Devonian Radiolarians of Russia

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Abstract—This study is devoted to the comprehensive description of radiolarians, the discussion of their morphology, problems of classification, and their role in the history of the Earth's biosphere. It contributes to the solution of the fundamental problems of the evolution of the organic world, aiming at the reconstruction of the dynamics of radiolarian diversity in the Devonian and chorology of units composing it; this is required for a better understanding of patterns and evolutionary pathways and revealing the biostratigraphic potential of radiolarians. The history of the study of Devonian radiolarians is described. The results of original and published studies have allowed the improvement of the radiolarian scale of the Devonian System and recognition of 18 Devonian biostratigraphic radiolarian assemblages and subassemblages, 11 of which are new. General patters of existence of Devonian radiolarians in the Russian Platform are considered. The patterns and adaptation pathways of radiolarians to various environments are determined. Special attention is paid to coevolution of Frasnian radiolarians and ammonoids in the Timan–Pechora Basin. Features of life of radiolarians under conditions of hydrosulphuric contamination are analyzed and a model for cyclic changes in ecological conditions in the basins of the Domanik type is developed. Four migration waves of radiolarians in the Famennian basins of Euramerica and the scenario of wave expansion of radiolarians in the Devonian are established. Seven genera are revised, including *Bisphaera, Entactinia, Entactinosphaera, Radiobisphaera, Somphoentactinia, Stigmosphaerostylus*, and *Trilonche*; ten new species are described, namely, *Archocyrtium amoenus* sp. nov., *Bientactinosphaera zuraevi* sp. nov., *Entactinia bella* sp. nov., *Haplentactinia kuzminae* sp. nov., *Haplentactinia vilvaensis* sp. nov., *Palaeodiscaleksus saturniformis* sp. nov., *Pluristratoentactinia trisphaerata* sp. nov., *Somphoentactinia multisphaerata* sp. nov., *Spongentactinia marina* sp. nov., and *Spongentactinia polaris* sp. nov. The study is expected to be of use to a broad range of readers in paleontology, biostratigraphy, paleoecology, paleobiogeography and as a textbook for the university courses. It contains 40 figures, 17 tables, 40 plates. The list of references includes 444 names.

Keywords: Radiolaria, paleoecology, paleobiogeography, evolution, biodiversity, new species, biostratigraphy, Devonian, Russia.

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INTRODUCTION

Research works in many micropaleontological laboratories of the world provide extensive new data on spatial and temporal distribution of radiolarians. On the one hand, new data expose unsolved problems, on the other hand, they induce changes and improvement of reconstructions of radiolarian evolution. Radiolariology develops rapidly and successfully. Radiolariologists obtain new data, formulate new hypotheses, and theories, critically revise early concepts, reject obvious mistakes and errors. The results and achievements in this field are widely used as an important means in the study of geological development of regions, reconstruction of tectonic and paleobiogeographic conditions in the geological past.

In paleontological and biostratigraphic studies of ancient radiolarians, two approaches are traditionally used:

- description and systematization of new taxa, study of biodiversity and its fluctuation, aiming at the reconstruction of paleoenvironments and paleobiogeographic conditions;
- study of new localities of fossil radiolarians and description of new assemblages for the determination of biostratigraphic potential, development of previous and new biostratigraphic schemes.

An important place among scientific studies of abundance and diversity of the biosphere is occupied by investigation of both its modern state and characteristics of the previous biospheres, which existed on the Earth during the past geological epochs. This knowledge provides an understanding of the dynamics and major trends in the evolution of biospheres and causes (probably catastrophic) of replacement of one biosphere by another. In turn, the knowledge of the dynamics and main developmental trends provides prediction of conditions of the modern biosphere in the nearest and remote future.

The study of modern and previous biospheres considered as an integral system is impossible without a detailed study of their elements, communities of various groups of organisms and interactions between them. In this connection, it is urgent to study particular features of biodiversity and paleobiogeography in the geological history of the Earth of particular groups, for example, radiolarians. The paleontological past of radiolarians is much more prominent and more diverse than in the Recent. Therefore, the study of the past geological epochs provide new information supplementing the knowledge of biodiversity and ecology of living organisms.

Crucial events in the biosphere history frequently occur at the level of protists, including radiolarians. They often display symbiotic relationships with the development of stable consortia, reproduction without sexual process, and innovation changes in morphotypes frequently mediated by viruses and bacteria.

The analysis and estimation of morphological diversity and evolution of radiolarians in the geological past is an important element in the knowledge of paleobiogeographic features of distribution of radiolarians in the World Ocean in different epochs of the Phanerozoic.

In the present study, the biodiversity dynamics, evolutionary trends, spatial–temporal distribution, and biostratigraphic potential of radiolarian faunas in the Devonian of the Russian Platform, Ural Mountains, and Western Siberia are analyzed.

Paleobiogeographic studies of radiolarians are characterized by novelty in the problem statement, since they naturally combine two closely connected aspects:

- on the one hand, paleobiogeographic reconstruction requires the data on biodiversity and skeletal morphology of radiolarians, reconstruction of the scenario of wave distribution of evolutionary innovations, and recognition of patterns of morphological changes in the major evolutionary lineages;
- on the other hand, reconstruction of the paleobiogeography of regional radiolarian faunas, i.e., the reconstruction of geographical ranges, directions and routes of migrations, provides an understanding of causes of certain trends in evolutionary changes of radiolarians and patterns of distribution of these changes in space and time.

The study of Devonian radiolarians of the Timan–Pechora Basin, Greater Urals, and Rudny Altai provided new data on the morphology, biodiversity, paleoecology, and paleobiogeography of Devonian radiolarians, which were a missing unit in available information on Paleozoic radiolarians and allowed the reconstruction of particular episodes in the Devonian history of epicontinental marginal seas of the Russian and Siberian platforms and Ural Paleocean (*Istoriya* ..., 1984; Scotese, 1997; Puchkov, 2000, Yolkin et al., 2003a, 2003b; Rikhter, 2008). Our studies have displayed the mechanisms of rearrangement of the taxonomic structure of regional radiolarian associations of the Devonian under conditions of considerable changes in environmental parameters from coastal–shallow water to water areas of the open shelf, from normal marine conditions to bottom waters with hydrosulphuric contamination.

Radiolarians were regarded for many decades as an astratigraphic faunal group and only recently were appreciated as an orthostratigraphic group. At present, radiolarians are more and more often used in practical biostratigraphy at the zonal level, they are more widely used as an important means in the study of features of geological development of particular regions and reconstruction of tectonic and paleogeographic conditions in the geological past; from an exotic paleontological object, they have turned into a working tool of geologists.

Devonian radiolarians have been studying for more than 100 years, beginning from works of Hinde (1890, 1899a, 1899b) devoted to Devonian radiolarians of southern Scotland, southern England (Cornwall), and New South Wales of Australia and a monograph of Rüst (1892), in which Devonian radiolarians of Germany and Russia were described.

Morphological studies of Foreman (1963) of Devonian radiolarians of North America opened a new stage in the understanding of Paleozoic radiolarians.

The first attempt to develop a zonal biostratigraphy on radiolarians was undertaken by Holdsworth and Jones (1980a, 1980b) for the Upper Devonian–Permian of the Yukon River Basin (eastern Alaska).

The first integrated radiolarian biostratigraphic scale of the Paleozoic was developed by Nazarov (1981b, 1988, 1989) and, later, supplemented by Nazarov and Ormiston (1985, 1986, 1990, 1993) based on detailed analysis of temporal and spatial distribution of all Paleozoic radiolarians known at that time.

Comprehensive approach to the resolution of the problem of morphological diversity and patterns of radiolarian evolution and new data on spatial–temporal distribution of radiolarians in Eastern Europe, the Ural and Siberian regions allowed us to revise the biostratigraphic potential of Devonian radiolarians and improve the Devonian biostratigraphic scale.

New paleobiogeographic and biostratigraphic results reported in the present study of Devonian radiolarians, involving all available data on geology, paleogeography, and biostratigraphy of the Russian Platform, Greater Urals, and Rudny Altai as well as the analysis of published data on foreign areas allowed us to resolve for the first time the following questions:

(1) to establish new Devonian biostratons with characteristic biostratigraphic radiolarian assemblages;

(2) to display the dynamics of biodiversity and evolutionary trends of radiolarians in space and time at regional and global levels;

(3) to develop the scenario of expansion of morphological evolutionary innovations of radiolarians;

(4) to reconstruct the centers of origin of regional radiolarian faunas and to determine the main directions of migration flows;

(5) to reconstruct the basins and environments of radiolarians in the geological past;

(6) to establish and describe new, previously unknown species of Devonian radiolarians.

The present study bridges the gap in the knowledge of Paleozoic radiolarians and provides a new understanding of the matter, since to date, complete paleobiogeographic and biostratigraphic studies on Devonian radiolarians have not been published.

Such a wide systematic study of biodiversity, evolutionary patterns, paleobiogeographic and spatial–temporal distribution of Devonian radiolarians has not yet been performed. Unfortunately, paleobiogeographic and paleoecological studies play a minor role in general discussion of fossil radiolarians. In works of Russian and foreign researchers dealing with fossil radiolarians, paleobiogeographic aspects are considered rarely and superficially. The incompleteness of the fossil record and poor data on paleobiology and paleoecology of radiolarians prevent to certain extent the application of methods and approaches used in the study of modern ecology and biogeography.

An important study of paleobiogeography of ancient radiolarians was performed by Kiessling (2002), who considered the global radiolarian biota at the Jurassic–Cretaceous boundary and, among other things, reconstructed the system of prevailing currents. Interesting paleobiogeographic studies were performed for boreal radiolarian biota of the Jurassic–Lower Cretaceous of northern Eurasia (Vishnevskaya and Pral'nikova, 1999; Vishnevskaya, 2001). Kemkin (2006) performed paleobiogeographic analysis of ranges of radiolarian species and species groups in the Jurassic and Cretaceous, which allowed the recognition of geodynamic evolution of the Sikhote Alin and Sea of Japan Region in the Mesozoic.

In the Paleozoic, only Nazarov (1988) studied the dynamics of radiolarian biodiversity, although without paleoecological analysis of the data and paleobiogeography of reconstruction of paleobasins. The only related study was analytical work of Racki (1999) devoted to a global catastrophe at the Frasnian–Famennian boundary, which is manifested in the radiolarian composition.

In addition, a serious methodological problem is connected with the fact that radiolarian analysis conflicts with paleobiogeographic reconstructions based on other groups of the marine fauna.

At the same time, during the past decades, an essentially new methodological and factual basis for the study of pathways and patterns of the evolution of life on the Earth was created. For integration of biological, paleontological, and geological data, the Presidium of the Russian Academy of Sciences supported the multidisciplinary program "Origin of Biosphere and Evolution of Geobiological Systems," which is performed by research teams of 52 academic institutes, including the Borissiak Paleontological Institute of the Russian Academy of Sciences.

The morphology of radiolarians was studied using a CamScan scanning electron microscope in the Borissiak Paleontological Institute.

We examined Devonian radiolarians from the Rudny Altai (collection no. 5253), Southern Urals (no. 5247), Timan–Pechora Basin (no. 5311), Polar Urals (no. 5312), Prague Basin (no. 5323), and Middle Urals (no. 5369), which are stored in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). The collection of thin sections of radiolarians from the Upper Frasnian Substage of the Middle Urals is stored in the Zavaritskii Institute of Geology and Geochemistry of the Ural Branch of the Russian Academy of Sciences, Yekaterinburg (IGG, collection no. 5510).

CHAPTER 1. HISTORY OF THE STUDY OF DEVONIAN RADIOLARIA OF RUSSIA

Ancient radiolarites rich in remains of Devonian radiolarians from the region of the Greater Urals were mentioned for the first time by F.N. Chernyshev and A.P. Karpinsky at the beginning the 1890s and accompanied by microphotographs (Khabakov et al., 1959). Chernyshev transferred the material of radiolarians to the German naturalist Rüst for monographic study. Unfortunately, Rüst did not work in the Ural Mountains.

The history of the study of Devonian radiolarians of Russia begins with the monograph of Rüst (1892), in which, along with Paleozoic radiolarians of Germany, a number of radiolarian genera and species from the Southern Urals were described.

Rüst (1892) described 36 species of 17 genera of relatively well-preserved radiolarians based on thin sections from Lower Devonian red jaspers of the following southern Ural localities: Yukaly Mountain, villages of Abzelilovo and Kirdasovo near the city of Magnitogorsk, vicinity of the town of Verkhneural'sk, deposits of light red jaspers in the Orenburg Region (Fig. 1, V–VIII, XII).

Unfortunately, the data on localities, of these radiolarian specimens are very poor and absent from explanations to paleontological plates; it is only indicated that they come from the Devonian of the Southern Urals, as was typical for monographs in the 19th century. In this connection, it is impossible to refer the data reported by Rüst to a particular unit of the modern stratigraphic scale of the Paleozoic. It is only possible to propose that all radiolarians described were found in the upper strata of red South Ural jaspers, most likely, of the Early Devonian age.

Judging from the great delight and assiduity seen in Rüst's detailed descriptions of rocks, Rüst was lithologist by vocation, while paleontology was only in the second place; when determining radiolarians, Rüst, a disciple of Haeckel, used atlases known at that time, which contained mostly Mesozoic and Cenozoic radiolarians. Therefore, Rüst assigned new Devonian species to known Cretaceous and Paleogene genera (Fig. 2): *Amphibrachium devoniense, A. bacillum, A. inaequale, A. pulchellum, Cenellipsis areolata, C. citrus, C. curvatopora, C. cyrpidina, C. rectipora, Cenosphaera apiaria, C. rossica, C. uralensis, Cromyosphaera distans, Cyphanta piscis, C. quiniseriata, Cyrtocalpis obtusa, C. serieporata, Druppula cembra, Liosphaera devoniensis, Lithocampe lossenii, L. orenburgensis, L. tschernytschewii, Peripanartus deficiens, Porodiscus intricatus, P. rossicus, Sethocapsa obstipa, Sphaeropyle dreyeri, S. laevis, Spongodictyon triquetrum, Spongosphaera induta, Stichocapsa anguillula, S. conglobata, S. elpenor, S. taenia, S. zinckenii*, and *Tricolocapsa obesa.*

However, the paleontological plates presented by Rüst give an ambiguous impression. On the one hand, they are the first figures of Devonian radiolarians, but, on the other hand, figures of skeletons in the plates disagree with morphological features typical of Devonian radiolarians.

First, the drawings of radiolarian skeletons were made in thin sections and, hence, many elements of the internal structure remain indiscernible.

Second, the drawings are undoubtedly supplemented by some structural details, i.e., certain elements and skeleton fragments are invented and added, although they are likely invisible in thin sections. Moreover, it is as if the drawings of radiolarians are forced to fit the images of Mesozoic genera known at that time from the literature (Ehrenberg, 1854a, 1854b; Haeckel, 1881, 1887).

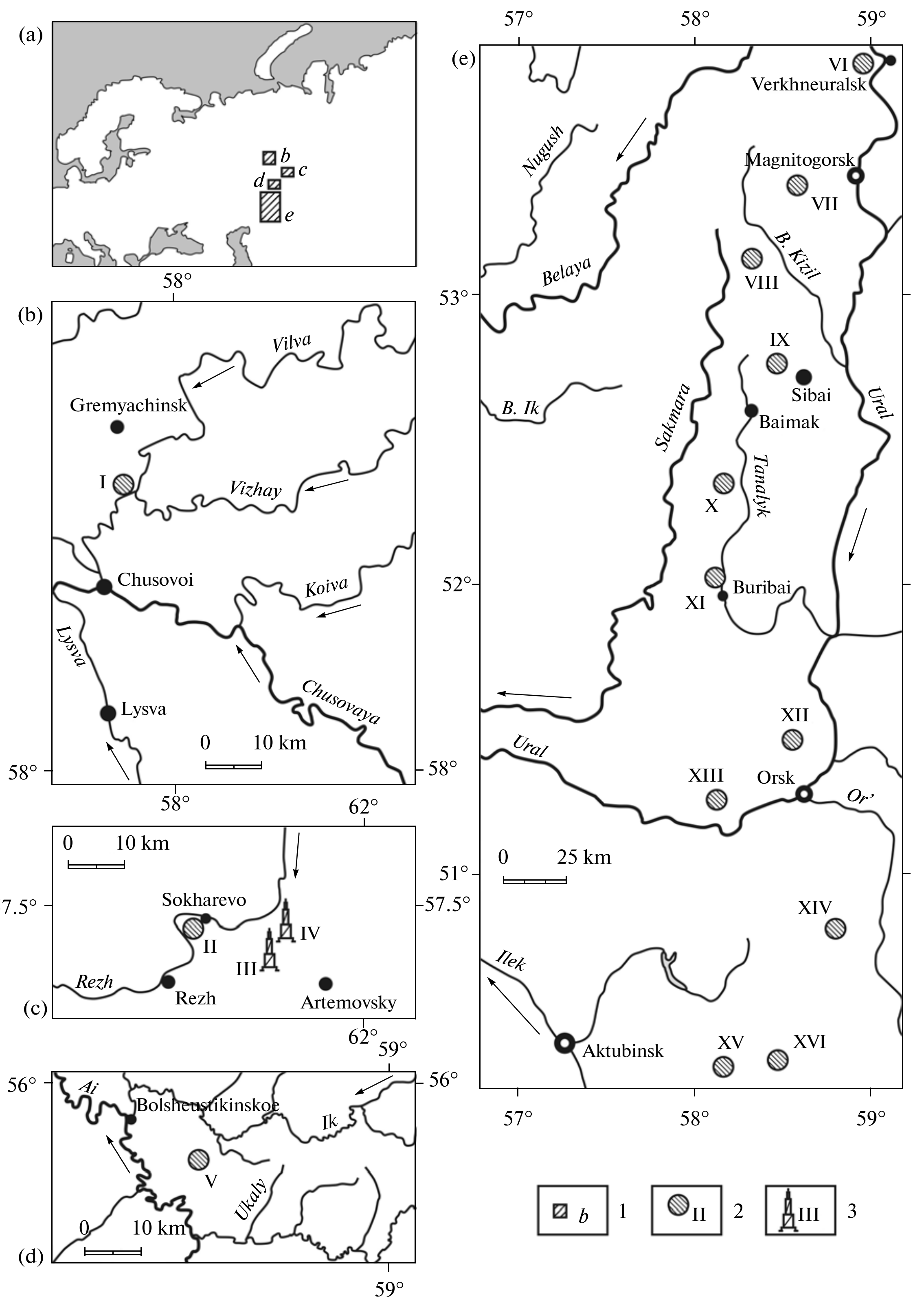
Third, the drawings display only typical Mesozoic and, partly, Cenozoic radiolarians figured in the manner accepted in the 19th century.

As a result of the above imperfections, it is hardly possible to recognize characteristic Paleozoic morphotypes. In addition, in the study cited, dating of samples often conflicts with the morphological types of radiolarians. For example, the forms described by Rüst under the names *Lithocampe lossenii, L. orenburgensis, L. tschernytschewii, Sethocapsa obstipa, Stichocapsa anguillula, S. conglobata, S. elpenor, S. taenia, S. zinckenii*, and *Tricolocapsa obesa* (Figs. 2x–2ac) show typical morphological characters of Mesozoic forms rather than Early Devonian radiolarians, as stated by Rüst (1892).

At the same time, as Khabakov (1934) remarked, for a long time after Rüst, who examined the collection of Chernyshev, nobody succeeded in finding in the Ural Moutains of fossils of ancient radiolarians of satisfactory preservation; thus, actually, South Ural Devonian radiolarian localities have been lost (Khabakov, 1934).

The presence of radiolarians in the Devonian beds of the Southern Urals and Northern Mugodzhary was reported by Teodorovich (1935), Strakhov (1939), and Balaev (1946); however, the first paper about radiolarians from the Greenstone Belt of the Southern Urals E.A. Kuznetsov published only in 1947.

Kuznetsov recorded Devonian radiolarians in thin sections of quartz schist in localities near Polevskaya and Ufalevskaya dachas, which are situated south of Yekaterinburg. The stratigraphic position of these quartz schists is uncertain. Kuznetsov proposed that they belong to the strata accompanying orthophyres and clayey tuffs and tuffites connected with them, which were then assigned to the Lower Devonian. Kuznetsov (1947, p. 127) indicated that radiolarian skeletons consist of very small crystals of garnet, many small dodecahedrons of which are scattered in enclos-



ing matter. Kuznetsov was the first to report a unique case of replacement of silica by garnet in radiolarian skeletons and later this has not been observed. He described eight species, including six new. Most of these forms have thorns and resemble at the generic level Lower Devonian radiolarians described by Rüst from jaspers of the Southern Urals; however, it is impossible to identify these species more precisely.

Fig. 1. Radiolarian localities in the Devonian of the Middle and Southern Urals and Northern Mugodzhary: (a) position of working areas; (b–d) Middle Urals; (e) Southern Urals and Northern Mugodzhary; radiolarian localities: (I–IV) Middle Urals: (I) Perm Region, Vilva River, southeast of the town of Gremyachinsk; (II–IV) Sverdlovsk Region, Rezhevskii District: (II) type "Sokharevo" section near the village Sokharevo, (III) borehole P-21, (IV) borehole P-31; (V–XIII) Southern Urals: (V, VII–XI) Bashkortostan: (V) Yukaly Mountain, (VII) village of Abzelilovo, (VIII) village of Kirdasovo, (IX) Karyukmas Mountain, northwest of the town of Sibai, (X) Argagan Mountain, village of Sultantimirovo, (XI) Kamennaya Gora locality, Tanalyk River, north of the town of Buribai; (VI) Chelyabinsk Region, town of Verkhneural'sk; (XII, XIII) Orenburg Region: (XII) of light red jaspers, (XIII) gully Temnaya valley, left bank of the Ural River; (XIV–XVI) Northern Mugodzhary, Kazakhstan, Aktyubinsk Region: (XIV) Aitpaika River, (XV) Shanda River Basin, (XVI) Shuldak River. Radiolarian localities: (I, II) Afanasieva and Amon, this paper; (III, IV) Amon and Korovko, 1992; (V–VIII, XII) Rüst, 1892; (IX–XI) Afanasieva and Amon, 2008b, 2009a; (XIV) Nazarov, 1975; (XIII) Ivanov and Puchkov, 1984; (XV) Ivanov et al., 1984; (XVI) Nazarov, 1988. Designations: (*1*) working areas, (*2*) outcrops, and (*3*) boreholes.

On the western slope of the Greater Urals and Volga–Ural Basin, Bykova (1955) was the first to investigate Devonian radiolarians from thin sections of carbonate rocks (Fig. 3).

Kushnareva (1959) reported for the first time about abundant radiolarians in the stratotype of the Domanik Formation on the Domanik River in the Ukhtinskii District of the Timan–Pechora Basin (Fig. 3). The first figures of Domanik radiolarians in thin sections (without identification or description) was provided by Maksimova (1970).

Results of long-term work of Sadrislamov (1970, 1983, 1987, 1990) devoted to Paleozoic radiolarians of the Southern Urals were inaccessible and unclaimed in connection with almost complete absence of his results in open publications. At the same time, Sadrislamov was the first to work with thin sections alone without data on other faunal groups and tried to understand the biostratigraphic significance of radiolarians for gaining an insight into the geological situation in this region.

In a brief paper, Sadrislamov (1970) reported that he had established based on thin sections 15 radiolarian assemblages ranging in age from the Cambrian (?) and Ordovician to the Permian in the volcanogenic–sedimentary Baimak–Buribai Formation of the Southern Urals.

Subsequently, Sadrislamov (1983) listed five radiolarian biostratons recognized in the Lower and Middle Devonian beds of the Southern and Northern Urals, ranked beds with characteristic faunas. In the Lower Devonian of the Southern Urals, these are beds with *Cubentactinia orensis–Entactinia karpinskaja*, beds with *Entactinia biktashevensis*, and beds with *Entactinia zinzilbanensis*; in the Middle Devonian, beds with *Cubentactinia dzhausensis dzhausensis* in the Northern Urals and beds with *Cubentactinia shakirtauensis–Entactinia aptchakensis* in the Southern Urals. Sadrislamov (1983) established these beds with radiolarians based on thin sections and published without figures of radiolarians; therefore, it is impossible to compare these data with recent finds of radiolarians. However, the results received by Sadrislamov confirmed the possibility of the presence of Early and Middle Devonian radiolarians in the Southern Urals.

Then, Sadrislamov (1987, 1990) elaborated in more detail the Silurian and Devonian radiolarian scales of the Southern Urals, with 12 (!) Silurian and 16 (!) Devonian radiolarian beds with characteristic radiolarian assemblages. As Maslov and Artyushkova (2002, p. 20) noted, from one report to another, Sadrislamov changed his conclusions about the age of the Baimak–Buribai Formation without comment concerning the basis of these changes, whether species were reidentified or radiolarians were transferred to other faunal groups; the latter is more probable."

In geological literature devoted to the Paleozoic and, in particular, Devonian of the Greater Urals, many works contain references to the above studies of Sadrislamov (1970, 1983, 1987, 1990) or reprint information from them. Researchers often use references to local research reports inaccessible to wide scientific community.

Unfortunately, the data on Devonian radiolarians published before the mid-1970s have become out of date and should not be regarded as reliably established because of the following.

(1) Beginning from the studies of Hinde (1890, 1899a, 1899b) and Rüst (1892) up to the mid-1970s, fossil radiolarians from dense rocks were only studied in thin sections based on accidental sections. This method was considered to be the main and the only possible, since many researchers a priori believed that it is impossible to extract radiolarians from siliceous, carbonate, and other types of lithified rocks. In addition, radiolarian remains were occasionally recorded in thin sections, as an incidental result of lithologic–petrographic investigation of rocks, which was regarded as more important.

At the same time, the technique of extraction of complete radiolarian skeletons was developed by Hinde as early as the 19th century. Hinde (1899a) described an extremely diverse well-preserved radiolarian assemblage from limestone lenses of the Tamworth Series[1] of New South Wales of Australia, which was obtained by treatment with hydrochloric acid of the surface of samples. In doing so, radiolarians retained all features of external morphology and partially damaged specimens displayed some internal structures. Despite positive results, this experiment had been forgotten for a long time (Nazarov et al., 1990).

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[1] Yarrimie Formation after Aitchison and Stratford (1997).

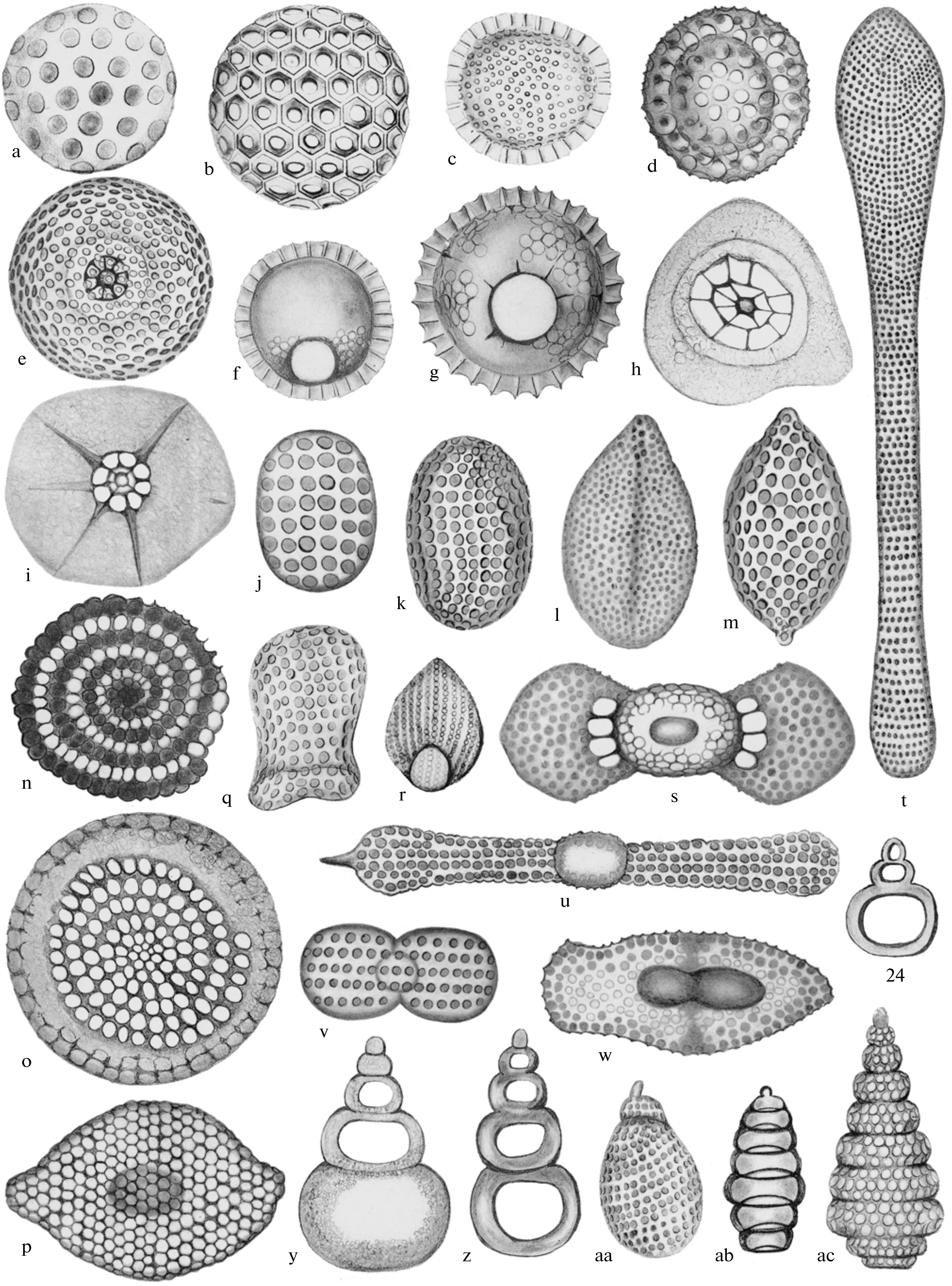
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Fig. 2. Radiolarians from the Devonian of the Southern Urals described by Rüst (1892): (a) *Cenosphaera uralensis* Rüst, 1892 (Pl. 6, fig. 3), ×265; (b) *C. apiaria* Rüst, 1892 (Pl. 6, fig. 6), ×270; (c) *C. rossica* Rüst, 1892 (Pl. 6, fig. 9), ×280; (d) *Liosphaera devoniensis* Rüst, 1892 (pl. 7, fig. 5), ×200; (e) *Cromyosphaera distans* Rüst, 1892 (pl. 8, fig. 6), ×250; (f) *Sphaeropyle laevis* Rüst, 1892 (pl. 9, fig. 5), ×270; (g) *S. dreyeri* Rüst, 1892 (pl. 9, fig. 6), ×300; (h) *Spongodictyon triquetrum* Rüst, 1892 (pl. 8, fig. 10), ×100; (i) *Spongosphaera induta* Rüst, 1892 (pl. 15, fig. 3), ×265; (j) *Cenellipsis rectipora* Rüst, 1892 (pl. 15, fig. 6), ×240; (k) *C. curvatoporata* Rüst, 1892 (pl. 15, fig. 7), ×220; (l) *C. cyrpidina* Rüst, 1892 (pl. 15, fig. 9), ×120; (m) *C. citrus* Rüst, 1892 (pl. 15, fig. 8), ×130; (n) *Porodiscuc intricatus* Rüst, 1892 (pl. 23, fig. 5), ×325; (o) *P. rossicus* Rüst, 1892 (pl. 22, fig. 6), ×260; (p) *Druppula cembra* Rüst, 1892 (pl. 17, fig. 8), ×245; (q) *Cyrtocalpis obtusa* Rüst, 1892 (pl. 26, fig. 15), ×170; (r) *C. serieporata* Rüst, 1892 (pl. 26, fig. 16), ×275; (s) *Peripanartus deficiens* Rüst, 1892 (pl. 19, fig. 7), ×195; (t) *Amphibrachium inaequale* Rüst, 1892 (pl. 23, fig. 10), ×200; (u) *A. devoniense* Rüst, 1892 (pl. 20, fig. 8), ×100; (v) *Cyphanta quiniseriata* Rüst, 1892 (pl. 19, fig. 6), ×200; (w) *C. piscis* Rüst, 1892 (pl. 19, fig. 5), ×150; (x) *Tricolocapsa obesa* (Rüst, 1888) (Rüst, 1892, pl. 28, fig. 2), ×150; (y) *Stichocapsa conglobata* Rüst, 1885 (Rüst, 1892, pl. 30, fig. 3), ×180; (z) *S. zinckenii* Rüst, 1885 (Rüst, 1892, pl. 30, fig. 4), ×180; (aa) *Sethocapsa obstipa* Rüst, 1892 (pl. 27, fig. 6), ×125; (ab) *Lithocampe orenburgensis* Rüst, 1892 (pl. 29, fig. 5), ×150; and (ac) *L. tschernytschewii* Rüst, 1892 (pl. 29, fig. 8), ×185.

The imperfection of studying radiolarians in thin sections was repeatedly remarked by many researchers (Lipman, 1952, 1979; Khabakov et al., 1959; Nazarov, 1975). This was particularly clearly formulated in *Osnovy paleontologii ...* (Fundamentals of Paleontology: Khabakov et al., 1959, p. 425), indicating that "this approach should not be regarded as perfect, because thin sections usually show incomplete accidental sections of skeletons, which are very difficult to determine to species, even when radiolarians are extremely abundant and many sections are observed. In thin sections, it is impossible to see simultaneously

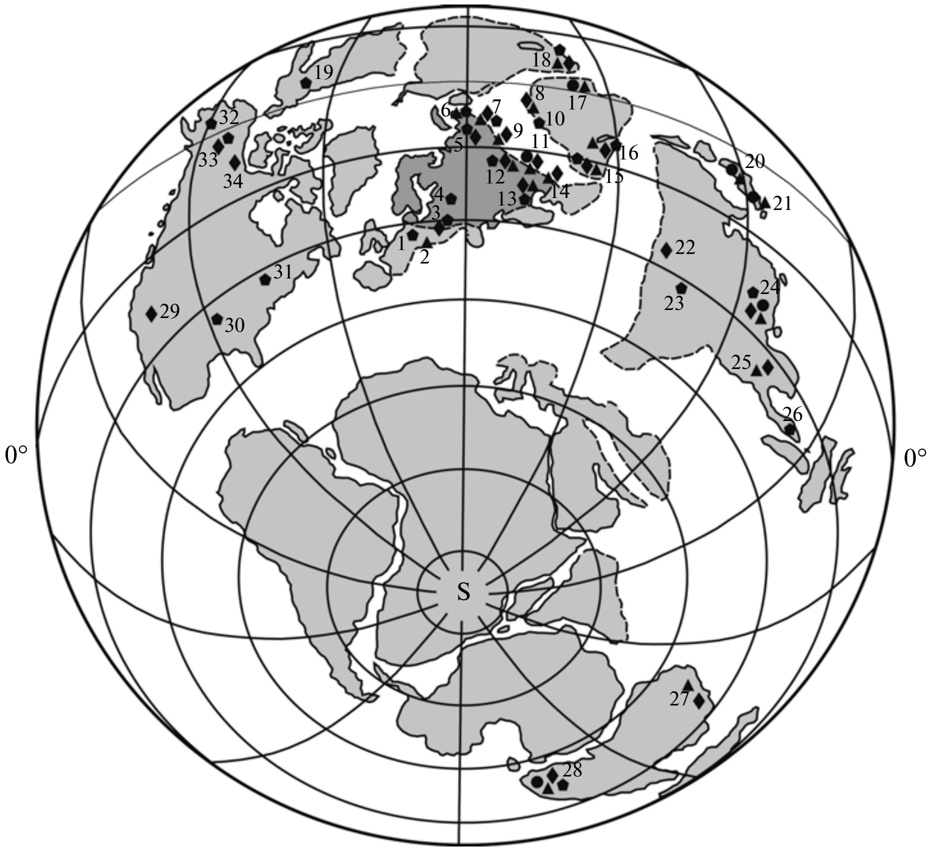

Fig. 3. Distribution of Devonian radiolarians. (●) Early Devonian, (▲) Middle Devonian, (◆) Late Devonian, Frasnian, (⬟) Late Devonian, Famennian Age: (1) Germany, (2) Czechia, (3) Poland, (4) Pripyat Depression, Belarus, (5) Timan–Pechora Basin, (6) Polar Urals, (7) Northern Urals, western slope, (8) Northern Urals, eastern slope, (9) Middle Urals, western slope, (10) Middle Urals, eastern slope, (11) Southern Urals, (12) Volga–Ural Province, (13) Caspian Depression, western Kazakhstan, (14) Northern Mugodzhary, western Kazakhstan, (15) Chara Zone, eastern Kazakhstan, (16) Alai Mountains, Kyrgyzstan, (17) southern Western Siberia, (18) Rudny Altai, (19) Eastern Siberia, Kolyma Uplift, (20) Central Japan, (21) southwestern Japan, (22) Central Mongolia, (23) northwestern China, (24) southern China, (25) northern Thailand, (26) Malaysia, Malacca Peninsula, (27) western Australia, (28) New South Wales of Australia, (29) USA, Nevada, (30) USA, Oklahoma, (31) USA, Ohio, Lake Erie, (32) central Alaska, (33) eastern Alaska, and (34) northwestern Canada. Radiolarian localities are shown in the global reconstruction of continents and oceans for the Late Devonian (Khramov et al., 1982).

complete structure of the skeleton and its outer shell; this complicates systematic identification. Very similar rounded sections are observed in many different genera and families of the Sphaeroidea, Discoidea, Prunoidea, and even different families of Nassellaria. It is impossible to determine radiolarian species based on isolated sections, because complete sets of species and even generic characters of radiolarians are not observed in individual sections, while good and complete skeletons are almost impossible to prepare from very firm rock samples."

(2) Dating based on radiolarians was not confirmed by other fossil groups, including conodonts. In other words, the geological age of radiolarian assemblages was often estimated based on the "position in the section" between the strata with a more or less confidently established stratigraphic position.

(3) In works of Russian researchers published before the mid-1970s, taxonomic descriptions or, more often, lists of Paleozoic radiolarians were given according to the classification developed by Haeckel (1887), monograph of Zittel (1934), and *Osnovy paleontologii* (Khabakov et al., 1959). However, the classification of Haeckel (1887) is based on the study of radiolarians from Recent benthic deposits and on plankton stations during the circumnavigation expedition of the corvette *H.M.S. Challenger* (1872–1876)[2] (Amon et al., 2009). Therefore, works devoted to ancient Paleozoic forms frequently display lists of Recent genera and even Recent species, because they were determined based on the system of Haeckel.

Thus, a more than centenary-long history of the study of fossil radiolarians from the Ural Mountains has provided a few thematic studies and special paleontological publications on this faunal group. The myth of a ***perfect*** understanding of Paleozoic radiolarians of the Ural Mountains appeared because extensive literature on the geology of the Ural Mountains contains ***mentioning*** of the presence of radiolarians as light points in certain Paleozoic stratons. This true or imaginary[3] fact of the presence of radiolarian skeletons in rocks is often regarded as a lithologic–mineralogical or petrographic characteristic of the rock or, rarely, as a parameter of paleogeographic and paleogeodynamic conditions.

Only rare biostratigraphic works provide detailed and precise evidence of the presence of radiolarians in sections of sedimentary and volcanogenic–sedimentary strata, with the ranges of their stratigraphic distribution. Paleontological studies of Devonian radiolarians, containing descriptions of radiolarians, their taxonomy, and figures are extremely rare.

Skeletal remains of Frasnian radiolarians were extracted for the first time from carbonate nodules of the Egindy Formation of the Southern Urals and examined in detail only in the mid-1970s (Nazarov, 1973, 1975). In addition, Nazarov established the distribution of a Frasnian radiolarian assemblage in limestone interbeds of the Evtropin Formation on the Unya River in the Evtropiny Noski locality of the Northern Urals (Nazarov, 1988) (Fig. 3).

Ten years later, new determination of radiolarians from the Frasnian and Famennian beds of the eastern slope of the Middle Urals were reported by Amon (1995, 1999a) (Fig. 3).

The first comprehensive study of rich radiolarian assemblages from the Frasnian and Famennian beds of the Timan–Pechora Basin (Fig. 3) allowed Afanasieva to develop a new system of Paleozoic radiolarians, create detailed biostratigraphy of the Frasnian Stage, reconstruct ecological conditions of the Timan–Pechora Basin, and develop a model for the formation of rocks of the Domanik type under conditions of hydrosulphuric contamination (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2000, 2001; Afanasieva and Aitchison, 2001).

To date, we have accumulated original and published data on Devonian radiolarians, which require a new generalization of available information on radiolarians, including revision of old data, which form the foundation of the regional and global radiolarian scales of the Paleozoic. This enables refinement and detailed elaboration of radiolarian zones of the Devonian System within the Paleozoic radiolarian scale of Western Siberia, the eastern Russian Platform, and Greater Urals.

Recent studies of Devonian radiolarians, involving new collections, revision of the former data, and analysis of published data, allowed us to establish for the first time (1) new Devonian biostratons, with characteristic radiolarian assemblages; (2) the centers of origin of regional radiolarian faunas and determine their migration directions; (3) the dynamics of radiolarian diversity in space and time; and (4) new, previously unknown radiolarian species.

CHAPTER 2. RUSSIAN PLATFORM AND GREATER URALS

Devonian deposits of the Russian Platform show wide facies and formational variations caused by developmental features of various paleotectonic structures. In general, these deposits are characterized by cyclic sedimentation. Each cycle of Devonian development of the Russian Platform corresponds to one

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[2] *H.M.S. Challenger* is a three-master steam wooden corvette of 2306 t displacement, the circumnavigation expedition of which took five years, 1872–1876. Research work of the corvette was supported by the British Government and it collected extensive oceanographic material from 362 plankton stations, 492 stations of depth measurements, and 133 stations of dredging the ocean bottom.

[3] During field works and description of samples, geologists are frequently inclined to treat microscopic white, light gray, or slightly yellowish points in a fresh chip of rock as radiolarian fossils, although, in fact, this may well be whatever one likes rather than radiolarian skeletons.

expansion and regression of the area of marine deposits (Tikhomirov, 1967, 1995).

Ecological changes occurred synchronously with changes in general physiographic conditions. The Ural Devonian Sea was an open marine basin with normal salinity, situated in the equatorial and tropical belts with a warm climate (Tikhii, 1975). During the Devonian, there were many westward transgressions of the Ural Paleocean, involving adjacent areas of the Russian Platform, and subsequent regressions; this resulted in rhythmic alternation and wide facies diversity of deposits and had certain effect on paleobiogeographic occurrence of radiolarian associations.

On the western slope of the Ural Mountains, conditions of the marginal marine basin in the Devonian were extremely favorable for the development of organic life, where chemogenic formations were accompanied by various widely developed organogenic deposits; algal, coral, stromatoporoid, crinoid, pteropod, and other limestones were formed.

In the central Russian Platform, physiographic conditions were different. The sea penetrated there only in the Late Givetian Time, after the period of dry land in this area. Beginning from deposits of the Upper Givetian Substage, which overlie the basement rocks, up to the Frasnian Stage inclusive, the section is characterized by frequently interbedding rocks, with the prevalence of siliciclastic differences. In this part of the section, limestones play a subordinate role and are obviously of coastal–marine shallow-water nature, since they show fossil traces of crawling, drilling, and attachment benthic organisms. These beds are considered to be lagoons (with some decrease in salinity). Beginning from the Evlanovo beds up to the end of the Frasnian Stage, limestones with a marine fauna prevail in the section. In the Famennian Stage, limestones are in places replaced by dolomites, which, in opinion of many researchers, are deposits of shallow salinated lagoons.

A distinctive feature of the Devonian of the western slope of the Ural Mountains and the eastern marginal area of the Russian Platform is the prevalence of radiolarians over benthic foraminifers. The data on environments of planktonic and benthic foraminifers and radiolarians in the Recent oceans and seas and sharply manifested confinement of various groups of protists to certain facies types of Devonian rocks enable us to judge the paleoecological and paleobiogeographic character of these paleobasins and recognize some patters in the distribution of radiolarians.

EARLY DEVONIAN

The Early Devonian deserves the name geocratic epoch in the development of the Earth. At the beginning of the Devonian Period, the Russian Platform underwent the maximum upraise, becoming an extensive peripheral land of Euramerica (Fig. 4). At that time, it had completely become free from the epicontinental seas. Only eastern and northeastern marginal areas of the Russian Plate and the northeastern part of the Timan–Pechora Plate were below the sea level (Tikhii, 1975). Based on the general patterns of sedimentary formations of the Early Devonian, Tikhomirov (1967, 1995) assigned them to the final part of the Silurian geological cycle of sedimentation, which completed the Early Paleozoic stage in the development of the Russian Platform.

In the western Urals and west of it, the Early Devonian marine basin was reduced because of the general regional upraise (Fig. 4). The base of the Devonian sequence of the western slope of the Ural Mountains is formed of massive, frequently reef-building limestones. In the Early Devonian, this was probably a barrier reef in the tropical Ural Sea. At the same time, the southeastern Ural Sea was an active eastern marginal area of the paleocean, known under different names, including the Ural Paleocean (Burtman et al., 2000). The area of this oceanic basin was estimated differently, from rather narrow, splitlike (Seravkin et al., 1992) to wide extending along the paleomeridian for 2500 km or more in width (Puchkov, 2000).

In general, within the extensive Russian Platform and Greater Urals in the Early and Middle Devonian, the following units have been established: (1) in the western part, there were formations of a passive marginal area of Ancient Russian Continent, including shallow and deep shelves, continental slope, and continental foot; (2) in the east, there were oceanic formations connected with an island arch; (3) in the southeast, there was Eastern Ural (Eastern Mugodzhary) microcontinent, submerged below the sea level for different depths (Puchkov, 2000; Mizens, 2002, 2003).

In the Early Devonian, radiolarians clearly preferred relatively shallow and quiet conditions of continental marginal areas on both Ancient Russian Continent and Eastern Ural microcontinent (Fig. 4). These events could have been caused by hydrodynamics and hydrochemistry of basins inhabited in these areas, which were more favorable for radiolarians than easterly lumpy oceanic water areas.

Until recently, Early Devonian radiolarians have not been recorded in Russia or abroad, except for Early Devonian radiolarians of the Southern Urals described by Rüst (1892) in the 19th century (Fig. 4). Only 100 years later, in the 1990s, the first studies devoted to Early Devonian radiolarians were published. The first reliable Early Devonian (Late Emsian) radiolarians of Russia were described by Lipnitskaja (1995, 2002) in the south of Western Siberia, including four species of three genera (Fig. 3; Table 1).

Nazarov (1988) noted that Pridolian–Emsian radiolarians have not been recorded with certainty in Russia, although Usoltseva (1973, 1981) had already established a radiolarian assemblage in the Lower Devonian beds of the Milyashinsk Formation of the Greenstone Zone of Western Mugodzhary. However, it is very difficult to use the data of Usoltseva (1973,

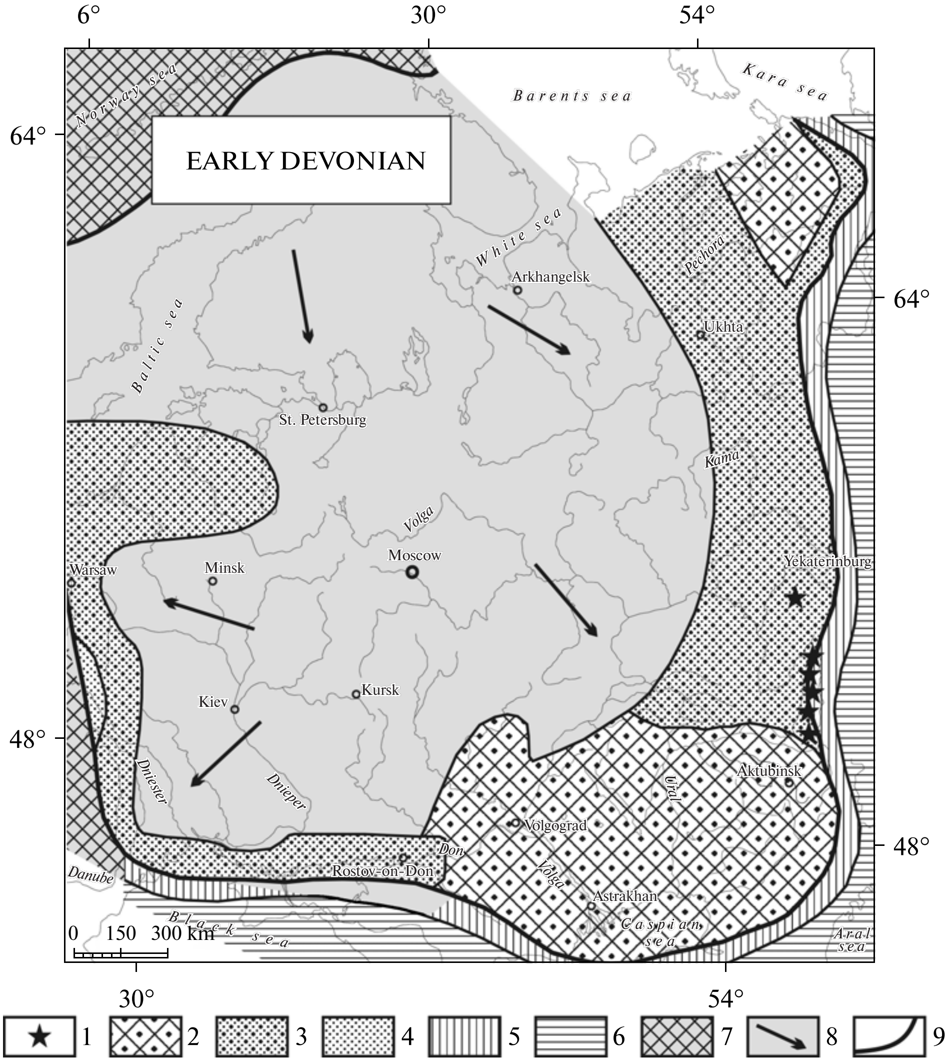

Fig. 4. Paleobiogeographic scheme of the Early Devonian of the Russian Platform and Greater Urals, with a radiolarian locality: (1) radiolarian locality; (2) sea of increased salinity; (3–6) sea of normal salinity: (3) coastal region, (4) internal shelf, (5) continental slope, (6) bottom of paleocean; (7) active fold belt; (8) main directions of transportation of clastic material from land; (9) boundary of the Russian Platform. The paleobiogeographic scheme is based made on the data of Tikhomirov (1967, 1995), Tikhii (1975), Racki (1992, 1997), Rodionova et al. (1995), Nikishin et al. (1996), Yunusov et al. (1997).

1981), since she examined radiolarians in thin sections and determined specimens based on the system of Haeckel, so that the taxonomic list contained Recent genera.

At the same time, Early Devonian radiolarians are rather common in Russia, although, as Nazarov indicated, ***reliably dated*** Early Devonian radiolarians are rare.

In the West Mugodzhary Synclinorium, thick volcanogenic strata are divided into a number of formations occurring transgressively with angular unconformity. In particular, the Silurian corresponds to the Aktogai, Mugodzhary, and Kurkuduk formations, the second and third of which contain jaspers with radiolarian fossils, which have been determined in thin sections to genus. The Lower Devonian is represented by the Milyashinsk Formation, in which interbeds of jasper tuffites contain many radiolarians (nine genera). Upward in the section, there is the Bugulygyr Formation of the Upper Eifelian (dated based on brachiopods) with abundant radiolarians in jasper differences. It is followed by Givetian deposits, with scarce radiolarians in tuff–sandstone interbeds. The section is crowned by the Frasnian strata, with a poor radiolarian assemblage in limestone lenses and the flyschoid Famennian strata also poor in radiolarians (Abdulin, 1973).

According to other data, the stratigraphic position of these stratons in the region considered is essentially different. Ivanov et al. (1984, p. 65) concluded with irony that “such datings were based on the determination of radiolarians in thin sections, isolated plant

Table 1. Stratigraphic and geographic distribution of Early Devonian radiolarians

Radiolarians	Early Devonian							Central Japan	SW Japan	NSW, Australia	S China	W Siberia	S Urals
	D_1lo		D_1pr		D_1em								
	lo$_1$	lo$_2$	pr$_1$	pr$_2$	em$_1$	em$_2$	em$_3$						
Zadrappolus aff. spinosus Furutani, 1990	—	—						▨					
Zadrappolus sp.	—	—						▨					
Pseudospongoprunum ? sp.	—	—						▨					
Secuicollacta sp.	—	—						▨					
Futobari morishitai Furutani, 1990	—	—						▨					
Zadrappolus yoshikiensis Furutani, 1990	—	—	—					▨					
Zadrappolus tenuis Furutani, 1990	—	—					—	▨	▨				▨
Palaeoscenidium sp.	—	—			—	—	—	▨	▨				
Ceratoikiscum amiger Furutani, 1990	—	—			—	—	—	▨					
Radiolaria gen. et sp. indet., sp. C	—				—	—	—	▨					
Stylosphaera ? sp. A et sp. B		—	—	—	—	—	—	▨					
Futobari solidus Furutani, 1990			—	—				▨	▨				
Helenifore laticlavium Nazarov et Ormiston, 1983			—	—						▨			
Entactiniidae gen. et sp. indet., sp. F			—	—						▨			
Entactiniidae gen. et sp. indet., sp. J			—	—						▨			
Entactiniidae gen. et sp. indet., sp. M			—	—						▨			
Entactiniidae gen. et sp. indet., sp. P			—	—						▨			
Entactiniidae gen. et sp. indet., sp. B			—	—	—	—	—			▨			
Ceratoikiscum sp. A			—	—	—	—	—	▨		▨	▨		
Palaeoscenidium cladophorum Deflandre, 1953			—	—	—	—	—	▨		▨	▨		
Palaeoscenidium ishigai Wakamatsu, Sugiyama et Furutani, 1990				—	—	—	—	▨					
Deflantrica furutanii Kurihara et Sashida, 2000				—	—	—	—	▨					
Deflantrica solidum Wakamatsu, Sugiyama et Furutani, 1990					—	—	—	▨					
Deflantrica sp. A					—	—	—	▨					
Deflantrica sp.					—	—	—	▨					
Palaeoscenidium simplum Kurihara et Sashida, 2000					—	—	—	▨					
Palaeoscenidium hakogasensis Kurihara et Sashida, 2000					—	—	—	▨					
Palaeoscenidium fragilis Kurihara et Sashida, 2000					—	—	—	▨					
Palaeoscenidium sp. A					—	—	—	▨					
Palaeoscenidium sp. B					—	—	—	▨					
Palaeoscenidium sp. C					—	—	—	▨					
Tlecerina sp. A					—	—	—	▨					
Tlecerina horrida Furutani, 1990					—	—	—	▨					▨
Tlecerina isensis Kurihara et Sashida, 2000					—	—	—	▨					▨
Pactarentinia holdsworthi (Furutani, 1990)					—	—	—	▨					▨
Pactarentinia intermedia Kurihara et Sashida, 2000					—	—	—	▨					
Pactarentinia igoi Kurihara et Sashida, 2000					—	—	—	▨					
Pactarentinia sp. A					—	—	—	▨					
Pactarentinia sp. B					—	—	—	▨					
Palaeoumbraculum hidense Kurihara et Sashida, 2000					—	—	—	▨					
Palaeoumbraculum sp.					—	—	—	▨					
Spumellaria gen. et sp. indet., sp. A					—	—	—	▨					
Spumellaria gen. et sp. indet., sp. B					—	—	—	▨					
Spumellaria gen. et sp. indet., sp. C					—	—	—	▨					
Palaeopyramidium ramosum Kurihara et Sashida, 2000					—	—	—	▨					
Palaeopyramidium sp.					—	—	—	▨					
Ceratoikiscum ichinotaniense Ishiga, 1992					—	—	—	▨					
Ceratoikiscum izumiensis Kurihara et Sashida, 2000					—	—	—	▨					
Ceratoikiscum kurosegum Aitchison, Hada, Ireland et Yoshikura, 1996					—	—	—	▨					
Radiolaria gen. et sp. indet., sp. A et sp. B					—	—	—	▨					
Entactiniidae gen. et sp. indet., sp. K					—	—	—			▨			
Entactiniidae gen. et sp. indet., sp. L					—	—	—			▨			

Table 1. (Contd.)

Radiolarians	Early Devonian							Central Japan	SW Japan	NSW, Australia	S China	W Siberia	S Urals
	D_1lo		D_1pr		D_1em								
	lo$_1$	lo$_2$	pr$_1$	pr$_2$	em$_1$	em$_2$	em$_3$						
Stylosphaera (=Bientactinosphaera) vetusta Hinde, 1899					—	—	—			▨			▨
Trilonche (=Bientactinosphaera) vetusta Hinde, 1899					—	—	—			▨	▨		
Trilonche (=Bientactinosphaera) pittmani Hinde, 1899					—	—	—						▨
Trilonche (=Bientactinosphaera) elegans Hinde, 1899					—	—	—			▨			▨
Trilonche (=Bientactinosphaera) hindea Aitchison et Stratford, 1997					—	—	—			▨			
Trilonche (=Radiobisphaera) echinata Hinde, 1899					—	—	—			▨	▨	▨	
Trilonche (=Bientactinosphaera) ? sp.					—	—	—			▨	▨		
Trilonche (=Bientactinosphaera) sp. A					—	—	—	▨	▨	▨			
Trilonche (=Bientactinosphaera) sp. B					—	—	—			▨			
Palaeoephippium sp.					—	—	—	▨					
Circulaforma admissarius Stratford et Aitchison, 1997					—	—	—			▨			
Circulaforma sp. A					—	—	—			▨			
Ceratoikiscum calvum Stratford et Aitchison, 1997					—	—	—			▨			
Ceratoikiscum lyratum Ishiga, 1988					—	—	—	▨	▨				
Ceratoikiscum turgidum Umeda, 1998						—			▨				
Helenifore sp. B						—			▨				
Glanta fragilis Wakamatsu, Sugiyama et Furutani, 1990						—	—	▨	▨				
Glanta sp.						—	—	▨	▨				
Protoholoeciscus hindea Aitchison, 1993						—	—	▨	▨				
Protoholoeciscus spinosus Umeda, 1998							—		▨				
Protoholoeciscus sp.							—		▨				
Helenifore sp. A							—		▨				
Ceratoikiscum coroniferum Luo, Aitchison et Wang, 2002							—				▨		
Ceratoikiscum planistellare Foreman, 1963							—				▨		
Spongentactinia sp.							—				▨		
Stigmosphaerostylus cubicus Luo, Aitchison et Wang, 2002							—				▨		
Stigmosphaerostylus hystricuosa (Aitchison, 1993)							—				▨		
Stigmosphaerostylus sp.							—				▨		
Trilonche (=Bientactinosphaera) davidi Hinde, 1899							—				▨		
Trilonche (=Bientactinosphaera) minax Hinde, 1899							—				▨		
Trilonche (=Bientactinosphaera) nanningensis Luo, Aitch., Wang, 2002							—				▨		
Trilonche (=Bientactinosphaera) remosa Luo, Aitchison et Wang, 2002							—				▨		
Trilonche (=Bientactinosphaera) tanheensis Luo, Aitch. et Wang, 2002							—				▨		
Trilonche (=Bientactinosphaera) xinpoensis Luo, Aitch. et Wang, 2002							—				▨		
Helioentactinia cf. *multa* (Won, 1997)							—				▨		
Magnisphaera sp.							—				▨		
Bientactinosphaera limpida (Lipnitskaja, 2002)							—					▨	
Bientactinosphaera (?) *tortilispina* (Lipnitskaja, 2002)							—					▨	
Bientactinosphaera sp. A							—					▨	
Pseudospongoprunum sagittatum Wakamatsu, Sugiyama, Furutani, 1990							—						▨
Spongentactinia fungosa Nazarov, 1975							—						▨
Theodiscus hastatus Hinde, 1899							—						▨
Trochodiscus planatus Hinde, 1899							—						▨
Palacantholithus stellatus Deflandre, 1973							—						▨
Primaritripus patella (Hinde, 1899)							—						▨
Palaeodiscaleksus punctus (Hinde, 1899)							—						▨
Palaeodiscaleksus cribrarius (Hinde, 1899)							—						▨
Palaeodiscaleksus tumefactus Afanasieva et Amon, 2008							—						▨
Primaritripus buribayensis Afanasieva et Amon, 2008							—						▨
Primaritripus chuvashovi Afanasieva et Amon, 2008							—						▨
Radiobisphaera rozanovi Afanasieva et Amon, 2009							—						▨
Entactinia rostriformis Afanasieva et Amon, 2008							—						▨

specimens, and, to a great extent, general geological reasoning. Originally, these datings were considered to be tentative and, then, according to tradition, regarded as proved. It is interesting that the age of formations was initially established based on radiolarians (Abdulin, 1973) and, later, in the course of more detailed studies, radiolarians were dated based on the age of formations."

Thus, the above geological formations with radiolarians were dated based on conodonts as follows: the Aktogai Assemblage corresponds to the Middle Devonian; the Mugodzhary Assemblage, to the Middle Devonian, Eifelian–Givetian; the Kurkuduk Assemblage, to the Upper Eifelian–Lower Givetian to the *ensensis* Zone inclusive; the Milyashinsk Assemblage, to the period from the Upper Eifelian to the middle of the Givetian, to the *cristatus* Zone; the Shuldak (=Bugulygyr) Assemblage, to the uppermost Givetian, probably, the bottom of the Frasnian, *varcus–asymmetricus* zones. Upward in the section, they are followed by tuffs, tuff–sandstones, and siliceous tuffites with olistiliths of shallow-water limestones of the Givetian Alabass (Ulutauss) Assemblage (Ivanov, 1983, 1998; Ivanov et al., 1984).

All the above does not necessary mean that it is impossible to find Early Devonian radiolarians in the Ural Mountains. The point is that the entire geological material requires more thorough analysis.

Thus, finds of Early Devonian radiolarians in the Ural Mountains are possible. Early Devonian radiolarians of the Ural Mountains await a discoverer. This statement is inspired by the finds of radiolarians[4] in the Sakmara Zone of the Southern Urals (Ivanov and Puchkov, 1984):

- in the upper part of the stratotype section of the Kosistek Formation on the right bank of the Kos-Istek River, where in a member of red platy clayey jaspers has yielded conodonts, which are tentatively treated as representatives of the *serotinus* Zone of the Emsian Stage;
- in interbeds rich in radiolarians up to the formation of radiolarites, among deposits of the Kyzylflot Formation dated based on conodonts as the Pragian (?) and Emsian (sections on the Zhaksy-Kargala, Karabutak, Ural, and other rivers);
- in a member of even-platy gray cherts–radiolarites in the upper part of the so-called Sugralin Formation (section in the Kyzymbadzha gully), where Emsian conodonts were found;
- in radiolarites of the section on the Kolymbai Creek (upper reaches of the Terekla River), in which conodonts of the Pragian (?) Age were found.

Northerly, in the Sibai–Baimak region of the Magnitogorsk Megasynclinorium, radiolarians are frequent in jaspers and flinty slates among volcanites of the Baimak–Buribai Formation dated based on conodonts as the Late Emsian, *serotinus–patulus* zones (Maslov and Artyushkova, 2002; Artyushkova and Maslov, 2007).

The study of a new collection of radiolarians from the Lower Devonian in the section of the Kamennaya Gora locality of Bashkiria and analysis of the entire set of data on the geology and stratigraphy of the Southern Urals allowed us to establish for the first time a new biostraton ranked beds with characteristic radiolarian assemblage of the Late Emsian (Figs. 1, XI; 3; Table 2) and to describe new, previously unknown radiolarian taxa (Afanasieva and Amon, 2008b).

Late Emsian Assemblage with *Primaritripus buribayensis–Entactinia rostriformis*

Early Devonian radiolarians were found for the first time by us in the Southern Urals (Figs. 3, 4) in the section of the Kamennaya Gora locality, north of the town of Buribai on the Tanalyk River (Fig. 1, XI; Table 2) in siliceous tuff–siltstones of the third sequence of the Baimak–Buribai Formation (Afanasieva and Amon, 2008b). The division of the Baimak–Buribai Formation into three sequences was proposed by Seravkin (1986; Seravkin et al., 1992). He and many other researchers dated the Baimak–Buribai Formation to the Eifelian. However, the third sequence of the Baimak–Buribai Formation has yielded the conodont *Polygnathus* cf. *linguiformis bultyncki* Wedd. and, at present, the Baimak–Buribai Formation is assigned to the Upper Emsian, the *serotinus–patulus* conodont zones (Maslov and Artyushkova, 2002; Artyushkova and Maslov, 2007).

The new Late Emsian radiolarian assemblage is represented by 20 species of 11 genera (Table 2).

The spherical porous Sphaerellaria comprise nine species of four genera (Pl. 1, figs. 2–14): *Astroentactinia tenuis* (Furutani), *Bientactinosphaera elegans* (Hinde), *B. pittmani* (Hinde), *B. vetusta* (Hinde), *Entactinia horrida* (Furutani), *E. isensis* (Kurihara et Sashida), *E. rostriformis* Afanasieva et Amon, *Pactarentinia holdsworthi* Furutani, and *Radiobisphaera rozanovi* Afanasieva et Amon.

The spherical spongy Spumellaria are only represented by one species, *Spongentactinia fungosa* Nazarov (Pl. 1, fig. 1).

The spiny Aculearia (Pl. 1, fig. 15) and spindle-shaped Stauraxonaria (Pl. 2, figs. 1, 2) are represented by the species *Palacantholithus stellatus* Deflandre and *Pseudospongoprunum sagittatum* Wakamatsu, Sugiyama et Furutani.

Discoidal radiolarians of the class Stauraxonaria comprise eight species of four genera (Pl. 2, figs. 3–15): *Palaeodiscaleksus cribrarius* (Hinde), *P. punctus* (Hinde), *P. tumefactus* Afanasieva et Amon, *Primaritripus patella* (Hinde), *P. buribayensis* Afanasieva et

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[4] Hereinafter, undescribed radiolarian assemblages established during field work and in thin sections are considered.

Plate 1

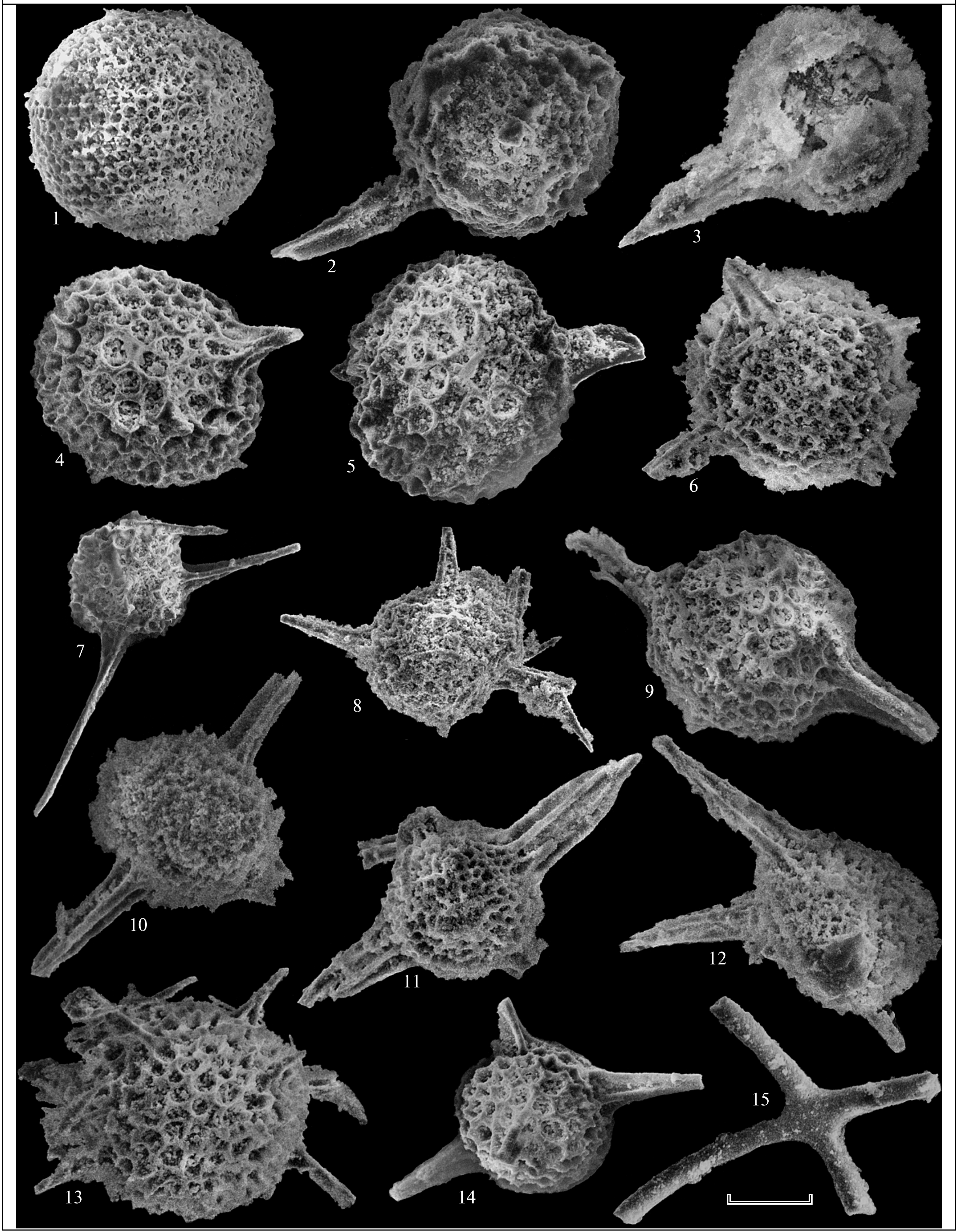


Table 2. Stratigraphic distribution of Devonian radiolarians of the Southern Urals

System	Devonian			
Series	Lower		Middle	Upper
Stage	Emsian		Eifelian	Frasnian
Substage	Upper		Upper	Middle
Formation/Regional Substage	Baimak-Buribay Formation (third unit)		Karamalytash Formation	Mukasov Regional Substage
Biostraton	Beds with *Primaritripus buribayensis – Entactinia rostriformis*		Beds with *Primaritripus kariukmasensis*	Beds with *Primaritripus chuvashovi*
Location, Samples	Kamennaya Gora Locality		Kariukmas Mountain	Argagan Mountain
Radiolarians	0551/3146	0551/3149	7653/4066-6	0434/3156-1
Bientactinosphaera elegans (Hinde, 1899)	—	—		
Spongentactinia fungosa Nazarov, 1975	—	—	—	
Entactinia horrida (Furutani, 1983)	—	—	—	
Theodiscus hastatus Hinde, 1899	—	—	—	
Astroentactinia tenuis (Furutani, 1990)	—	—	—	—
Bientactinosphaera pittmani (Hinde, 1899)	—	—	—	—
Bientactinosphaera vetusta (Hinde, 1899)	—	—	—	—
Trochodiscus planatus Hinde, 1899	—	—	—	—
Palaeodiscaleksus punctus (Hinde, 1899)	—	—	—	—
Primaritripus buribayensis Afanasieva et Amon, 2008	—	—	—	—
Palaeodiscaleksus tumefactus Afanasieva et Amon, 2008	—	—	—	—
Primaritripus chuvashovi Afanasieva et Amon, 2008	—	—	—	—
Palaeodiscaleksus cribrarius (Hinde, 1899)	—	—	—	—
Primaritripus patella (Hinde, 1899)	—	—		—
Pseudospongoprunum sagittatum Wakam., Sugiyam. et Furut., 1990		—		
Entactinia isensis (Kurihara et Sashida, 2000)		—		
Entactinia rostriformis Afanasieva et Amon, 2008		—		
Pactarentinia holdsworthi Furutani, 1983		—		
Radiobisphaera rozanovi Afanasieva et Amon, 2009		—	—	—
Palacantholithus stellatus Deflandre, 1973		—	—	—
Bientactinosphaera obtusa (Hinde, 1899)			—	
Hozmodia ozawai Sugiyama, 1992			—	
Primaritripus kariukmasensis Afanasieva et Amon, 2009			—	—
Radiobisphaera domanicensis (Bykova, 1955)				—

Explanation of Plate 1

Late Emsian radiolarians of the Southern Urals; *Primaritripus buribayensis–Entactinia rostriformis Assemblage*: Spherical spongy Spumellaria (1), porous Sphaerellaria (2–14), and spiny Aculearia (15).

Fig. 1. *Spongentactinia fungosa* Nazarov, 1975, specimen PIN, no. 5247/14404; scale bar, 59 μm.

Figs. 2 and 3. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009: (2) specimen PIN, no. 5247/14333; scale bar, 40 μm; (3) specimen PIN, no. 5247/14516; scale bar, 27 μm.

Figs. 4 and 5. *Entactinia rostriformis* Afanasieva et Amon, 2008: (4) specimen PIN, no. 5247/14834; scale bar, 40 μm; (5) holotype no. 5247/14833; scale bar, 40 μm.

Fig. 6. *Entactinia horrida* (Furutani, 1983), specimen PIN, no. 5247/14306; scale bar, 37 μm.

Fig. 7. *Pactarentinia holdsworthi* Furutani, 1983, specimen PIN, no. 5247/14925; scale bar, 68 μm.

Fig. 8. *Entactinia isensis* (Kurihara et Sashida, 2000), specimen PIN, no. 5247/14318; scale bar, 68 μm.

Fig. 9. *Bientactinosphaera vetusta* (Hinde, 1899), specimen PIN, no. 5247/14515; scale bar, 44 μm.

Figs. 10–12. *Bientactinosphaera pittmani* (Hinde, 1899): (10) specimen PIN, no. 5247/14315; scale bar, 37 μm; (11) specimen PIN, no. 5247/14323; scale bar, 37 μm; (12) specimen PIN, no. 5247/14317; scale bar, 40 μm.

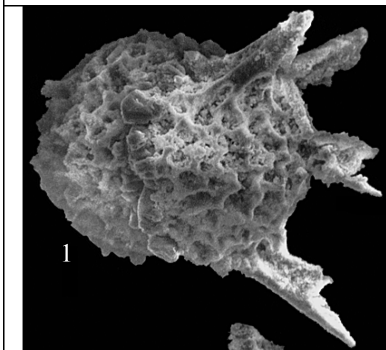
Fig. 13. *Astroentactinia tenuis* (Furutani, 1990), specimen PIN, no. 5247/14325; scale bar, 40 μm.

Fig. 14. *Bientactinosphaera elegans* (Hinde, 1899), specimen PIN, no. 5247/14828; scale bar, 55 μm.

Fig. 15. *Palacantholithus stellatus* Deflandre, 1973, specimen PIN, no. 5247/14824; scale bar, 37 μm.

Lower Devonian, Upper Emsian Substage; Southern Urals, section of Kamennaya Gora on the Tanalyk River, north of the town of Buribai: (1–3, 6, 8, 9, 11–14) sample 0551/3149 and (4, 5, 7, 10, 15) sample 0551/3146.

Plate 2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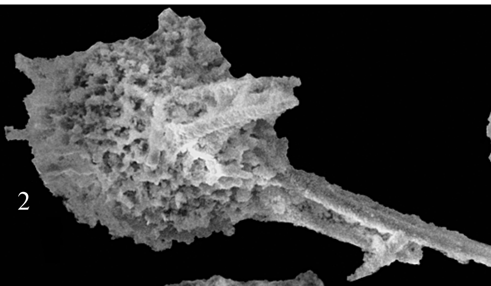
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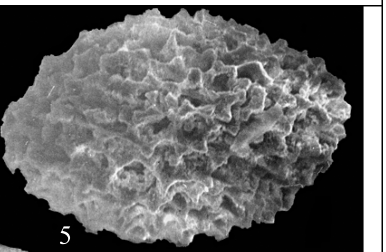
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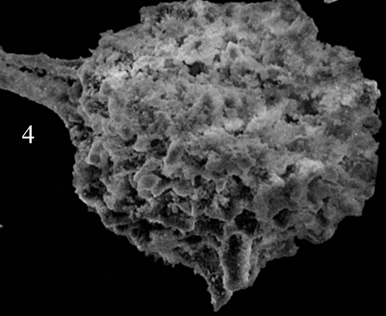
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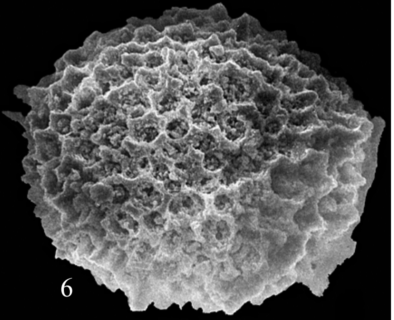
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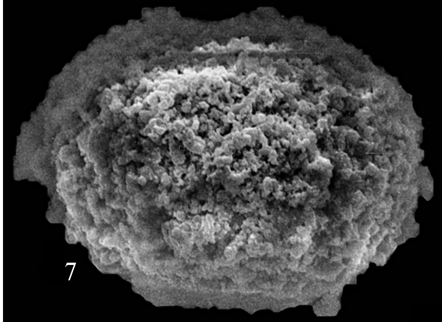
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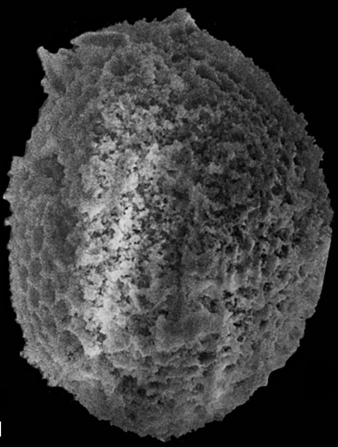
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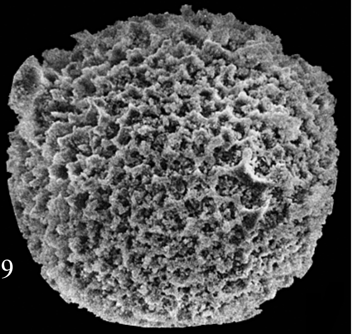
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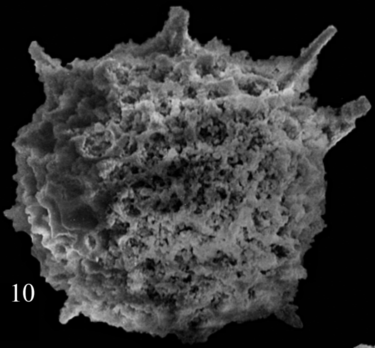
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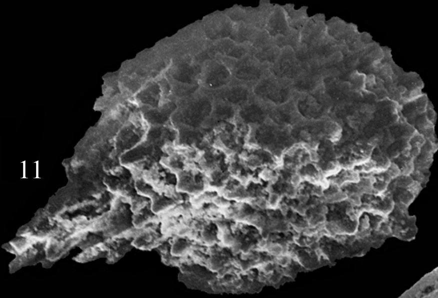
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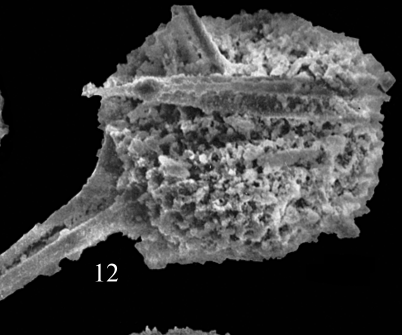
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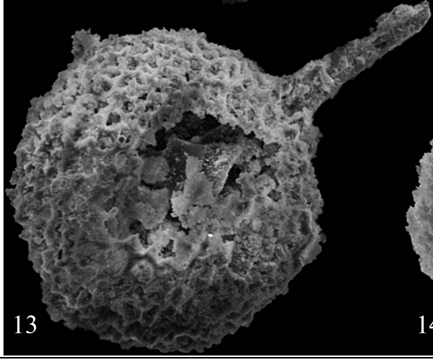
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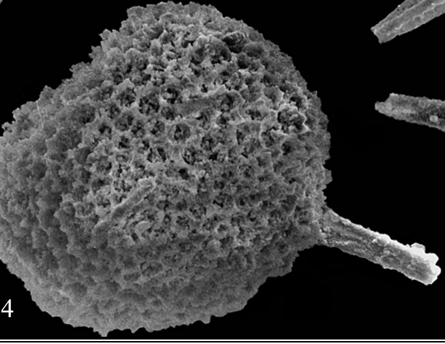
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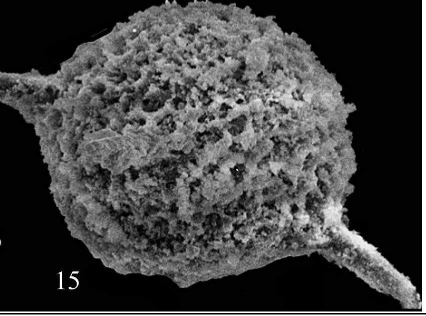
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Explanation of Plate 2

Late Emsian radiolarians of the Southern Urals; *Primaritripus buribayensis—Entactinia rostriformis* Assemblage: spindle-shaped (1, 2) and discoidal (3—15) Stauraxonaria.

Figs. 1 and 2. *Pseudospongoprunum sagittatum* Wakamatsu, Sugiyama et Furutani, 1990: (1) specimen PIN, no. 5247/14520; scale bar, 55 μm; (2) specimen PIN, no. 5247/14521; scale bar, 33 μm.

Figs. 3 and 4. *Theodiscus hastatus* Hinde, 1899: (3) specimen PIN, no. 5247/14424; scale bar, 44 μm; (4) specimen PIN, no. 5247/14408; scale bar, 48 μm.

Figs. 5 and 6. *Palaeodiscaleksus cribrarius* (Hinde, 1899): (5) specimen PIN, no. 5247/15003, lateral view; scale bar, 37 μm; (6) specimen PIN, no. 5247/15106; scale bar, 37 μm.

Fig. 7. *Palaeodiscaleksus punctus* (Hinde, 1899), specimen PIN, no. 5247/14531, lateral view; scale bar, 33 μm.

Figs. 8 and 9. *Palaeodiscaleksus tumefactus* Afanasieva et Amon, 2008: (8) specimen PIN, no. 5247/14528, lateral view; scale bar, 44 μm; (9) holotype PIN, no. 5247/14505; scale bar, 55 μm.

Fig. 10. *Trochodiscus planatus* Hinde, 1899, specimen PIN, no. 5247/14407; scale bar, 40 μm.

Fig. 11. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5247/14931; scale bar, 33 μm.

Fig. 12. *Primaritripus chuvashovi* Afanasieva et Amon, 2008, specimen PIN, no. 5247/14415; scale bar, 34 μm.

Figs. 13—15. *Primaritripus buribayensis* Afanasieva et Amon, 2008: (13) specimen PIN, no. 5247/14412; scale bar, 55 μm; (14) specimen PIN, no. 5247/15014; scale bar, 55 μm; (15) holotype PIN, no. 5247/14511; scale bar, 33 μm.

Lower Devonian, Upper Emsian Substage; Southern Urals, section of Kamennaya Gora on the Tanalyk River, north of the town of Buribai: (1—4, 7—10, 12, 15) sample 0551/3149 and (4, 5, 11, 13, 14) sample 0551/3146.

Amon, *P. chuvashovi* Afanasieva et Amon, *Theodiscus hastatus* Hinde, and *Trochodiscus planatus* Hinde.

The prevalence in oryctocoenosis of discoidal radiolarians (up to 60% of the total number of individuals) suggests relatively shallow marine character of the sedimentation basin of the Southern Urals in the Early Devonian (Fig. 4).

We treat the Late Emsian radiolarian association according to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006) as a characteristic assemblage of a new biostraton, Beds with *Primaritripus buribayensis—Entactinia rostriformis* (Tables 2, 3), which correspond to the Upper Emsian *patulus* Conodont Zone.

The Beds with *Primaritripus buribayensis—Entactinia rostriformis* occur and are valid within the Southern Urals and Northern Mugodzhary. The new biostraton corresponds in stratigraphic position (Table 3) to the Upper Emsian *Protoholoeciscus hindea* Zone of central and southwestern Japan (Umeda, 2002; Kurihara, 2003a, 2003b), the middle part of the Middle Emsian—Lower Eifelian *Circulaforma admissarius* Zone of eastern Australia (Metcalfe et al., 1997; Stratford and Aitchison, 1997), and to the Upper Emsian Beds with *Bientactinosphaera limpida* of Western Siberia (Lipnitskaja, 1995, 2002).

Geographical Distribution of Early Devonian Radiolarians

The analysis of published data has shown that, to date, 106 species of 28 radiolarian genera have been recorded in the Early Devonian of the world fauna; 42 of these species are described in open nomenclature (Table 1). Most of the Early Devonian radiolarians are spherical forms, comprising 54 species of 14 genera. Spiny members are represented by 42 species of nine genera, and stauraxonic radiolarians are ten species of five genera.

Beyond Russia, Early Devonian radiolarians were established for the first time by Furutani (1990) in central Japan and provided the basis for the recognition of two assemblages of Early Devonian radiolarians (Fig. 3; Tables 1, 3): *Zadrappolus yoshikiensis* for the lower horizons of the Lochkovian Stage and *Stylosphaera?* sp. A—*Stylosphaera?* sp. B for the upper part of the Lochkovian—Emsian.

Early Devonian radiolarians of eastern Australia (Fig. 3), comprising 20 species of six genera (Table 1), were described for the first time by Aitchison and coauthors (Metcalfe et al., 1997; Stratford and Aitchison, 1997) from interbedding tuffaceous siliceous shales and limestones and clayey shales of the Gemilaroi terrane (New England, New South Wales). Stratford and Aitchison (1997) established two Lower Devonian radiolarian assemblages: Pragian with *Helenifore laticlavium* and Middle Emsian—Early Eifelian with *Circulaforma admissarius* (Table 3).

The radiolarian assemblage of the Pragian Age includes the species *Helenifore laticlavium* Nazarov et Ormiston, *Palaeoscenidium cladophorum* Deflandre, *Ceratoikiscum* sp. A, Entactiniidae gen. et sp. indet. (sp. B, sp. F, sp. J, sp. M) (Stratford and Aitchison, 1997). A Middle Emsian—Early Eifelian radiolarian assemblage is characterized by the species *Circulaforma admissarius* Stratford et Aitchison, *Circulaforma* sp. A, *Ceratoikiscum calvum* Stratford et Aitchison, *Palaeoscenidium cladophorum* Deflandre, *Trilonche*[5] *hindea* (Hinde), *T. vetusta* Hinde, *T. echinata* (Hinde), *T. elegans* (Hinde), *Trilonche* sp. A, *Trilonche* sp. B, and Entactiniidae gen. et sp. indet. (sp. B, sp. K, sp. L) (Metcalfe et al., 1997; Stratford and Aitchison, 1997) (Table 1).

In southwestern Japan (Fig. 3), in the Kurosegawa Fold Belt Terrane, Lower—Middle Devonian beds have yielded ten Emsian radiolarian species of five genera (Umeda and Yamagiwa, 1997; Umeda, 1998a): *Ceratoikiscum, Glanta, Helenifore, Palaeoscenidium,*

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[5] In the revision of Devonian radiolarians of eastern Australia, Aitchison and Stratford (1997) proposed to return to the generic names used in works of Hinde (1890, 1899a, 1899b) (see Chapter 6).

Table 3. Biostratigraphy of Lower and Middle Devonian radiolarian assemblages

System	Series	Stage	Substage	Australia, New South Wales, New England Range, Gamilaroi terrane Stratford, Aitchison, 1997	Southwest Japan, Kurosegawa Belt		Central Japan, Hida Gaien Belt				Russia, South Urals Afanasieva, Amon, 2008, 2009	Czech Republic, Prague Basin (Barrandian) Afanasieva, Amon, 2010, 2011
					Umeda, 1998a, 1998b	Umeda et al., 2002 (after Kurihara, 2003a, 2003b)	Furutani, 1990	Kurihara, Sashida, 2000	Kurihara, 2003a, 2003b	Kurihara, 2004		
Devonian	Middle	Eifelian		*Ceratoikiscum regalinodus*			*Stylosphaera?* sp. C	*Pactarentinia holdsworthi*			Beds with *Primaritripus kariukmasensis*	Beds with *Apophysisphaera hystricuosa – Spongentactinia fungosa*
				Protoholoeciscus hindea	*Protoholoeciscus hindea*							
				Helenifore sp. A	*Glanta fragilis*							
				Circulaforma admissarius								
	Lower	Emsian	Upper		*Trilonche* (?) sp. A	*Protoholoeciscus hindea*	*Stylosphaera?* sp. A – *Stylosphaera?* sp. B		*Protoholoeciscus hindea*		Beds with *Primaritripus buribayensis – Entactinia rostriformis*	
			Middle			*Glanta fragilis*			*Glanta fragilis*			
			Lower			*Trilonche* (?) sp. A			*Trilonche* (?) sp. A	*Pactarentinia intermedia–Pactarentinia igoi*		
		Pragian	Upper	*Helenifore laticlavium*		*Futobari solidus*			*Futobari solidus*	*Palaeoscenidium ishigai–Deflantrica furutanii*		
			Lower		*Futobari solidus*				*Zadrappolus yoshikiensis*	*Futobari solidus–Zadrappolus tenuis*		
		Lochkovian	Upper									
			Lower				*Zadrappolus yoshikiensis*	*Zadrappolus* sp. aff. *spinosus*				

and *Protoholoeciscus* (Table 1). In the Lower Devonian beds, Umeda (1998a, 1998b) established two radiolarian zones and, then, four (Umeda, 2002) (Table 3), including *Futobari solidus* (Pragian), *Trilonche* (?) sp. *A* (Lower Emsian), *Glanta fragilis* (Middle Emsian), and *Protoholoeciscus hindea* (Upper Emsian).

In central Japan, Fukui Prefecture (Fig. 3), interbedding clastic and carbonate rocks (sandstones and limestones) of the Yoshiki and Fukuji formations of the Hida Gaien Belt have yielded an Emsian–Eifelian radiolarian assemblage of good preservation (Kurihara and Sashida, 1998, 2000; Kurihara, 2000). The assemblage consists of 47 species of 16 genera (Table 1), including a large part of Early Devonian forms of the genera *Palaeoscenidium, Deflantrica, Pactarentinia, Tlecerina* (=*Entactinia*), *Ceratoikiscum, Glanta*, and *Protoholoeciscus*. In the Early–Middle Devonian, these researchers recognized two radiolarian assemblages (Table 3), with *Zadrappolus* aff. *spinosus* (Late Silurian–Early Devonian, Pridolian–Lochkovian) and *Pactarentinia holdsworthi* (Early–Middle Devonian, Emsian–Eifelian).

Kurihara (2003a, 2003b) extended Emsian radiolarian zones recognized by Umeda (2002) to central Japan and added a Pragian assemblage with *Futobari solidus* (Table 3). One year later, Kurihara (2004) proposed a new zonal stratification of the Lower Devonian beds (Lochkovian–Lower Emsian) based on radiolarians for central Japan (Table 3): *Futobari solidus–Zadrappolus tenuis* (Upper Pridolian–Lower Pragian), *Palaeoscenidium ishigai–Deflantrica furutanii* (Upper Pragian), *Pactarentinia intermedia–P. igoi* (Lower Emsian).

From siliceous interbeds of the Tanhe Formation in Guangxi Province of southern China (Fig. 3), Luo et al. (2002) described a relatively rich Late Emsian–Early Givetian radiolarian assemblage, consisting of 19 species of seven genera (Table 1), and established six new species. The assemblage is rich in local endemic taxa, which were described for the first time by Chinese researchers.

MIDDLE DEVONIAN

At the beginning of the Middle Devonian, a new developmental stage of the region began. The main feature of this stage was gradual submerging of the Russian Platform and, consequently, transgression of the Ural Paleocean from the east (Fig. 5a). In the eastern part of the Russian Platform, Middle Devonian deposits are similar in lithology, cyclicity, and paleontological features to the Western Urals.

Eifelian Age

At the beginning of the Early Eifelian, the Russian Platform was still rather high and abundant clastic material was transported from it to the eastern basins. The central part of the platform was occupied by a lagoon with increased salinity, which had only one-way connection with the shallow sea in the eastern part of the Russian Platform; this did not promote the development of radiolarians. In the eastern Russian Platform, shallow marine conditions of a marginal sea of the Ural Paleocean gradually formed (Tikhii, 1975) (Fig. 5a).

At the end of the Early Eifelian, the eastern part of the platform began lowering and, during the Late Eifelian, marine transgression of the Ural Paleocean gradually expanded. Thus, the northwestern part of the platform turned into an extensive coastal–marine plain. The Late Eifelian transgression considerably expanded the Ural Sea and resulted in the formation of a shallow open marginal basin with carbonate deposits and, in the south, with siliceous deposits (Tikhii, 1975).

Notwithstanding generally adverse paleogeographic background in the eastern Russian Platform and Ural Mountains, radiolarians continued adaptation to water areas of these regions in the Eifelian Time (Fig. 5a).

The frequent occurrence of Eifelian radiolarians was marked for the first time by Shatrov and Petrova (1984) in thin sections from the rocks of the lower part of red beds in the interfluve of the Manya and Lopsiya rivers in the Northern Sos'va Basin on the eastern slope of the Northern Urals (Figs. 3; 6, III, IV).

In the Sakmara Zone of the Southern Urals, among diabases of the so-called Sugralin Formation (gully of the Temnaya valley, right tributaries of the Chebakly River on the left bank of the Ural River), Ivanov and Puchkov (1984) recorded a member of contorted red jaspers–radiolarites about 12 m thick, with a Late Eifelian conodont assemblage (*Polygnathus* cf. *pseudofoliatus* Witt., *P.* cf. *eiflius* Bisch. et Zieg., *P.* ex gr. *linguiformis* Hinde) (Fig. 1, XIII).

In an outcrop on the Shuldak River (Fig. 1, XVI) in the southern peripheral area of the Sakmara Zone of the Southern Urals (including Northern Mugodzhary) (Fig. 3), Nazarov (1988) established a radiolarian assemblage with *Spongentactinella windjanensis–Bientactinosphaera nigra*, which, in his opinion, was characteristic of not only Givetian but also Eifelian Stage. In our opinion, this assemblage is confined to the Givetian, while the Late Eifelian Age is marked by a new radiolarian assemblage with *Primaritripus kariukmasensis* (Table 3).

Late Eifelian assemblage with *Primaritripus kariukmasensis*. We found the new radiolarian assemblage with *Primaritripus kariukmasensis* of Late Eifelian Age in the Southern Urals, Bashkortostan (Fig. 3), in a section on the southeastern slope of Karyukmas Mountain in an interbed of red jaspers among volcanites of the Karamalytash Formation (Fig. 1, IX; Table 2) (Afanasieva and Amon, 2009a). The jaspers have yielded a conodont assemblage, including *Tortodus kockelianus kockelianus* Bisch. et Ziegl., *Polygnathus* aff. *angusticostatus* Witt., *P.* cf. *eiflius* Bisch. et Zieg., *P. robusticostatus* Bisch. et Ziegl., and *P. trigonicus* Bisch. et Zieg. Somewhat northerly, at the top of Karyukmas

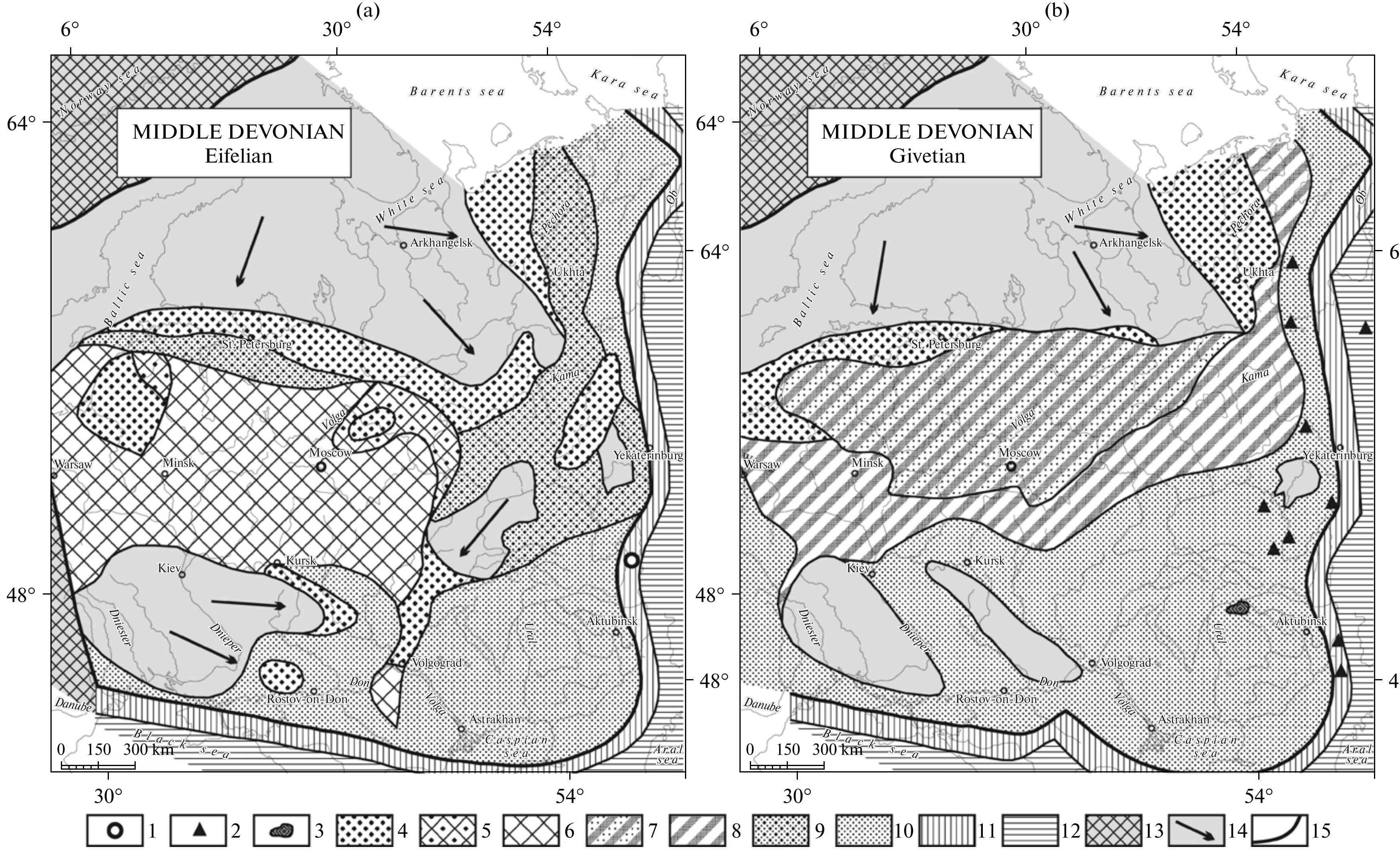

Fig. 5. Paleobiogeographic scheme for the Eifelian (a) and Givetian (b) of the Russian Platform and Greater Urals, with radiolarian localities: (1, 2) radiolarian localities: (1) Eifelian, (2) Givetian; (3) Karachaganak bioherm; (4) continental fluvial plains; (5, 6) sea of increased salinity: (5) coastal region, (6) shallow internal shelf; (7, 8) sea of low salinity: (7) coastal region, (8) internal shelf; (9–12) sea of normal salinity: (9) coastal region, (10) internal shelf, (11) continental slope, (12) bottom of paleocean; (13) active fold belt; (14) main directions of transportation of clastic material from land; and (15) boundary of the Russian Platform. Paleobiogeographic schemes are based on the data of Tikhomirov (1967, 1995), Tikhii (1975), Racki (1992, 1997), Rodionova et al. (1995), Nikishin et al. (1996), and Yunusov et al. (1997).

Mountain, the following conodonts were found: *Polygnathus eiflius* Bisch. et Zieg., *P. linguiformis linguiformis* Hinde, *P.* aff. *robusticostatus* Bisch. et Zieg., *P. trigonicus* Bisch. et Zieg., *Tortodus kockelianus australis* (Jack.), and *T. kockelianus kockelianus* Bisch. et Zieg. These assemblages are characteristic of the *australis–kockelianus* zones of the Upper Eifelian (Maslov and Artyushkova, 2002; Kononova and Kim, 2005).

The new Late Eifelian radiolarian assemblage consists of 17 species of 11 genera.

The spherical porous Sphaerellaria are represented by six species of four genera (Pl. 3, figs. 3–7, 9–15): *Astroentactinia tenuis* (Furutani), *Bientactinosphaera obtusa* (Hinde), *B. pittmani* (Hinde), *B. vetusta* (Hinde), *Entactinia horrida* (Furutani), and *Radiobisphaera rozanovi* Afanasieva et Amon.

The spherical spongy Spumellaria are only represented by one species, *Spongentactinia fungosa* Nazarov (Pl. 3, fig. 8).

Radiolarians with pylome from the order Pylomariata (Pl. 3, fig. 1) and spiny Aculearia (Pl. 3, fig. 2) are represented by the species *Hozmadia ozawai* Sagiyama and *Palacantholithus stellatus* Deflandre.

Discoidal radiolarians of the class Stauraxonaria are represented by eight species of four genera (Table 4): *Palaeodiscaleksus*[6] *cribrarius* (Hinde), *P. punctus* (Hinde), *P. tumefactus* Afanasieva et Amon, *Primaritripus buribayensis* Afanasieva et Amon, *P. chuvashovi* Afanasieva et Amon, *P. kariukmasensis* Afanasieva et Amon, *Theodiscus hastatus* Hinde, and *Trochodiscus planatus* Hinde.

The prevalence in the oryctocoenosis of discoidal radiolarians (more than 60% of the total number of individuals), as in the Early Devonian, is evidence of relatively shallow marine character of the sedimentation basin in the Middle Devonian of the Southern Urals (Fig. 5a) (Afanasieva and Amon, 2008b, 2009a).

According to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006), we consider the Late Eifelian radiolarian association as a characteristic assemblage of the new biostraton: Beds with *Primaritripus kariukmasensis* (Table 2), which correspond to the Late Eifelian *australis–kockelianus* conodont zones.

The new Middle Devonian Upper Eifelian radiolarian biostraton (Table 3) occurs and is valid within the Southern Urals and Northern Mugodzhary (Afanasieva and Amon, 2009a) and corresponds in stratigraphic position to the *Ceratoikiscum regalinodus* Zone of New South Wales of Australia (Stratford and Aitchison, 1997).

Late Eifelian assemblage with *Apophisisphaera hystricuosa–Spongentactinia fungosa*. A diverse Late Eifelian radiolarian assemblage has been found at the extreme western marginal area of the Russian Platform in the Prague Basin of Czechia (Figs. 3, 7) (Afanasieva and Amon, 2009d).

The first radiolarians of the Prague Basin were recorded in the Barrandian stratotype, in thin sections from a 2-m-thick limestone strata of the Chotec Beds of the Chotec Formation, within the *Polygnathus costatus partitus, Tortodus kockelianus australis*, and *Tortodus kockelianus kockelianus* conodont zones, which covers almost entirely the Eifelian Stage (Fabian, 1933; Petránek, 1946; Čejchan, 1987).

Later, Budil (1995a, 1995b) and Braun and Budil (1999) extracted and described for the first time radiolarians from the upper part of the Chotec Formation, 50 cm below the boundary of the Kačák beds (Fig. 7). The radiolarian biota comes from the uppermost part of the *Tortodus kockelianus* Conodont Zone, which is characteristic of the Upper Eifelian. The study of these radiolarians allowed these researchers to characterize in more detail the Barrandian radiolarian association.

The fauna is not always well preserved, although, among the taxa determined with certainty, the authors cited recognized 19 species of nine radiolarian genera (Budil, 1995a, 1995b; Braun and Budil, 1999) (Table 4).

They include 13 species of six genera of spherical porous radiolarians of the class Sphaerellaria: *Astroentactinia* cf. *stellata* Nazarov, *A. paronae* (Hinde), *Entactinia* cf. *additive* Foreman, *Entactinia* spp., *Entactinosphaera* cf. *polyacanthina* Foreman, *Entactinosphaera* sp. 1, *Entactinosphaera* sp. 2, *Helioentactinia ?* sp., *Stigmosphaerostylus*[7] (=*Entactinia*) *herculea* (Foreman), *S.* aff. *proceraspinus* (Aitchison), *S.* (*Apophisisphaera*) aff. *hystricuosa* (Aitchison), *Trilonche* (=*Bientactinosphaera*[8]) *riedeli* (Foreman), and *T.? echinata*[9] (Hinde).

Spherical spongy radiolarians of the class Spumellaria are only represented by one species, *Spongenactinella ?* sp. 2 Nazarov et Ormiston.

Spiny radiolarians of the class Aculearia are represented by five species of two genera: *Ceratoikiscum* sp., *Ceratoikiscum* sp. 2 sensu Čejchan, *Ceratoikiscum* sp. 5 sensu Čejchan, *Palaeoscenidium cladophorum* Deflandre, and *Palaeoscenidium* sp.

Our new study of radiolarians from limestones of the Chotec Formation, collected 60 cm below the boundary with the Kačák Beds (Fig. 7), has shown the presence of a more diverse assemblage, including 31 species of 15 radiolarian genera (Afanasieva and Amon, 2009d) (Table 4).

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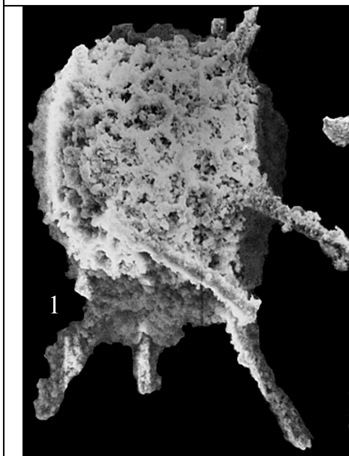
[6] *Palaeodiscaleksus* is the new name of the genus *Palaeodiscus* Afanasieva, 2000 introduced according to the principle of homonymy (Afanasieva, 2008).

[7] See revision of the genera *Entactinia* Foreman and *Stigmosphaerostylus* Rüst in Chapter 6.

[8] See Footnote 5.

[9] Hereinafter, we use the name *Trilonche echinata* when citing different authors; however, it should be kept in mind that this species is composite (see chapter 6).

Plate 3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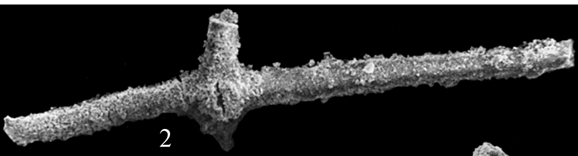
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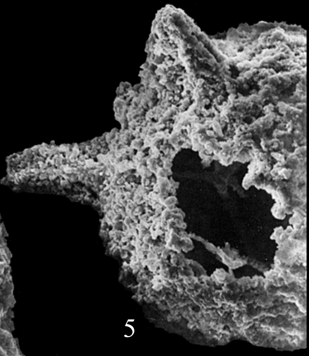
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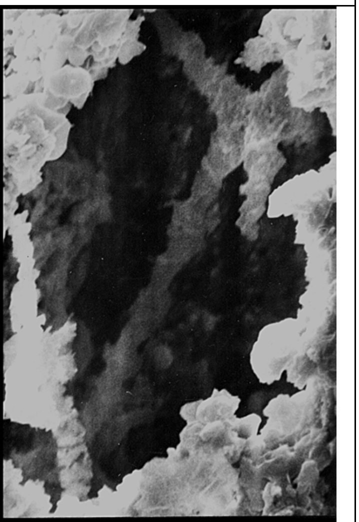
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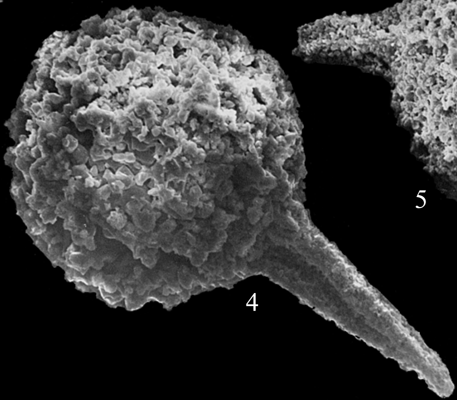
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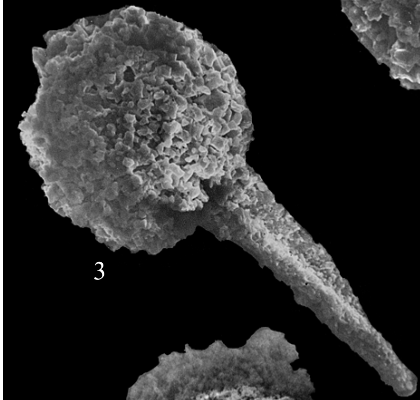
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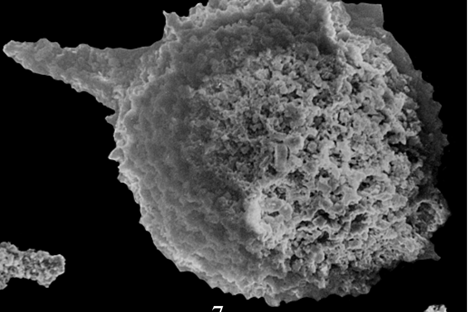
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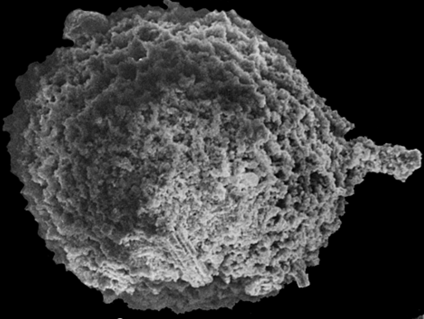
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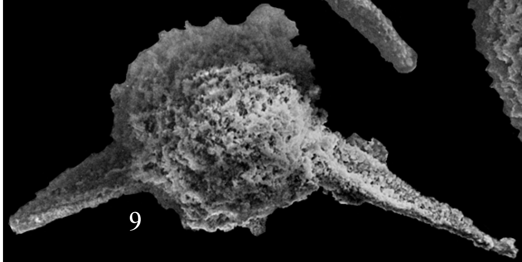
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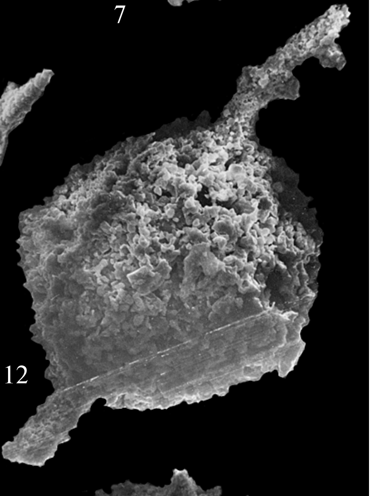
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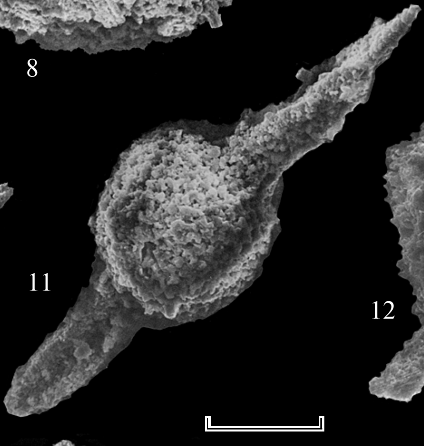
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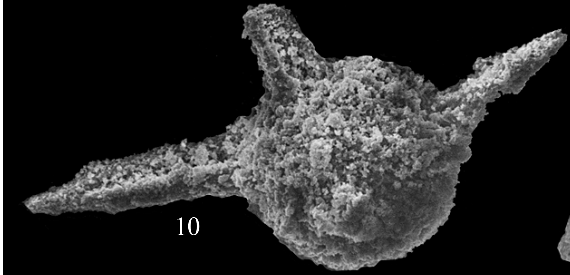
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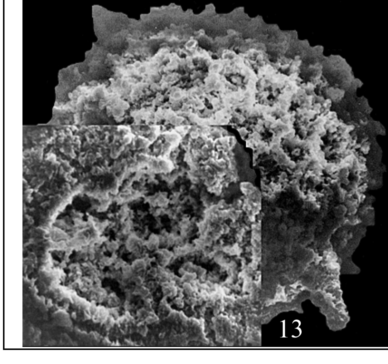
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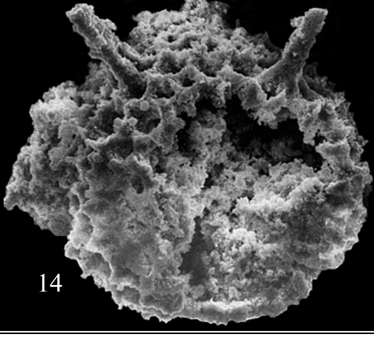
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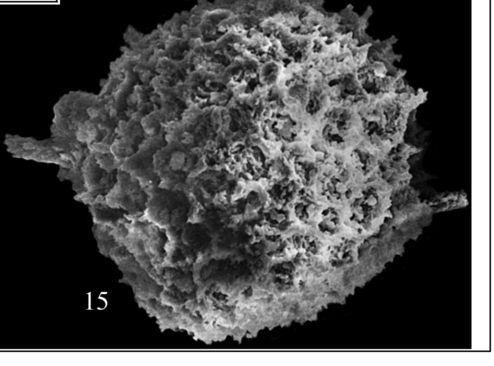
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Spherical porous radiolarians of the class Sphaerellaria are represented by 13 species of five genera (Pl. 5, figs. 1–13): *Apophysisphaera hystricuosa* (Aitchison), *Astroentactinia stellata* Nazarov, *Bientactinosphaera cancellicula* (Foreman), *B. clavata* (Hinde), *B. elegans* (Hinde), *B. pittmani* (Hinde), *Entactinia crustescens* Foreman, *E. echinata* (Hinde), *E. faveolata* Nazarov, *E. parva* Won, *E. paula* Foreman, *E. proceraspina* Aitchison, and *Radiobisphaera rozanovi* Afanasieva et Amon.

Spherical spongy members of the class Spumellaria include 11 species of five genera (Pl. 6, figs. 1–10): *Pluristratoentactinia conspissata* Nazarov, *P. trisphaerata* Afanasieva et Amon, sp. nov., *Polyentactinia circumretia* Nazarov et Ormiston, *Somphoentactinia multisphaerata* Afanasieva et Amon, sp. nov., *Spongentactinella exilispina* (Foreman), *S. intracata* Aitchison, *S. veles* (Foreman), *S. windjanensis* Nazarov, *Spongentactinia diplostraca* (Foreman), *S. fungosa* Nazarov, and *S. marina* Afanasieva et Amon, sp. nov.

Spiny radiolarians of the class Aculearia are represented by seven species of five genera: *Ceratoikiscum lyratum* Ishiga, *Nazarovites bioculus* Afanasieva, *Palacantholitus stellatus* Deflandre, *Palaeothalomnus quadriramosum* (Foreman) (Pl. 5, figs. 14–17), *Palaeoscenidium cladophorum* Deflandre, *P. robustum* Aitchison, and *P. tabernaculum* Aitchison (Pl. 6, figs. 11–13).

In this radiolarian assemblage, *Apophysisphaera hystricuosa* (Aitchison) and members of the genus *Spongentactinia* prevail in number, and the radiolarian morphotype with two porous spheres and one main spine, represented by the species *Radiobisphaera rozanovi* Afanasieva et Amon, is recorded for the first time.

We propose to regard the new Late Eifelian radiolarian association as a characteristic assemblage of the new biostraton (Afanasieva and Amon, 2009d): Beds with *Apophysisphaera hystricuosa–Spongentactinia fungosa* (Table 3), which correspond in age to the Late Eifelian *kockelianus* Conodont Zone.

At the same time, Čejchan (1987, 2006) believes that the radiolarian biota from the Chotec Formation correlates with the radiolarian association described by Hinde (1899a) from the volcanogenic–siliceous Tamworth Series of New South Wales, Australia. However, in the revisions of Aitchison (1988b, 1990) and Aitchison and Stratford (1997), the radiolarian assemblage from New South Wales was dated Givetian. The taxonomic composition of the new radiolarian assemblage from the Chotec Formation in general agrees with this point of view. However, the presence in the section of Late Eifelian conodonts suggests that the new assemblage should be dated Late Eifelian.

The new Upper Eifelian radiolarian biostraton, Beds with *Apophysisphaera hystricuosa–Spongentactinia fungosa*, occurs and is valid within Czechia and corresponds in stratigraphic position to the radiolarian Beds with *Primaritripus kariukmasensis* of the Southern Urals (Afanasieva and Amon, 2009a) and the *Ceratoikiscum regalinodus* Zone of New South Wales of Australia (Stratford and Aitchison, 1997) (Table 3).

The stratigraphic equivalents and analogues of the new biostraton *Apophysisphaera hystricuosa–Spongentactinia fungosa* are recognized in regional radiolarian associations of the same age of the eastern continental block of Euramerica (Southern Urals) in the Northern Hemisphere and the superplatform of Gondwana in the Southern Hemisphere (Australia, New South Wales).

Braun and Budil (1999) believe that changes in taxonomic composition and abundance of radiolarians are observed from the bottom of the Chotec beds (Fig. 7). This begins approximately 2 m below a sharp shift in sedimentation conditions, i.e., the beginning of accumulation of black shales of the Kačák Member (Fig. 7), which are usually regarded as evidence of the onset of the biotic crisis.

The data of Čejchan (2006) and results of our new study in general confirm and develop these observations. Fluctuations in qualitative and quantitative

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Explanation of Plate 3

Late Eifelian radiolarians of the Southern Urals; assemblage with *Primaritripus kariukmasensis*: Radiolarians with pylome from the order Pylomariata, Nassellaria (1); spiny Aculearia (2); spherical porous Sphaerellaria (3–7, 9–15); and spongy Spumellaria (8).

Fig. 1. *Hozmadia ozawai* Sugiyama, 1992, specimen PIN, no. 5247/15216; scale bar, 44 μm.

Fig. 2. *Palacantholithus stellatus* Deflandre, 1973, specimen PIN, no. 5247/15202; scale bar, 98 μm.

Figs. 3 and 4. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009: (3) specimen PIN, no. 5247/15220; scale bar, 40 μm; (4) specimen PIN, no. 5247/15214; scale bar, 37 μm.

Figs. 5–7. *Entactinia horrida* (Furutani, 1983): (5, 6) specimen PIN, no. 5247/15233: (5) scale bar, 40 μm; (6) fragment, scale bar, 15 μm; (7) specimen PIN, no. 5247/15213; scale bar, 40 μm.

Fig. 8. *Spongentactinia fungosa* Nazarov, 1975, specimen PIN, no. 5247/15206; scale bar, 56 μm.

Figs. 9 and 10. *Bientactinosphaera pittami* (Hinde, 1899): (9) specimen PIN, no. 5247/15212; scale bar, 55 μm; (10) specimen PIN, no. 5247/15203; scale bar, 37 μm.

Fig. 11. *Bientactinosphaera obtusa* (Hinde, 1899), specimen PIN, no. 5247/15217; scale bar, 37 μm.

Fig. 12. *Bientactinosphaera vetusta* (Hinde, 1899), specimen PIN, no. 5247/15225; scale bar, 37 μm.

Figs. 13–15. *Astroentactinia tenuis* (Furutani, 1990): (13) specimen PIN, no. 5247/15226; scale bar, 37 μm; (14) specimen PIN, no. 5247/15205; scale bar, 40 μm; (15) specimen PIN, no. 5247/15231; scale bar, 37 μm.

Middle Devonian, Upper Eifelian Substage. Southern Urals, section in the Karyukmas Mountain, northwest of the village of Staryi Sibai, sample 7653/4066-6.

Fig. 6. Radiolarian localities in the Timan–Pechora Basin and northern and Polar Urals: (a) position of working area, (b) Timan–Pechora Basin, (II–IV) Northern and (V–IX) Polar Urals; (c) Ukhtinskii District of the Timan–Pechora Basin; radiolarian localities: (I) Ukhtinskii District, (II) Unya River, (III) Lopsiya River, (IV) Manya River, (V) Malaya Nadota River, (VI) Lemva River, (VII) Kharuta River, (VIII) Paga River, (IX) Palnik-Yu River, (X) borehole Zapadnaya Vissertynskaya-1, (XI) borehole Zapadno-Lekkeyaginskaya-65. Designations: (1) working area; (2) villages (*a*) and towns (*b*); (3) boreholes Ukhtinskaya-3B, Shuda-Yag-1002, Shuda-Yag-1003, and Vapovskaya-2056; (4) outcrops; (5) sections (*a*), quarries (*b*), and points (*c*); (6) paleoreefs; (7) axis of the Ukhta Anticlinal (*a*) and geological boundaries of formations and subformations (*b*); (8–16) stratigraphic units of the Upper Devonian: (8, 9) Lower Frasnian Substage: (8) Upper Timan Subformation, (9) Ust'-Yarenga Formation; (10) Middle Frasnian Substage, Domanik Formation; (11–15) Upper Frasnian Substage: (11) Vetlasyan Formation, (12) Sirachoi Formation, (13) Ukhta Formation, (14) Lyaiol Formation, 15) Sedyu Formation; and (16) Famennian Stage, Izhma Formation.

composition of radiolarian assemblages occur within the Chotec beds (Fig. 7). These fluctuations are not associated with changes in lithology and, hence, with bathymetry of the basin. However, at the end of the Late Eifelian, the radiolarian biota underwent a considerable stress before the onset of crisis events, which were caused by a sharp shift in sedimentation conditions in anoxic environments of bottom waters and connected with the beginning of the formation of black shales of the Kačák Member (Fig. 7).

The prevalence in the new oryctocoenosis of spherical radiolarians (77.4% of the total number of individuals) is probably evidence of normal marine, relatively deepwater environments of the ancient basin.

At the same time, the analysis of changes in the taxonomic composition of radiolarian assemblages upward in the section has shown that 54.8% of radiolarians became extinct near the boundary with black slates of the Kačák Member (Table 4). In particular, note predominant disappearance of more deepwater spherical spongy species of Spumellaria (90.9%) against the background of extinction of 30.8% of spherical porous Sphaerellaria and 42.9% of spiny Aculearia.

On the other hand, three species of spherical porous Sphaerellaria new to this region appeared: *Astroentactinia paronae* (Hinde), *Entactinosphaera* sp. 2, and *Helioentactinia?* sp.

Thus, our study of Late Eifelian radiolarians of the Prague Basin (Czechia) resulted in (1) the establishment of the new *Apophysisphaera hystricuosa–Spongentactinia fungosa* biostraton ranked beds with characteristic faunal assemblage, (2) correlation of the new biostraton with regional radiolarian associations of the Southern Urals and Australia (New South Wales) of the same age, (3) recognition of distinctive evolutionary features of regional radiolarian faunas of the Middle Devonian in the paleobasin of central Europe.

Givetian Age

At the Eifelian–Givetian boundary, during regression, the Ural Sea left a significant part of the Russian Platform. This resulted in a long break in sedimentation, which separated two stages of the development of the basin (Tikhomirov, 1967, 1995).

In the Givetian, a new extensive transgression (sometimes accompanied by hypoxic conditions) of the Ural Paleocean began and reached a maximum in the Russian Platform at the middle of this stage (Tikhii, 1975) (Fig. 5b).

Givetian radiolarians were recorded by Nazarov (1975, 1988) in the Lemvin Zone of the Polar Urals. Puchkov (1979a, 1979b) also observed abundant recrystallized radiolarian skeletons in the siliceous Middle and Late Devonian strata of the Lemvin Zone (sections on the Paga, Palnik-Yu, Kharuta, and other rivers) (Figs. 3; 6, VII–IX).

Givetian radiolarians were recorded in siliceous strata of the section on the Unya River, in Evtropiny Noski locality on the western slope of the Northern Urals (Figs. 3; 6, II) (Puchkov, 1979b; Nazarov, 1988) and occurred on the eastern slope of the Northern Urals (Shatrov and Petrova, 1984).

In the Southern Urals, near the village of Sultantimirovo (Argagan Mountain) in the well investigated section of the Yarlykap strata, in banded siliceous siltstones with Givetian conodonts of the *disparilis* Zone (*Klapperina* aff. *disparilis* (Zieg. et Klap.), *Polygnathus* cf. *angustidiscus* Young., etc.), radiolarian remains[10] were recorded for the first time (Maslov and Artyushkova, 2002, p. 120).

In the northern marginal area of the Caspian Depression, in the Givetian deposits of the incipient Karachaganak bioherm, the earliest radiolarians of this region occurred (Figs. 3, 5b). Radiolarians were only examined in thin sections; they are very rare, represented by only two species, *Bientactinosphaera* cf. *variacanthina* (Foreman) and *Entactinia* sp. (Afanasieva, 1987, 2000a).

Givetian assemblage with *Spongentactinella windjanensis–Bientactinosphaera nigra*. The radiolarian assemblage with *Spongentactinella windjanensis–Bientactinosphaera*[11] *nigra* (Table 5) was established for the first time by Nazarov (1975, 1988) in the southern marginal area of the Sakmara Zone of the South-

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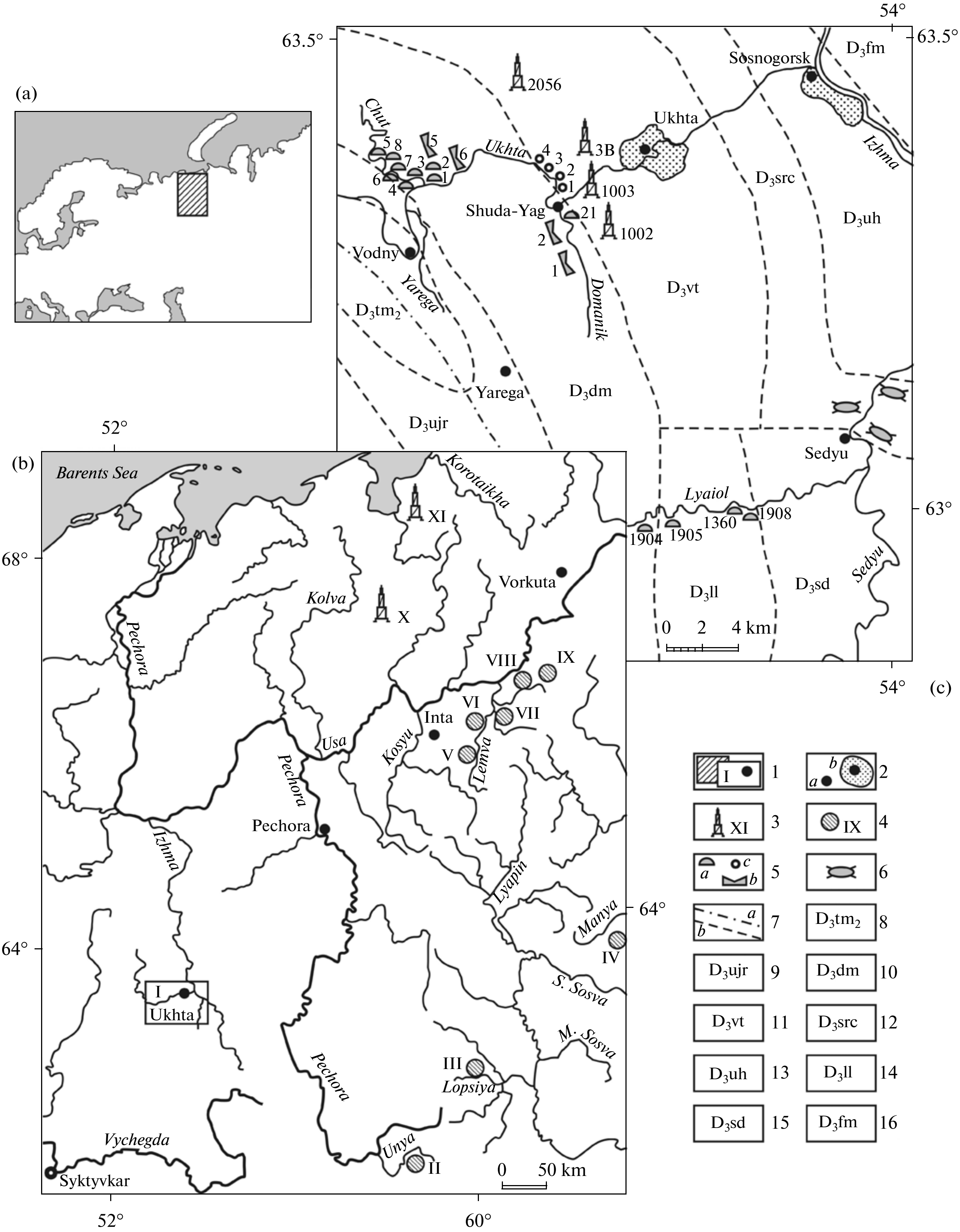
[10] See Footnote 4.

[11] Hereinafter, the Latin generic names are given according to the taxonomic revision (Afanasieva, 2000a; Afanasieva and Amon, 2003, 2006) and, therefore, differ from some generic names in works of Nazarov.


(a)
(b)
(c)
Barents Sea
Korotaikha
Kolva
Pechora
Usa
Kosyu
Lemva
Inta
Vorkuta
Lyapin
Manya
S. Sosva
M. Sosva
Izhma
Ukhta
Pechora
Lopsiya
Unya
Vychegda
Syktyvkar
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II
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Chut
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Vodny
Yarega
Domanik
Sedyu
Lyaiol
2056
3B
1003
1002
21
1904
1905
1360
1908
D_3fm
D_3src
D_3uh
D_3vt
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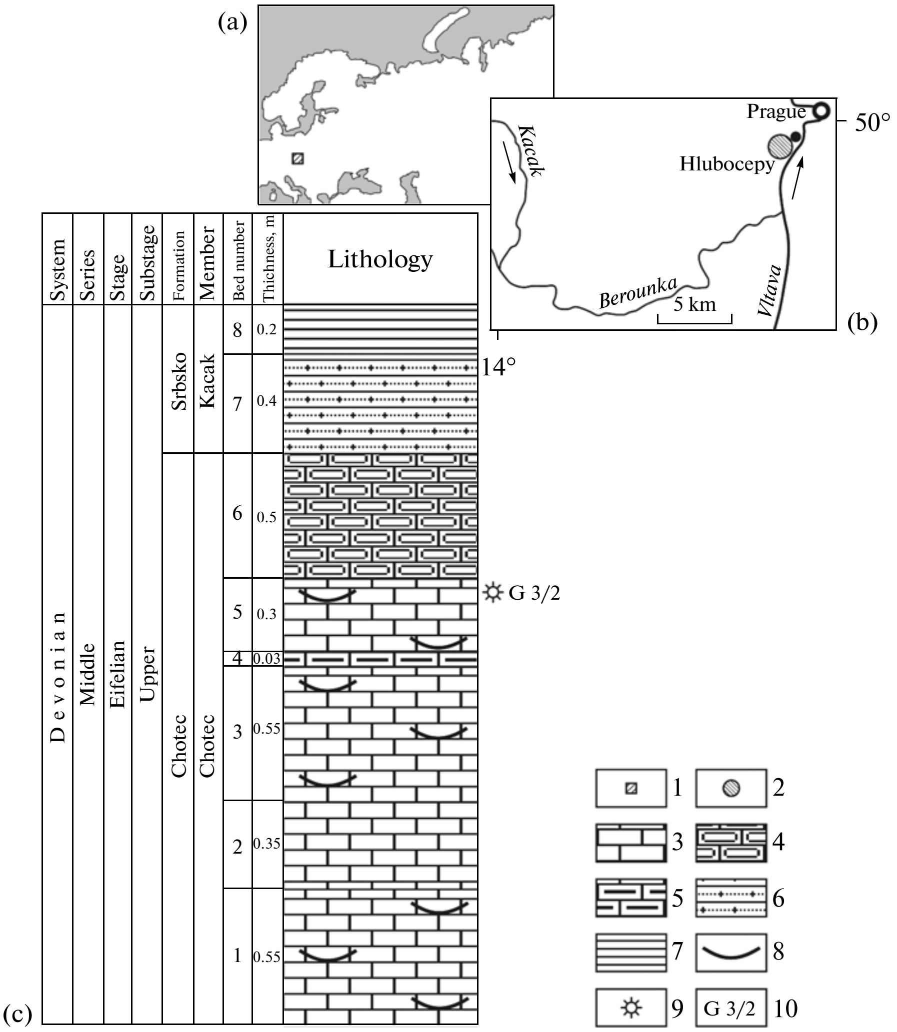

Fig. 7. Middle Devonian radiolarian locality in the Prague Basin of Czechia: (a) position of working area; (b) Prague Basin, Barrandian, village of Hlubocepy; and (c) section of the Chotec Formation (Yurina et al., 2009). Designations: (1) working area, (2) outcrop, (3) crystal limestone, (4) nodular limestone, (5) clayey limestone, (6) silicides, (7) high-carbon silicides, (8) shell detritus, (9) radiolarians, and (10) sample no.

ern Urals (including Northern Mugodzhary) (Fig. 3) in syngenetic lenticular interbeds of limestones among jaspery, siliceous, and siliceous–clayey formations of the Shuldak Formation, outcropping on the Shuldak River (Fig. 1, XVI).

The radiolarian assemblage includes 32 species of eight genera, the most typical of which are the following (Table 7): *Apophysisphaera hystricuosa*[12] (Aitchison), *Astroentactinia biaciculata* Nazarov, *Bientactinosphaera* cf. *cancellicula* (Foreman), *Bientactinosphaera nigra* (Hinde), *Entactinia manalloea* Foreman, *Helioentactinia* cf. *polyacanthina* (Foreman), *Palaeoscenidium cladophorum* Deflandre, *Polyentactinia circumretia* Nazarov et Ormiston, *Radiobisphaera* cf. *assidera* (Nazarov), *Spongentactinella spongites* (Foreman), and *S. windjanensis* Nazarov.

The lower boundary of the assemblage is marked by the first appearance of *Bientactinosphaera nigra, Spongentactinella windjanensis*, and *Astroentactinia biaciculata* (Nazarov and Ormiston, 1990; Nazarov and Ormiston, 1993).

The radiolarian assemblage described from the Shuldak Formation Nazarov (1988, 1989) dated Late Eifelian–Givetian based on the co-occurrence in siliceous rocks with limestone lenses of radiolarians and the conodonts *Polygnathus* aff. *linguiformis* (Hinde) and *P.* ex gr. *pseudofoliatus* Witt.

This conclusion is quite reasonable, because these conodonts have a wide stratigraphic range, appear for the first time in the Eifelian or even in the Emsian and continue to the Givetian. At the same time, Nazarov

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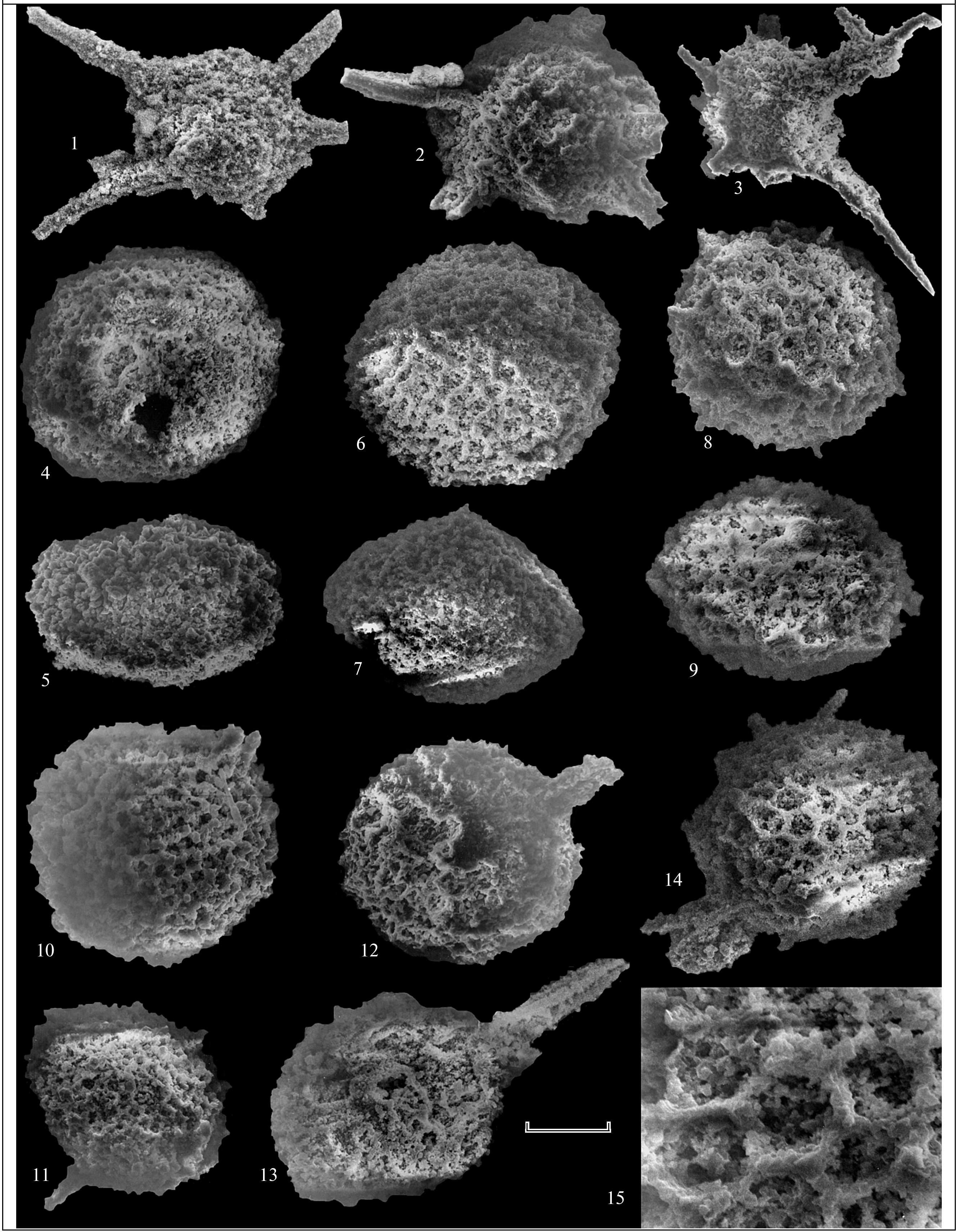
[12] Nazarov (1988, pl. XIII, fig. 6) determined this species as *Entactinia additiva* Foreman.

Table 4. Late Eifelian radiolarians of the Prague Basin (Barrandian, Czechia)

Afanasieva and Amon, 2009a, this study	Braun and Budil, 1999	Budil, 1995a, 1995b
		Astroentactinia paronae (Hinde, 1899)
		Entactinosphaera sp. 2
		Helioentactinia? sp.
Apophisisphaera hystricuosa (Aitchison, 1993)	*Stigmosphaerostylus* aff. *hystricuosa* (Aitchison, 1993)	*Entactinosphaera* sp. 1 ?*Entactinosphaera* cf. *polyacanthina* Foreman, 1963 *Entactinia* cf. *additive* Foreman, 1963
Astroentactinia stellata Nazarov, 1975		*Astroentactinia* cf. *stellata* Nazarov, 1975
Bientactinosphaera cancellicula (Foreman, 1963)	*Stigmosphaerostylus* aff. *herculea* (Foreman, 1963)	?*Entactinosphaera* cf. *polyacanthina* Foreman, 1963
Bientactinosphaera clavata (Hinde, 1899)	*Trilonche*? *echinata* (Hinde, 1899)	
Bientactinosphaera elegans (Hinde, 1899)	*Trilonche riedeli* (Foreman, 1963)	
Entactinia crustescens Foreman, 1963	*Stigmosphaerostylus* aff. *herculea* (Foreman, 1963)	
Entactinia proceraspina Aitchison, 1993	*Stigmosphaerostylus* aff. *proceraspinus* (Aitchison, 1993)	
Entactinia parva Won, 1983	*Stigmosphaerostylus herculea* (Foreman, 1963)	*Entactinia* spp. ?*Entactinosphaera* cf. *polyacanthina* Foreman, 1963 *Entactinia* cf. *additive* Foreman, 1963
Entactinia paula Foreman, 1963		
Ceratoikiscum lyratum Ishiga, 1988	*Ceratoikiscum* sp.	*Ceratoikiscum* sp. 5 sensu @ejchan, 1987
Nazarovites bioculus Afanasieva, 2000		*Ceratoikiscum* sp. 2 sensu @ejchan, 1987
Palaeoscenidium cladophorum Deflandre, 1953	*Palaeoscenidium cladophorum* Deflandre, 1953	*Palaeoscenidium* cladophorum Deflandre, 1953
Palaeoscenidium tabernaculum Aitchison, 1993		
Palaeoscenidium robustum Aitchison, 1993		*Palaeoscenidium* sp.
Spongentactinella intracata Aitchison, 1993		*Spongenactinella*? sp. 2 Nazarov et Ormiston, 1983
Bientactinosphaera pittmani (Hinde, 1899)		
Entactinia echinata (Hinde, 1899)		
Entactinia faveolata Nazarov, 1975		
Palacantholitus stellatus Deflandre, 1973		
Palaeothalomnus quadriramosum (Foreman, 1963)		
Pluristratoentactinia conspissata Nazarov, 1981		
Pluristratoentactinia trisphaerata Afanasieva et Amon, sp. nov.		
Polyentactinia circumretia Nazarov et Ormiston, 1993		
Radiobisphaera rozanovi Afanasieva, Amon, 2009		
Somphoentactinia multisphaerata Afanasieva et Amon, sp. nov.		
Spongentactinella exilispina (Foreman, 1963)		
Spongentactinella veles (Foreman, 1963)		
Spongentactinella windjanensis Nazarov, 1982		
Spongentactinia marina Afanasieva et Amon, sp. nov.		
Spongentactinia diplostraca (Foreman, 1963)		
Spongentactinia fungosa Nazarov, 1975		

Plate 4



Explanation of Plate 4

Late Eifelian radiolarians of the Southern Urals; assemblage with *Primaritripus kariukmasensis*, discoidal Stauraxonaria.

Figs. 1–3. *Primaritripus kariukmasensis* Afanasieva et Amon, 2009: (1) specimen PIN, no. 5247/15313; scale bar, 40 μm; (2) specimen PIN, no. 5247/15306; scale bar, 44 μm; (3) specimen PIN, no. 5247/15325; scale bar, 59 μm.

Figs. 4 and 5. *Palaeodiscaleksus punctus* (Hinde, 1899): (4) specimen PIN, no. 5247/15312; scale bar, 59 μm; (5) specimen PIN, no. 5247/15406, lateral view; scale bar, 59 μm.

Figs. 6 and 7. *Palaeodiscaleksus tumefactus* Afanasieva et Amon, 2008: (6) specimen PIN, no. 5247/15420; scale bar, 37 μm; (7) specimen PIN, no. 5247/15411, lateral view; scale bar, 44 μm.

Figs. 8 and 9. *Palaeodiscaleksus cribrarius* (Hinde, 1899): (8) specimen PIN, no. 5247/15419; scale bar, 37 μm; (9) specimen PIN, no. 5247/15426, lateral view; scale bar, 33 μm.

Figs. 10 and 11. *Primaritripus buribayensis* Afanasieva et Amon, 2008: (10) specimen PIN, no. 5247/15327; scale bar, 33 μm; (11) specimen PIN, no. 5247/15415, lateral view; scale bar, 44 μm.

Figs. 12 and 13. *Primaritripus chuvashovi* Afanasieva et Amon, 2008: (12) specimen PIN, no. 5247/15333; scale bar, 40 μm; (13) specimen PIN, no. 5247/15308; scale bar, 37 μm.

Figs. 14 and 15. *Trochodiscus planatus* Hinde, 1899, specimen PIN, no. 5247/15424: (14) scale bar, 37 μm; (15) fragment, scale bar, 15 μm.

Middle Devonian, Upper Eifelian Substage; Southern Urals, section in the Karyukmas Mountain, northwest of the village of Staryi Sibai, sample 7653/4066-6.

(1988, p. 126) believed that the age of the Shuldak Formation "requires additional study and revision."

The analysis of geological information on the Southern Urals and Western Mugodzhary allows us to conclude that the age of the assemblage described should be restricted to the Givetian (Table 5).

The Shuldak complex is composed of variegated jaspers or jaspery rocks, with abundant radiolarians[13] (radiolarites), in places, cherts, flinty slates, and other rocks with interbeds of siliceous sandstones, rarely, with lenses of clayey or brecciated limestones. The jaspers, cherts, and flinty slates have yielded conodonts of the Givetian, Late Givetian–Early Frasnian, and Late Eifelian–Early Givetian ages, including *Polygnathus* cf. *benderi* Wedd., *P.* ex gr. *varcus* Stauff., *P.* cf. *dobrogensis* Mirauta, *P.* ex gr. *linguiformis* Hinde, and *Bryantodus* sp. et al., from different points of Western Mugodzhary (western slope of the Kundyzdinsk Syncline, mouth of the Tlegensai River, Berchogur station, south of the Uisylkara River, Shanda River, etc.) (Ivanov, 1983, 1996, 1998; Ivanov et al., 1983, 1984; Ivanov and Puchkov, 1984).

Two conodont records from siliceous members with abundant radiolarians in sections of the Shanda River Basin are of particular significance: (1) *Polygnathus* ex gr. *varcus* Stauff. found near the mouth of the Tlegensai River and (2) *Polygnathus dubius* Hinde, *P.* aff. *dengleri* Bisch. et Zieg found in the vicinity of the village of Anastas'evka on the right bank of the Shanda River (Ivanov et al., 1984) (Fig. 1, XV). The first find is evidence of the Givetian Age (*varcus* Zone) and the second, of the boundary beds of the uppermost Givetian–lowermost Frasnian (bottom of the *falsiovalis* Zone).

These data, along with conodonts occurring in both the upper part of the Eifelian and the lower part of the Givetian, allow the conclusion about the Givetian age of the *Spongentactinella windjanensis*–*Bientactinosphaera nigra* assemblage (Table 5), which occurs throughout the Southern Urals and Northern Mugodzhary.

"Ural" Radiolarian Assemblage

Devonian radiolarians of the western slope of the Greater Urals and Volga–Ural Basin were described for the first time by Bykova (1955) in thin sections of carbonate rocks (Fig. 8). In addition to radiolarians, Bykova (1955) investigated in detail the so-called "primitive" small pelagic foraminifers (Fig. 9; Table 5), including *Archaesphaera crassa* Lipina, *Archaesphaera magna* Suleimanov, *Archaesphaera minima* Suleimanov, *Parathurammina magna* Antropov, *Parathurammina radiata* Antropov, *Parathurammina spinosa* Lipina, *Parathurammina gekkeri* Antropov, *Parathurammina subvasta* Bykova, *Parathurammina dagmarae* Suleimanov var. *crassitheca* Antropov, *Parathurammina paulis* Bykova, *Parathurammina tuberculata* Lipina, *Bisphaera parva* Bykova, *Bisphaera concavutas* Vissarionova, *Bisphaera elegans* Vissarionova, *Bisphaera elegans* var. *subsphaera* Vissarionova, and *Bisphaera malevkensis* Birina.

In our opinion (Afanasieva and Amon, 2010d, 2010e), it is possible to assign these forms to radiolarians based on the structure of their skeletons (Table 5). The similarity of shell morphology of *Archaesphaera, Parathurammina*, and *Bisphaera* to radiolarian skeletons was marked even by Bykova (1955, p. 110): "in shell structure, they are closer to ancient radiolarians than Recent or Mesozoic–Cenozoic planktonic foraminifers." Note that the generic names characterize the appearance of these microfossils and, in the shell structure, they show certain morphological features, such as "the spherical shape of the skeleton, from the surface of which radially positioned thorns diverge" (Bykova, 1955, p. 106) (Fig. 9):

(1) *Archaesphaera* is characterized by a regular spherical single-chamber shell, from the surface of which many narrow thorns diverge (Figs. 9a–9d);

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[13] See Footnote 4.

Plate 5

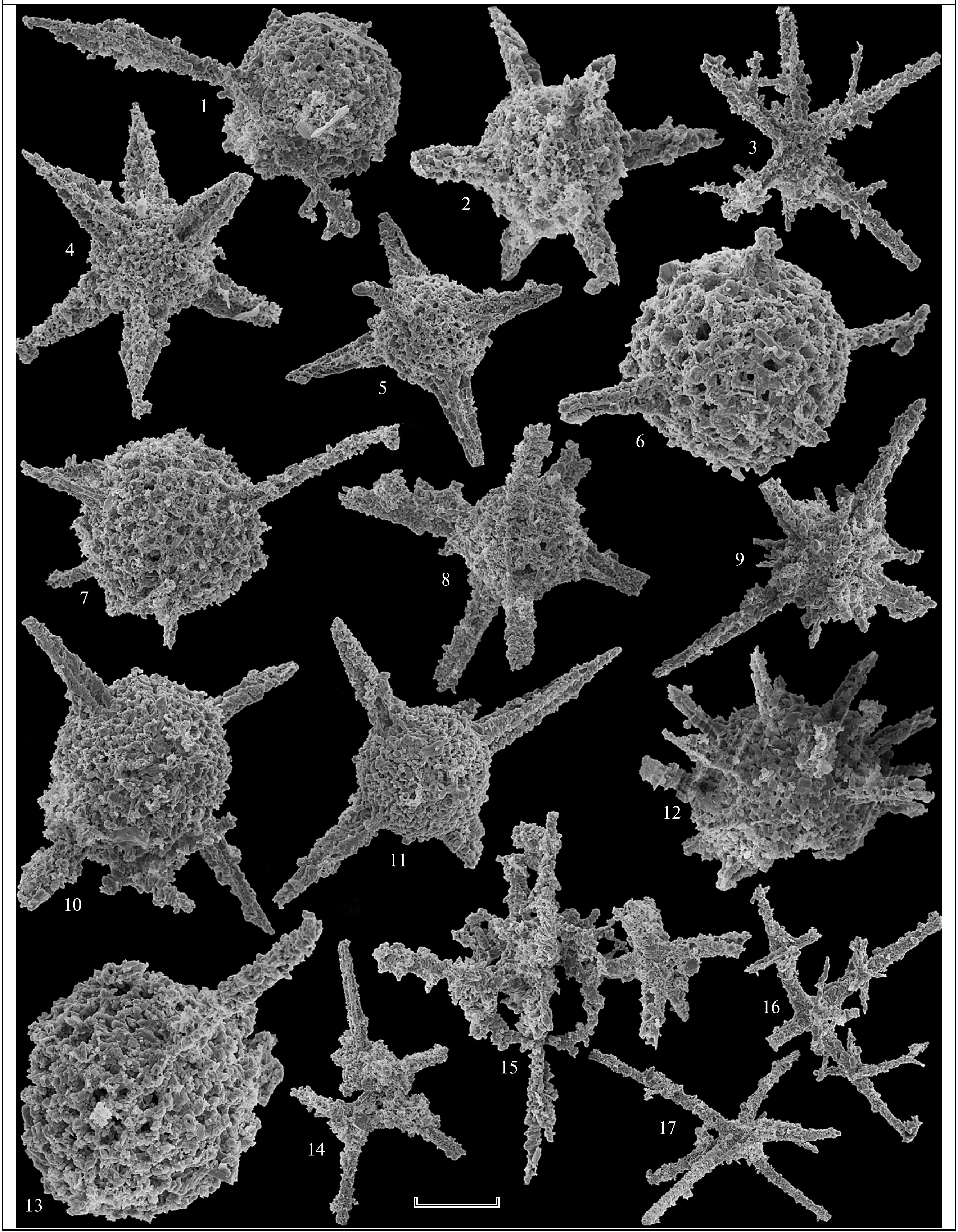


Table 5. Unification of the taxonomic composition of microfossils of the "Ural" Assemblage established by Bykova (1955)

Bykova, 1955	Afanasieva, Amon, 2010d, 2010e
Archaesphaera crassa Lipina, 1950	*Astroentactinia crassa* (Lipina, 1950)
Archaesphaera magna Suleimanov, 1945	*Astroentactinia* cf. *crassata* Nazarov, 1975
Archaesphaera minima Suleimanov, 1945	*Astroentactinia* cf. *stellata* Nazarov, 1975
Bisphaera elegans Vissarionova, 1950	*Trochodiscus elegans* (Vissarionova, 1950)
Bisphaera elegans var. *subsphaera* Vissarionova, 1950	*Trochodiscus elegans* var. *subsphaera* (Vissarionova, 1950)
Bisphaera aff. *concavutas* Vissarionova, 1950	*Trochodiscus* cf. *planatus* Hinde, 1899
Bisphaera malevkensis Birina, 1948	*Trochodiscus malevkensis* (Birina, 1948)
Bisphaera parva Bykova, 1955	*Trochodiscus* cf. *parva* (Bykova, 1955)
Parathurammina dagmarae var. *crassitheca* Antropov, 1950	*Entactinia dagmarae* var. *crassitheca* (Antropov, 1950)
Parathurammina gekkeri Antropov, 1950	*Entactinia* cf. *faveolata* Nazarov, 1975
Parathurammina magna Antropov, 1950	*Astroentactinia* cf. *biaciculata* Nazarov, 1975
Parathurammina paulis Bykova, 1955	*Entactinia paulis* (Bykova, 1955)
Parathurammina radiata Antropov, 1950	*Borisella* cf. *bykovae* Afanasieva, 2000
Parathurammina spinosa Lipina, 1950	
Parathurammina subvasta Bykova, 1955	*Entactinia* cf. *subvasta* (Bykova, 1955)
Parathurammina tuberculata Lipina, 1950	*Entactinia tuberculata* (Lipina, 1950)

(2) *Bisphaera* also has thorny structures. In any event, the species *Bisphaera* aff. *concavutas* Vissarionova and *B. parva* Bykova (Figs. 9o, 9p) undoubtedly have thorns filled with light calcite (Bykova, 1955, pl. V, figs. 2, 3). In addition, *Bisphaera* lacks an aperture, which is characteristic of all foraminifers.

(3) *Parathurammina* has a single-chamber skeleton, which is more or less spherical in outline, from the surface of which thorns also deviate. The thorns of *Parathurammina* increase in diameter and they obviously begin to play a role of apertural neck, i.e., combine two functions, provide outcome for cytoplasm and increase the body surface. With some economy of shell material, with a minor increase in weight, they result in a greater effect. In addition, the skeleton section of *Parathurammina gekkeri* Antropov (Bykova, 1955, pl. III, fig. 3) distinctly shows the presence of an internal spicule, which is only typical of radiolarian skeletons (Fig. 9k).

In opinion of Bykova (1955), the only difference of these organisms from radiolarians consists in the fact that their skeleton is carbonate, whereas that of radiolarians is siliceous. At the same time, it is well known that the primarily opalescent radiolarian skeleton

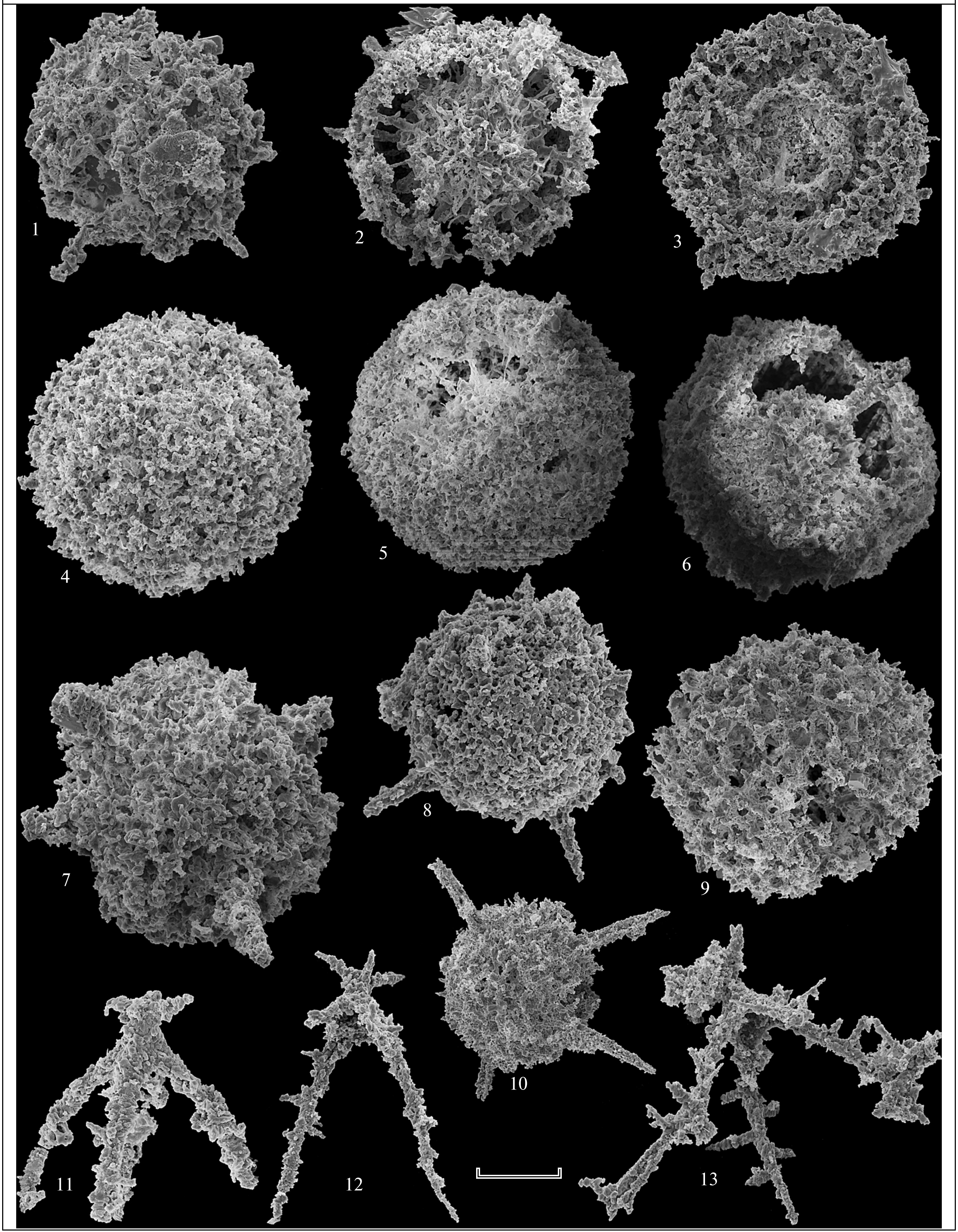
Explanation of Plate 5

Late Eifelian radiolarians of Czechia; assemblage with *Apophisisphaera hystricuosa—Spongentactinia fungosa*: spherical porous Sphaerellaria (1–13) and spiny Aculearia (14–17).

Fig. 1. *Entactinia echinata* (Hinde, 1899), specimen PIN, no. 5323/16061; scale bar, 68 μm.
Fig. 2. *Entactinia faveolata* Nazarov, 1975, specimen PIN, no. 5323/15970; scale bar, 56 μm.
Fig. 3. *Apophisisphaera hystricuosa* (Aitchison, 1993), specimen PIN, no. 5323/15966; scale bar, 79 μm.
Fig. 4. *Entactinia patorovaria* Afanasieva, 2000, specimen PIN, no. 5323/16047; scale bar, 74 μm.
Fig. 5. *Entactinia parva* Won, 1983, specimen PIN, no. 5323/16004; scale bar, 95 μm.
Fig. 6. *Entactinia paula* Foreman, 1963, specimen PIN, no. 5323/15992; scale bar, 57 μm.
Fig. 7. *Entactinia proceraspina* Aitchison, 1993, specimen PIN, no. 5323/15702; scale bar, 79 μm.
Fig. 8. *Bientactinosphaera cancellicula* (Foreman, 1963), specimen PIN, no. 5323/15959; scale bar, 95 μm.
Fig. 9. *Bientactinosphaera clavata* (Hinde, 1899), specimen PIN, no. 5323/16069; scale bar, 86 μm.
Fig. 10. *Bientactinosphaera elegans* (Hinde, 1899), specimen PIN, no. 5323/15973; scale bar, 69 μm.
Fig. 11. *Bientactinosphaera pittmani* (Hinde, 1899), specimen PIN, no. 5323/16057; scale bar, 69 μm.
Fig. 12. *Astroentactinia stellata* Nazarov, 1975, specimen PIN, no. 5323/15978; scale bar, 56 μm.
Fig. 13. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009, specimen PIN, no. 5323/16071; scale bar, 45 μm.
Fig. 14. *Ceratoikiscum lyratum* Ishiga, 1988, specimen PIN, no. 5323/16046; scale bar, 126 μm.
Fig. 15. *Nazarovites bioculus* Afanasieva, 2000, specimen PIN, no. 5323/16074; scale bar, 78 μm.
Fig. 16. *Palaeothalomnus quadriramosum* (Foreman, 1963), specimen PIN, no. 5323/15976; scale bar, 100 μm.
Fig. 17. *Palacantholitus stellatus* Deflandre, 1973, specimen PIN, no. 5323/15700; scale bar, 157 μm.

Middle Devonian, Upper Eifelian Substage, upper part of the Chotec Formation; Czechia, Prague Basin (Barrandian), village of Hlubocepy, sample g-3/2.

Plate 6



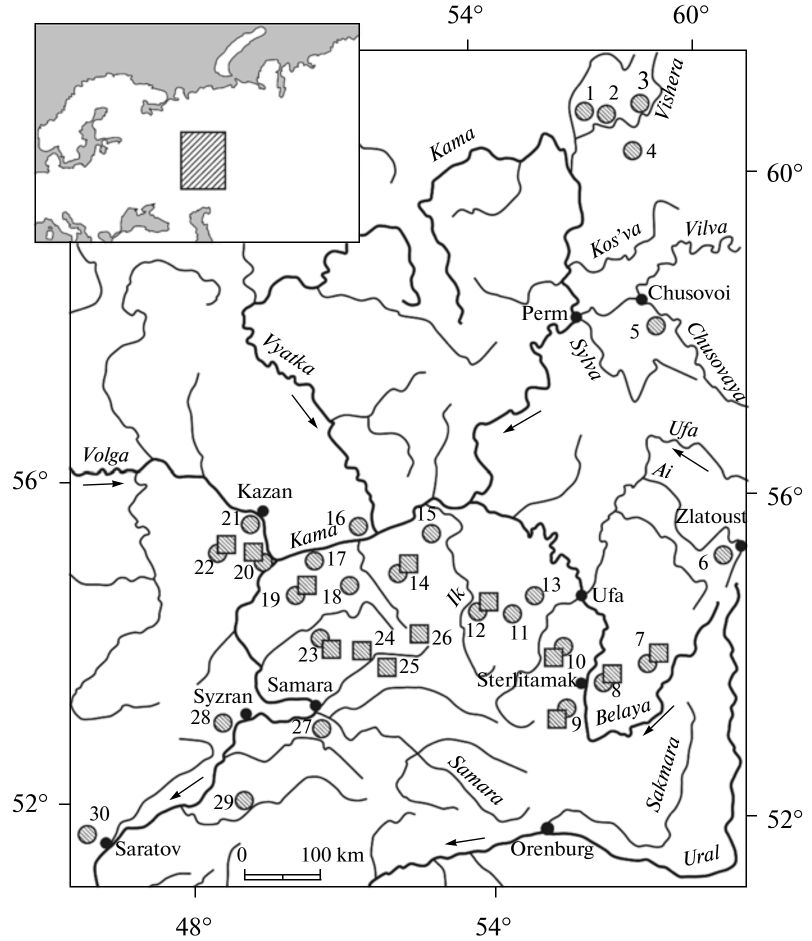


Fig. 8. Radiolarian localities on the western slope of the Greater Urals (1–8) and Volga–Ural Basin (9–30); Radiolarian localities (Bykova, 1955): (1–4) Northern Urals, Perm Region: (1) Petrunikha River, (2) Storozhevaya River, (3) Vishera River, (4) Yaz'va River; (5, 6) Middle Urals: (5) Chusovaya River, (6) Bolshaya Arsha River; (7, 8) Southern Urals: (7) Sikaza River, (8) Ryauzyak River; (9–13) western Bashkortostan: (9) town of Sterlibashevo, (10) village of Elatminki (=Novokonstantinovka), (11) village of Kopei-Kubovo, (12) town of Tuimazy, (13) village of Kargaly; (14–22) Tatarstan: (14) village of Aktash, (15) town of Aznakaevo, (16) village Yanga-Aul, (17) village of Staroe Romashkino, (18) village of Shugurovo, (19) village of Aksubaevo, (20) village of Kamskoe Ust'e, (21) village Verkhnii Uslon, (22) village of Cheremshan; (23–28) Samara Region: (23) village of Krasnovka, (24) village of Radaevka, (25) village of Sernovodsk, (26) Baitugan River, (27) village of Berezovka, (28) town of Syzran; (29, 30) Saratov Region: (29) town of Pugachev, and (30) village of Teplovka. Designations: (▨) radiolarian assemblage with *Radiobisphaera domanicensis–Radiobisphaera menneri* from the Domanik Formation of the Middle Frasnian and (⊘)) "Ural" Radiolarian Assemblage of the Devonian.

Explanation of Plate 6

Late Eifelian radiolarians of Czechia; assemblage with *Apophisisphaera hystricuosa–Spongentactinia fungosa*: spherical spongy Spumellaria (1–10) and spiny Aculearia (11–13).

Fig. 1. *Polyentactinia circumretia* Nazarov et Ormiston, 1993, specimen PIN, no. 5323/16062; scale bar, 59 μm.
Fig. 2. *Pluristratoentactinia trisphaerata* Afanasieva et Amon, sp. nov., specimen PIN, no. 5323/15705; scale bar, 68 μm.
Fig. 3. *Pluristratoentactinia conspissata* Nazarov, 1981, specimen PIN, no. 5323/15695; scale bar, 72 μm.
Fig. 4. *Spongentactinia fungosa* Nazarov, 1975, specimen PIN, no. 5323/15971; scale bar, 61 μm.
Fig. 5. *Spongentactinia marina* Afanasieva et Amon, sp. nov., specimen PIN, no. 5323/15991; scale bar, 68 μm.
Fig. 6. *Spongentactinia diplostraca* (Foreman, 1963), specimen PIN, no. 5323/16031; scale bar, 59 μm.
Fig. 7. *Spongentactinella veles* (Foreman, 1963), specimen PIN, no. 5323/15981; scale bar, 56 μm.
Fig. 8. *Spongentactinella windjanensis* Nazarov, 1982, specimen PIN, no. 5323/16011; scale bar, 64 μm.
Fig. 9. *Spongentactinella intracata* Aitchison, 1993, specimen PIN, no. 5323/15692; scale bar, 85 μm.
Fig. 10. *Spongentactinella exilispina* (Foreman, 1963), specimen PIN, no. 5323/15691; scale bar, 135 μm.
Fig. 11. *Palaeoscenidium robustum* Aitchison, 1993, specimen PIN, no. 5323/16022; scale bar, 59 μm.
Fig. 12. *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 5323/15977; scale bar, 72 μm.
Fig. 13. *Palaeoscenidium cladophorum* Deflandre, 1953, specimen PIN, no. 5323/15963; scale bar, 66 μm.

Middle Devonian, Upper Eifelian Substage, upper part of the Chotec Formation; Czechia, Prague Basin (Barrandian), village of Hlubocepy, sample g-3/2.

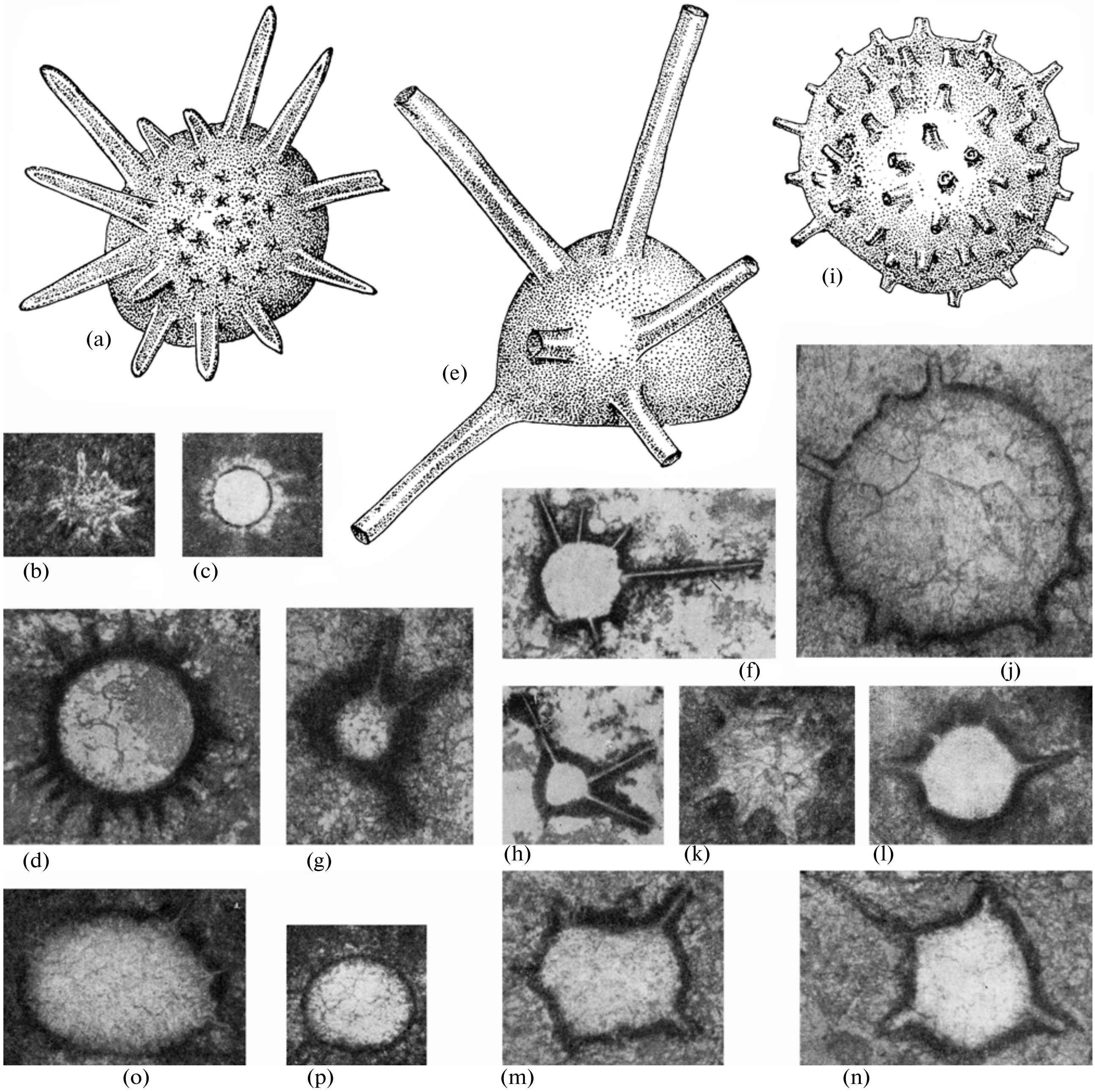


Fig. 9. "Ural" Radiolarian Assemblage after Bykova (1955): (a–h, l) Famennian Stage: (a, b) Syzran'skii District, (c, l) western Bashkortostan: (c) town of Sterlibashevo, (l) town of Tuimazy; (d–h) Northern Urals: Perm Region: (d) Petrunikha River, (e, f, h) Vishera River, (g) Storozhevaya River; (i, j, p) Upper Givetian Substage, Southern Urals, Sikaza River; (k, m–o) Upper Frasnian Substage: (k, m, n) Tatarstan, village of Shugurovo, and (o) Samara Region, village of Berezovka; (a–c) *Astroentactinia* cf. *stellata* Nazarov, 1975: (a) reconstruction (Bykova, 1955, pl. IV, fig. 3), ×330, (b) superficial section of the skeleton, without a fragment of the inner cavity (pl. I, fig. 2), ×100, (c) section of the skeleton, with a distinct dark fine-grained internal layer and light external layer, which forms spines (pl. I, fig. 8), ×100; (d) *Astroentactinia* cf. *crassata* Nazarov, 1975, skeleton section (pl. II, fig. 2), ×100; (e–h) *Borisella* cf. *bykovae* Afanasieva, 2000: (e) reconstruction (pl. IV, fig. 4), ×330, (f–h) skeleton section: (f) pl. II, fig. 6; ×100, (g) pl. II, fig. 7; ×100; (h) pl. II, fig. 9, ×100; (i, j) *Astroentactinia* cf. *biaciculata* Nazarov, 1975: (i) reconstruction, pl. IV, fig. 5, ×100; (j) skeleton section, pl. II, fig. 4, ×100; (k, l) *Entactinia* cf. *faveolata* Nazarov, 1975, skeleton section, ×100: (k) pl. III, fig. 3; (l) pl. III, fig. 1; (m, n) *Entactinia subvasta* (Bykova, 1955), skeleton section, ×100, pl. V, figs. 7 and 8; (o) *Trochodiscus concavutas* Vissarionova, 1950, skeleton section, with distinct subulate projections, pl. V, fig. 2, ×100; and (p) *Trochodiscus parva* (Bykova, 1955), skeleton section (pl. V, fig. 3), ×100.

often undergoes the processes of metasomatism and is replaced by other minerals because of changes in conditions during the animal's life, for example, hydrosulphuric contamination of waters, or catagenesis and metamorphism of ancient deposits (Braun and Amon, 1991; Afanasieva, 2000a).

As a result of field and laboratory studies, Braun and Amon (1991) concluded that, in radiolarians from many Devonian and Carboniferous localities, the primary organogenic skeletal opal is often replaced by minerals of groups of low-temperature quartz (including chalcedony), iron, manganese, carbonate, sometimes fluorite and garnet, and even gold. This fact clarify the cases of the presence of insufficient or unsatisfactory preservation of radiolarian skeletons in thin sections and the absence of a trace of radiolarians in powder of solid residual after decomposition of the same enclosing matter in strong or weak acids.

Under conditions of hydrosulphuric contamination, the primary amorphous opal of radiolarian skeletons could have been replaced by pyrite. In some skeletons, pyritization probably occurred in living organisms. This interesting phenomenon is evidenced by the fact of secondary replacement by pyrite of only the initial part of siliceous radiolarian skeletons (Afanasieva, 2000a, 2006).

During lithification of enclosing matter, many radiolarians undergo microbial corrosion and micritization. Radiolarian skeletons are gradually calcified, so that only spheres are retained. These spheres are frequently mistaken for remains of primitive small foraminifers, algae, or their reproductive organs (Vishnevskaya and Sedaeva, 2002; Sedaeva and Vishnevskaya, 2002, 2008).

The above suggests that the material examined by Bykova (1955) could have been radiolarian shells secondarily replaced by carbonates (calcite and dolomite) (Afanasieva and Amon, 2010e). These radiolarians, i.e., the so-called "small planktonic foraminifers" were combined by Bykova (1955) in the "Ural" Assemblage characterized by two features:

(1) strict confinement to limestones of the Ural Sea, where both benthic foraminifers and planktonic forms of the "Ural" Assemblage developed, with the prevalence of the latter;

(2) complete absence of the "Ural" Assemblage in terrigenous deposits of the central Russian Platform, where only benthic foraminifers occurred.

Features of paleoecological distribution of the organisms considered are an additional argument in favor of the assignment of small pelagic members of the "Ural" Assemblage to radiolarians. Radiolarians are typical organisms inhabiting oceans and open marine basins. The similarity of the shell structure of *Archaesphaera* and *Parathurammina* to radiolarian skeletons suggests the same lifestyle. The assumption of planktonic lifestyle of *Bisphaera* is based on the same shell shape and co-occurrence with *Archaesphaera* and *Parathurammina* and the same distribution pattern (Bykova, 1955).

In addition, recent studies of foraminifers have shown that they turned to planktonic mode of life only at the end of the Triassic (Korchagin et al., 2003). The benthic lifestyle of foraminifers was rather efficient, they well adapted to the existence on substrate and, only much later, in the Rhaetian Age of the Late Triassic, adapted to the pelagial.

The occurrence of Devonian planktonic microorganisms in the carbonate beds suggests that they, like recent pelagic foraminifers and radiolarians, were adapted to the life under conditions of normal or somewhat increased salinity of marine water. This explains the absence of small planktonic members of the "Ural" Assemblage in Devonian terrigenous matter.

Thus, forcible arguments for the radiolarian nature of planktonic forms of the "Ural" Assemblage are (1) the skeleton structure, which, even taking into account the carbonate composition, sharply differs from that of foraminiferal shells, (2) features of paleoecological distribution of the microorganisms in question, confinement to the pelagial of open seas and oceans with normal salinity. In the course of paleoecological reconstruction of the Devonian of the Russian Platform, Afanasieva (2000a) assigned particular members of *Archaesphaera, Parathurammina*, and *Bisphaera* to radiolarians.

The analysis of morphological and paleoecological features of the so-called small "primitive" pelagic foraminifers inclined us (Afanasieva and Amon, 2010d, 2010e) to determine some species of the genera *Archaesphaera, Parathurammina*, and *Bisphaera* as radiolarians of the genera *Astroentactinia, Borisella*, and *Trochodiscu* (Table 5). In doing so, we retain the name "Ural" Assemblage introduced by Bykova (1955) for these unusual planktonic organisms.

Early Givetian radiolarian assemblage. In the Givetian Age, the eastern marginal areas of the Russian Platform were probably occupied by a shallow shelf of the Ural Sea; as a result, the Volga–Ural Province and Southern Urals were mostly inhabited by benthic foraminifers and only the first rare spherical radiolarians of the "Ural" Assemblage (Bykova, 1955) (Figs. 10, 11; Table 5). Radiolarians either had not yet migrated there or the marginal waters of the Russian Platform differed from the Ural Sea in hydrological mode and planktonic organisms could not dwell there.

The carbonate beds of the Lower Givetian Substage of the Chusovaya River Basin on the Middle Urals contain pelagic forms of the "Ural" Assemblage, including *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), *T. malevkensis* (Birina), and *T. parva* (Bykova).

In the Southern Urals, a section of the Lower Givetian on the Sikaza River has yielded *Astroentac-*

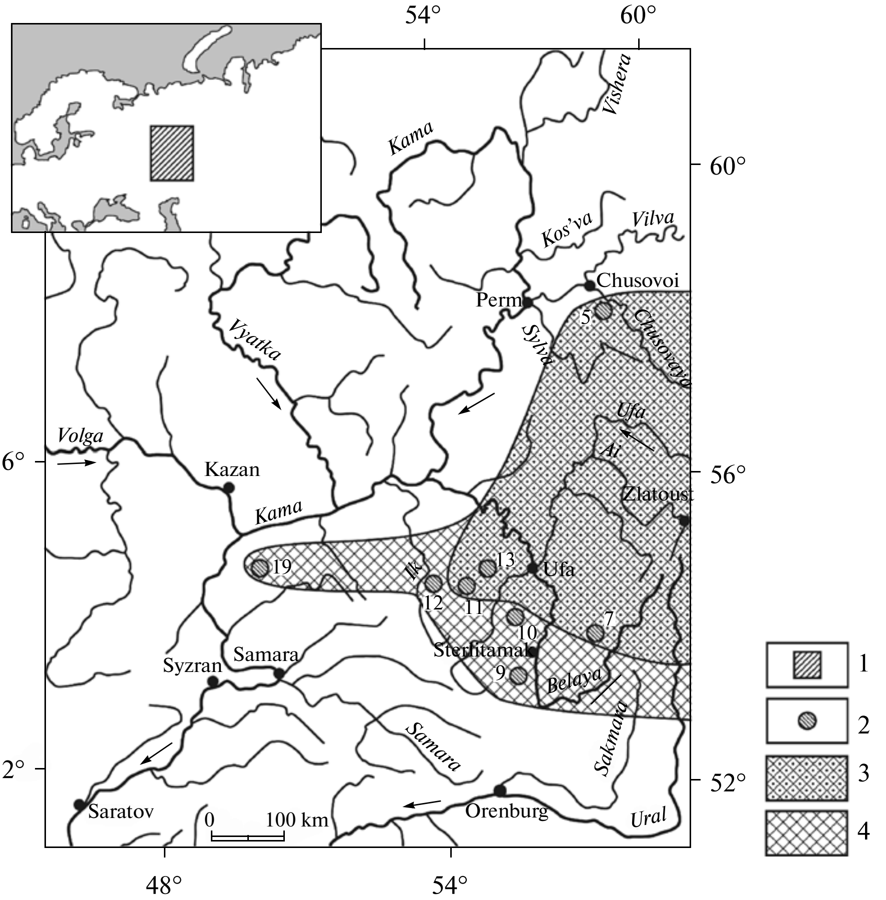


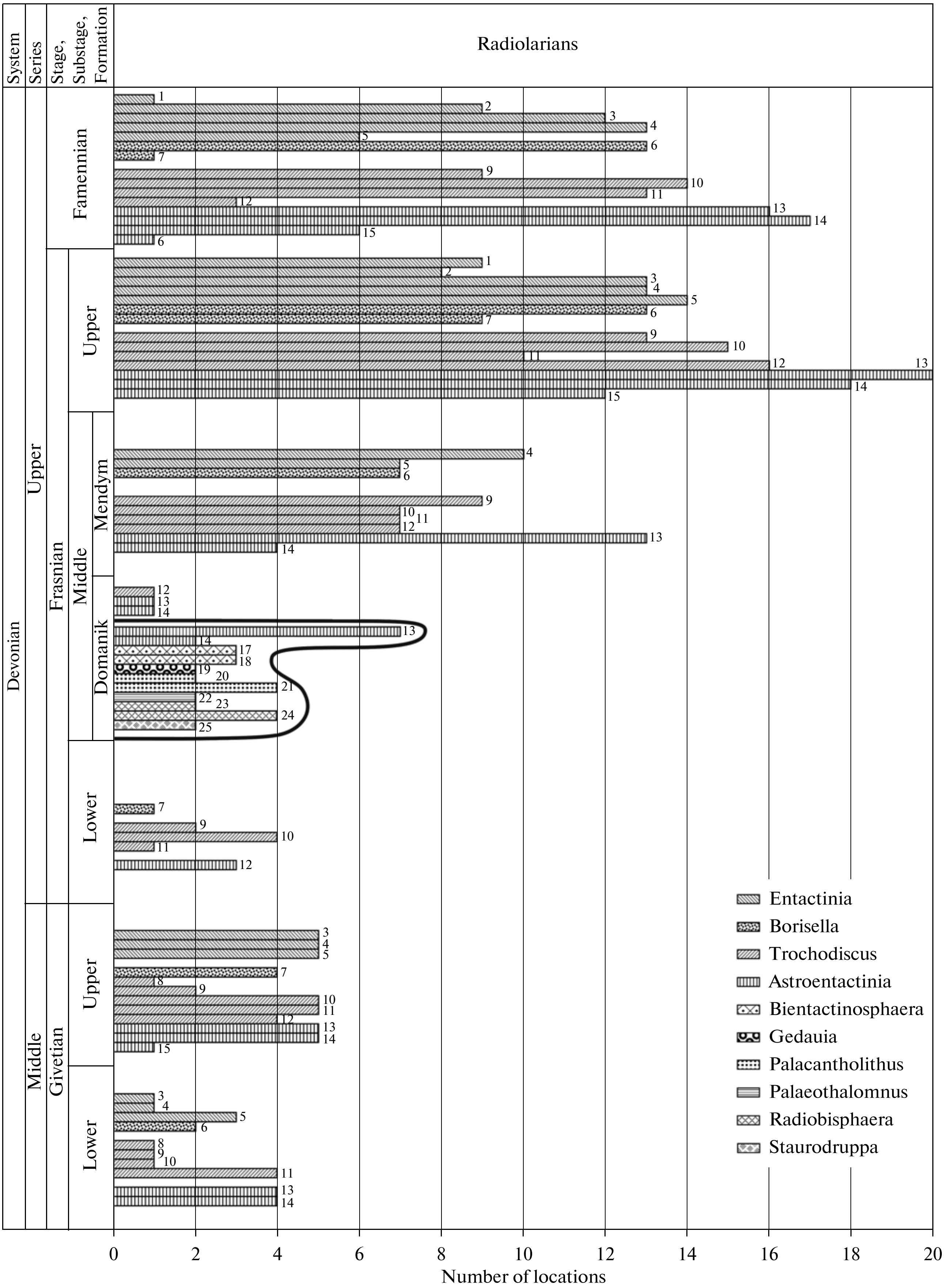
Fig. 10. Geographical ranges of radiolarians on the western slope of the Southern Urals and in the Volga–Ural Basin in the Givetian Age. Designations: (1) working area, (2) "Ural" Radiolarian Assemblage of the Devonian, (3) Early Givetian, (4) Late Givetian. For radiolarian localities (after Bykova, 1955), see Fig. 7.

tinia cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. tuberculata* (Lipina), and *Trochodiscus concavutas* Vissarionova.

In the vicinity of the villages of Kopei-Kubovo and Kargaly of western Bashkortostan, Early Givetian *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Entactinia paulis* (Bykova), *Trochodiscus concavutas* Vissarionova, and *T. parva* (Bykova) were recorded.

Late Givetian radiolarian assemblage. Late Givetian radiolarians of the "Ural" Assemblage were described in the Southern Urals (Sikaza River) (Figs. 10, 11; Table 5): *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), *T. malevkensis* (Birina), and *T. parva* (Bykova) (Figs. 9i, 9j, 9p). On the Chusovaya

Fig. 11. Age and spatial distribution of Devonian radiolarians of the "Ural" Assemblage (1–16) and assemblage with *Radiobisphaera domanicensis–Radiobisphaera menneri* (13, 14, 17–25) on the western slope of the Greater Urals and in the Volga–Ural Basin: (1–5) *Entactinia*: (1) *E. subvasta* (Bykova, 1955), (2) *E.* cf. *faveolata* Nazarov, 1975, (3) *E. dagmarae* var. *crassitheca* (Antropov, 1950), (4) *E. tuberculata* (Lipina, 1950), (5) *E. paulis* (Bykova, 1955); (6, 7) *Borisella*: (6) *B.* cf. *bykovae* Afanasieva, 2000, (7) *B. radiata* (Antropov, 1950); (8–12) *Trochodiscus*: (8) *T. malevkensis* (Birina, 1948), (9) *T. parva* (Bykova, 1955), (10) *T. elegans* (Vissarionova, 1950), (11) *T. concavutas* Vissarionova, 1899, (12) *T. elegans* var. *subsphaera* (Vissarionova, 1950); (13–15) *Astroentactinia*: (13) *A.* cf. *stellata* Nazarov, 1975, (14) *A.* cf. *crassata* Nazarov, 1975, (15) *A.* cf. *biaciculata* Nazarov, 1975, (16) *A. crassa* (Lipina, 1950); (17, 18) *Bientactinosphaera*: (17) *B.* cf. *grandis* (Nazarov, 1975), (18) *B.* cf. *variacanthina* (Foreman, 1963); (19) *Gedauia* (?) sp.; (20, 21) *Palacantholithus*: (20) *P. nana* (Bykova, 1955), (21) *P. simplex* (Hinde, 1899); (22) *Palaeothalomnus* cf. *quadriramosum* (Foreman, 1963); (23, 24) *Radiobisphaera*: (23) *R.* cf. *menneri* Afanasieva, 2000, (24) *R. domanicensis* (Bykova, 1955); and (25) *Staurodruppa nucula* Hinde, 1899. Bold line outlines an assemblage with *Radiobisphaera domanicensis–Radiobisphaera menneri* from the Domanik Formation of the Volga–Ural Basin.


System
Series
Stage, Substage, Formation
Radiolarians
Devonian
Upper
Middle
Famennian
Frasnian
Givetian
Upper
Middle
Lower
Mendym
Domanik
Upper
Lower
1
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Entactinia
Borisella
Trochodiscus
Astroentactinia
Bientactinosphaera
Gedauia
Palacantholithus
Palaeothalomnus
Radiobisphaera
Staurodruppa
0
2
4
6
8
10
12
14
16
18
20
Number of locations

Table 6. Biostratigraphy of radiolarian assemblages from the Middle and Late Devonian of the Russia

System	Series	Stage	Substage	Standard Conodont Zonation	Biostratigraphic radiolarian assemblages								
					Timan-Pechora Basin		Polar Urals	North Pre-Caspian Basin	Volga-Urals Basin and Southern Urals (west side)	Middle Urals		South Urals and Northern Mugodzhary	Rudny Altai
										west side	east side		
Devonian	Upper	Famennian	Lower	*crepida*	*Tetrentactinia barysphaera – Retientactinosphaera magnifica*		*Tetrentactinia barysphaera – Caspiaza spinifera*	Beds with *Tetrentactinia barysphaera – Holoeciscus auceps*	“Ural” Assemblage	Beds with *Haplentactinia alekseevi – Haplentactinia vilvaensis*	*Tetrentactinia barysphaera – Ceratoikiscum famennium*	*Tetrentactinia barysphaera – Ceratoikiscum famennium*	
				triangularis									
		Frasnian	Upper	*linguiformis*								*Polyentactinia circumretia – Bientactinosphaera egindyensis*	*Polyentactinia circumretia – Bientactinosphaera egindyensis*
				late *rhenana*	*Bientactinosphaera pittmani – Russirad kazintsovae*						*Bientactinosphaera pittmani – Russirad kazintsovae*		
			Middle	*early*	*Moskovistella allbororum – Ceratoikiscum ukhtensis*	*Rdm-3*			*Radiobisphaera domanicensis – Radiobisphaera menneri*				? *Moskovistella allbororum – Ceratoikiscum ukhtensis* ?
				jamieae									
				hassi		*Rdm-2*						Beds with *Primaritripus chuvashvi*	
				punctata		*Rdm-1*							
			Lower	*transitans*	Beds with *Palaeodiscaleksus punctus – Astroentactinia biaciculata*				“Ural” Assemblage				
				late *falsiovalis*									
	Middle	Givetian	Upper	*early*								*Spongentactinella windjanensis – Bientactinosphaera nigra*	
				disparilis									*Spongentactinella windjanensis – Bientactinosphaera nigra*
			Lower	*hermanni-cristatus*									
				varcus									
				hemiansatus									

Table 7. Stratigraphic distribution of Upper Devonian radiolarians of the Timan–Pechora Basin (1–6), Polar (7) and Middle (8) Urals, Pripyat Depression (9) and North America (10): (1) Chut River, borehole Zapadno-Visertynskaya-1 (3601–3616 m of depth) (Afanasieva, 2000); (2–5) Ukhtinskii District (Afanasieva, 2000a); (6) Saremboi–Lekkeyaga Swell, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth) (Afanasieva, 2000a); (7) Lemvin Zone, Palnik-Yu River (Afanasieva and Amon, this study); (8) Mikhailovskii–Niyayusskaya Zone, Vilva River (Afanasieva and Amon, this study); (9) Pripyat Depression (Kruchek and Nazarov, 1977); and (10) Huron Shale of Ohio, Erie Lake (Foreman, 1963)

Stage	Frasnian					Famennian				
Substage, Subassemblage	Lower	Middle			Upper	Lower				
		Rdm-1	Rdm-2	Rdm-3						
Location / Radiolarians	1	2	3	4	5	6	7	8	9	10
Astroentactinia paronae (Hinde, 1899)	▨	▨		▨						
Meschedea crassicortex Won, 1997	▨			▨						
Moskovistella deorsiacus (Nazarov et Ormiston, 1993)	▨			▨	▨					
Borisella bykovae Afanasieva, 2000	▨	▨		▨	▨					
Borisella maksimovae Afanasieva, 2000	▨	▨		▨	▨					
Palaeodiscaleksus punctus (Hinde, 1899)	▨	▨		▨	▨	▨				
Primaritripus patella (Hinde, 1899)	▨	▨		▨		▨				
Ceratoikiscum spinosiarcuatum Foreman, 1963	▨	▨		▨		▨				▨
Entactinia bogdanovi Afanasieva, 2000	▨	▨		▨		▨	▨			
Entactinia patorovaria Afanasieva, 2000	▨	▨		▨			▨			
Astroentactinia biaciculata Nazarov, 1975	▨	▨	▨	▨	▨	▨	▨		▨	
Borisella mediforma (Won, 1997)		▨								
Haplentactinia labyrinthica (Aitchison, 1993)		▨								
Helioentactinia gudymovae Afanasieva, 2000		▨								
Magnentactinia fragilis Won, 1997		▨								
Bientactinosphaera grandis (Nazarov, 1975)		▨	▨	▨						
Bientactinosphaera morozovi Afanasieva, 2000		▨	▨	▨						
Ceratoikiscum stellatum Aitchison, 1993		▨	▨	▨						
Circulaforma delicata Cheng, 1986		▨	▨	▨						
Nazarovites bioculus Afanasieva, 2000		▨	▨	▨						
Nazarovites pinnula Afanasieva, 2000		▨	▨	▨						
Palaeoscenidium robustum Aitchison, 1993		▨	▨	▨						
Moskovistella allbororum Afanasieva, 2000		▨	▨	▨						
Astroentactinia tantilla Nazarov, 1975		▨		▨						
Astroentactinia tikhomirovi Afanasieva, 2000		▨		▨						
Astroentactinia vishnevskayae Afanasieva, 2000		▨		▨						
Bientactinosphaera australis (Aitchison, 1993)		▨		▨						
Bientactinosphaera conglobata (Nazarov, 1975)		▨		▨						
Ceratoikiscum avimexpectans Deflandre, 1953		▨		▨						
Ceratoikiscum delicatum Cheng, 1986		▨		▨						
Ceratoikiscum goodbodyi Cheng, 1986		▨		▨						
Ceratoikiscum robustum Aitchison, 1993		▨		▨						
Ceratoikiscum spinosum Cheng, 1986		▨		▨						
Ceratoikiscum? cf. *vimenum* Nazarov et Ormiston, 1983		▨		▨						
Haplentactinia barskovi Afanasieva, 2000		▨		▨						
Haplentactinia bornazi Afanasieva, 2000		▨		▨						
Moskovistella rozanovi Afanasieva, 2000		▨		▨						
Nazarovites aprelevkensis Afanasieva, 2000		▨		▨						
Nazarovites mikhailovae Afanasieva, 2000		▨		▨						
Ornatoentactinia agarkovi Afanasieva, 2000		▨		▨						
Ornatoentactinia spartaci Afanasieva, 2000		▨		▨						
Ornatoentactinia spinisica Afanasieva, 2000		▨		▨						
Palaeoscenidium delicatum Aitchison, 1993		▨		▨						
Palaeoscenidium phalangium Aitchison, 1993		▨		▨						
Palaeoscenidium scaurum Afanasieva, 2000		▨		▨						
Retisphaera exquisita (Aitchison, 1993)		▨		▨						
Somphoentactinia gavrilovi Afanasieva, 2000		▨		▨						
Spongentactinella veles (Foreman, 1963)		▨		▨						

Table 7. (Contd.)

Stage	Frasnian					Famennian				
Location Radiolarians	1	2	3	4	5	6	7	8	9	10
Ceratoikiscum ukhtensis Afanasieva, 2000		■	■	■	■					
Moskovistella khaini Afanasieva, 2000		■	■	■	■					
Moskovistella victorialis Afanasieva, 2000		■		■	■					
Ornatoentactinia beljaevorum Afanasieva, 2000		■		■	■					
Palaeoscenidium tabernaculum Aitchison, 1993		■		■	■					
Polyentactinia kossistekensis Nazarov, 1975		■		■	■					
Polyentactinia zhamoidai Afanasieva, 2000		■		■	■					
Spongentactinella olafi Afanasieva, 2000		■		■	■					
Bientactinosphaera maslakovae Afanasieva, 2000		■		■		■				
Bientactinosphaera pinica Afanasieva, 2000		■		■	■	■				
Russirad kazintsovae Afanasieva, 2000		■		■	■	■				
Entactinia parva Won, 1983		■		■	■	■	■			
Ornatoentactinia solita Afanasieva, 2000		■		■		■	■			
Radiobisphaera menneri Afanasieva, 2000		■	■	■			■			
Haplentactinia alekseevi Afanasieva, 2000		■		■				■		
Astroentactinia crassata Nazarov, 1975		■		■			■		■	
Palacantholithus curvativus Afanasieva, 2000		■		■						■
Bientactinosphaera hystricosa (Foreman, 1963)		■		■						■
Palacantholithus stellatus Deflandre, 1973		■	■	■	■					■
Bientactinosphaera variacanthina (Foreman, 1963)		■		■	■		■		■	■
Ceratoikiscum planistellare Foreman, 1963		■	■	■	■				■	■
Palaeoscenidium cladophorum Deflandre, 1953		■	■	■			■		■	■
Radiobisphaera assidera (Nazarov, 1975)		■		■			■			■
Tetragregnon quadrispinosa (Foreman, 1963)		■		■			■		■	■
Moskovistella mira Afanasieva, 2000			■							
Entactinia bifida Afanasieva, 2000			■	■						
Moskovistella octoradiata Afanasieva, 2000			■	■						
Moskovistella sincera Afanasieva, 2000			■	■	■					
Retientactinosphaera clavata Afanasieva, 2011			■	■		■	■			
Ceratoikiscum incomptum Nazarov, 1975			■	■					■	
Bientactinosphaera symphypora (Foreman, 1963)			■	■		■			■	■
Apophysisphaera profundisculus (Aitchison, 1993)				■						
Astroentactinia rusaevi Afanasieva, 2000				■						
Bientactinosphaera aitpaiensis (Nazarov, 1973)				■						
Bientactinosphaera miletenkoi Afanasieva, 2000				■						
Bissylentactinia? cf. *rudicula* Nazarov, 1975				■						
Borisella invisitata Afanasieva, 2000				■						
Borisella mariae Afanasieva, 2000				■						
Borisella pantosompha (Foreman, 1963)				■						
Borisella primitiva Afanasieva, 2000				■						
Cancellosphaera varia (Won, 1997)				■						
Ceratoikiscum araneosum Afanasieva, 2000				■						
Ceratoikiscum simplum Cheng, 1986				■						
Entactinia diversita Nazarov, 1973				■						
Haplentactinia aperticuva (Aitchison, 1993)				■						
Helioentactinia aster Aitchison, 1993				■						
Helioentactinia perjucunda Nazarov et Ormiston, 1983				■						
Moskovistella baccata Afanasieva, 2000				■						
Moskovistella lucet Afanasieva, 2000				■						
Moskovistella viatoria Afanasieva, 2000				■						
Munzuwonella impedita (Won, 1997)				■						
Ornatoentactinia klevtsovae Afanasieva, 2000				■						
Palhindeolithus ambiguus Deflandre, 1973				■						
Palaeothalomnus timokhini Afanasieva, 2000				■						

Table 7. (Contd.)

Stage	Frasnian					Famennian				
Location / Radiolarians	1	2	3	4	5	6	7	8	9	10
Palhindeolithus cf. *pulcher* Deflandre, 1973				■						
Polyentactinia craticulata Foreman, 1963				■						
Polyentactinia polygonia Foreman, 1963				■						
Polyentactinia propinqua Nazarov, 1975				■						
Retentactinia kelleri Afanasieva, 2000				■						
Retentactinia longa Won, 1997				■						
Spongentactinella corynacantha Nazarov et Ormiston, 1983				■						
Spongentactinella windjanensis Nazarov, 1982				■						
Bientactinosphaera egindyensis (Nazarov, 1975)				■	■					
Helioentactinia stellaepolus Aitchison, 1993				■	■					
Moskovistella additiva (Foreman, 1963)				■	■					
Palaeothalomnus quadriramosum (Foreman, 1963)				■	■					
Bientactinosphaera guangxiensis (Li et Wang, 1991)				■			■			
Bientactinosphaera obtusa (Hinde, 1899)				■	■		■			
Radiobisphaera domanicensis (Bykova, 1955)				■		■	■			
Haplentactinia kuzminae Afanasieva et Amon, sp. nov.				■			■	■		
Polyentactinia circumretia Nazarov et Ormiston, 1993				■	■			■		
Polyentactinia rudihispida Nazarov et Ormiston, 1993				■	■	■	■		■	
Bientactinosphaera cancellicula (Foreman, 1963)				■						■
Bientactinosphaera inusitata (Foreman, 1963)				■						■
Entactinia micula Foreman, 1963				■						■
Helioentactinia polyacanthina (Foreman, 1963)				■						■
Ceratoikiscum bujugum Foreman, 1963				■	■	■	■		■	■
Entactinia crustescens Foreman, 1963				■		■	■			■
Palaeothalomnus arrhinia (Foreman, 1963)				■			■	■		■
Haplentactinia rhinophyusa Foreman, 1963				■			■	■		■
Entactinia paula Foreman, 1963				■					■	■
Bientactinosphaera pittmani (Hinde, 1899)					■					
Entactinia bella Afanasieva et Amon, sp. nov.						■	■			
Duplexia spinocurva Afanasieva, 2000						■				
Retientactinosphaera magnifica Afanasieva, 2011						■				
Adamasirad cathedrarius Afanasieva, 2000						■	■			
Radiobisphaera rozanovi Afanasieva et Amon, 2009						■	■			
Spongentactinia marina Afanasieva et Amon, sp. nov.						■	■			
Spongentactinia polaris Afanasieva et Amon, sp. nov.						■	■			
Bientactinosphaera spinofoliacea Nazarov et Afanasieva, 2000						■			■	
Polyentactinia suave (Nazarov, 1977)						■			■	
Helioentactinia valavica Nazarov et Ormiston, 1993						■	■		■	
Spongentactinia diplostraca (Foreman, 1963)						■	■		■	■
Tetrentactinia barysphaera Foreman, 1963						■	■		■	■
Archocyrtium amoenus Afanasieva et Amon, sp. nov.							■			
Archocyrtium riedeli Deflandre, 1960							■			
Bientactinosphaera zuraevi Afanasieva et Amon, sp. nov.							■			
Caspiaza collaricostulata Afanasieva, 1993							■			
Caspiaza spinifera Afanasieva, 1993							■			
Cyrtisphaeractenium mendax Deflandre, 1972							■			
Cyrtisphaeronemium spinosum (Cheng, 1986)							■			
Entactinia oumonhaoensis Wang, 1997							■			
Holoeciscus foremanae Cheng, 1986							■			
Holoeciscus quasiauceps Wang, 1997							■			
Pluristratoentactinia trisphaerata Afanasieva et Amon, sp.nov.							■			
Pylentonema antiqua Deflandre, 1963							■			
Robotium validum Cheng, 1986							■			
Tetragregnon sycamorensis Ormiston et Lane, 1976							■			

Table 7. (Contd.)

Stage	Frasnian					Famennian				
Radiolarians / Location	1	2	3	4	5	6	7	8	9	10
Astroentactinia stellata Nazarov, 1975							■		■	
Ceratoikiscum famennium Nazarov et Ormiston, 1993							■		■	
Pluristratoentactinia conspissata Nazarov, 1981							■		■	
Somphoentactinia multisphaerata Afanasieva et Amon, sp. nov.							■		■	
Archocyrtium cibdelosphaera (Foreman, 1963)							■			■
Holoeciscus auceps Foreman, 1963							■			■
Radiobisphaera palimbola (Foreman, 1963)							■			■
Ceratoikiscum perittacanthinum Foreman, 1963							■		■	■
Entactinia herculea Foreman, 1963							■		■	■
Spongentactinella exilispina (Foreman, 1963)							■		■	■
Haplentactinia vilvaensis Afanasieva et Amon, sp. nov.								■		
Archinella antiquus (Deflandre, 1973)									■	
Astroentactinia sp.									■	
Bientactinosphaera pulcherima (Nazarov et Ormiston, 1993)									■	
Borisella praenuntia (Nazarov et Ormiston, 1993)									■	
Haplentactinia flagellifera Nazarov et Ormiston, 1993									■	
Palacantholithus sp.									■	
Palaeoscenidium bicorne Deflandre, 1960									■	
Palaeothalomnus piletocladus Nazarov et Ormiston, 1993									■	
Palhindeolithus aff. *diductus* (Deflandre 1973)									■	
Retientactinosphaera unimana (Nazarov, 1977)									■	
Secuicollacta amoenitas Nazarov et Ormiston, 1993									■	
Spongentactinella faceta Nazarov et Ormiston, 1993									■	
Bientactinosphaera echinata (Hinde, 1899)									■	■
Bientactinosphaera euthlasta (Foreman, 1963)									■	■
Entactinia cometes Foreman, 1963									■	■
Entactinia monalloea Foreman, 1963									■	■
Entactinosphaera riedeli Foreman, 1963									■	■
Spongentactinia spongites (Foreman, 1963)									■	■
Tetrentactinia gracilispinosa Foreman, 1963									■	■
Tetrentactinia somphozona Foreman, 1963									■	■
Bientactinosphaera tretactinia (Foreman, 1963)										■
Bientactinosphaera hapala (Foreman, 1963)										■
Borisella pantosompha (Foreman, 1963)										■
Corythoecia dichoptera Foreman, 1963										■
Cyrtentactinia primotica Foreman, 1963										■
Entactinia quantilla Foreman, 1963										■
Entactinia? *sychnacanthina* Foreman, 1963										■
Entactinosphaera? erebenna Foreman, 1963										■
Entactinosphaera esostrongyla Foreman, 1963										■
Magnisphaera dystactotata (Foreman, 1963)										■
Moskovistella additiva (Foreman, 1963)										■
Palaeothalomnus quadriramosum (Foreman, 1963)										■
Polyentactinia craticulata Foreman, 1963										■
Polyentactinia leptosphaera Foreman, 1963										■
Polyentactinia polygonia Foreman, 1963										■
Polyentactinia? *plecta* Foreman, 1963										■
Retientactinosphaera fredericki (Foreman, 1963)										■
Spongentactinia somphorhips (Foreman, 1963)										■
Spongentactinella veles (Foreman, 1963)										■
Staurodruppa? *prolata* Foreman, 1963										■
Tetrentactinia somphosphaera Foreman, 1963										■
Tetrentactinia spongacea Foreman, 1963										■
Tetrentactinia teuchestes Foreman, 1963										■

River of the Middle Urals, only individual *Trochodiscus parva* (Bykova) have been found.

In western Bashkortostan (towns of Sterlibashevo and Tuimazy, villages of Kopei-Kubovo and Elatminki), the Upper Givetian radiolarians *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella radiata* (Antropov), *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), and *T. elegans* var. *subsphaera* (Vissarionova) occur.

In Tatarstan, a section of the Upper Givetian near the village of Aksubaevo has only yielded individual *Astroentactinia* and *Trochodiscus.*

Geographical Distribution of Middle Devonian Radiolarians

An analogue of the Givetian *Spongentactinella windjanensis–Bientactinosphaera nigra* Assemblage was established by Nazarov (Nazarov et al., 1982) at the base of a terrigenous–shaly section with limestone interbeds of the Middle–Upper Devonian in the Canning Basin of western Australia (Fig. 3).

The Givetian *Spongentactinella windjanensis–Bientactinosphaera nigra* Radiolarian Assemblage was traced by Nazarov (1988, 1989) in eastern Kazakhstan among ophiolitic deposits of the Chara Zone, in condensed sections of the Late Silurian–Early Carboniferous of the Alai Mountains, Kyrgyzstan (Fig. 3).

Unfortunately, it is impossible to use the data of Parfenova (1970) on the distribution of radiolarians in the Middle Devonian–Early Carboniferous beds of Central Asia on the northern slope of the Zeravshan Mountain Range (Vashan, Madm, Kum, Tagobi-Dzhuft, and Darkh river basins), because she examined radiolarians in thin sections and used the taxonomic system of Haeckel; therefore, the taxonomic list includes Recent genera.

At the end of the 19th century, Hinde (1899a) described a very diverse (54 species) radiolarian association from the volcanogenic–siliceous Tamworth Series of the New England Range of New South Wales of Australia (Fig. 3), dated Devonian (in the broad sense).

A century later, in revisions of Aitchison (1988b, 1990) and Aitchison and Stratford (1997), dealing with the Gemilaroi terrane of the New England Range, the age of this radiolarian assemblage was determined more precisely as Givetian.

In central Japan (Fig. 3; Table 3), Furutani (1990) established for the first time an Eifelian radiolarian assemblage with *Stylosphaera?* sp. *C.* Ten years later, Kurihara and Sashida (2000) described Emsian–Eifelian radiolarians from the strata of interbedding sandstones and limestones of the Hida Gaien Belt of the Fukui Prefecture of central Japan and established the Emsian–Eifelian assemblage with *Pactarentinia holdsworthi.*

In southwestern Japan, in the Kurosegawa Fold Belt (Fig. 3; Table 3), Umeda (1998a, 1998b) established two Middle Devonian Eifelian zones of radiolarians, *Glanta fragili* and *Protoholoeciscus hindea.*

The first Middle Devonian radiolarians of southern China (Fig. 3) were described by Sheng and Wang (1982) and Wang (1991) from the beds of Hunan Province, where they co-occurred with the Eifelian–Givetian conodonts *Bispathodus bipennatus* (Bisch. et Zieg.) and *Icriodus brevis.* The radiolarian assemblage is represented by *Stauroplegma pulcherrimum* Sheng et Wang, *S. robustospina* Sheng et Wang, *S. lepidum* Sheng et Wang, *Cubaxomum antiquorum* Sheng et Wang, *Spongodiscus punctus* Hinde, *S. cribrarius* Hinde, and *Spongotripus xintianensi* Sheng et Wang. Members of the genus *Stauroplegma* are most abundant and diverse.

At the beginning of the 21st century, Wang et al. (2000, 2003) described a radiolarian assemblage from the Middle–Upper Devonian of southern China, Yunnan, Guizhou, Guangxi, and Hunan provinces (Fig. 3). It consists of 30 species of 15 genera, which were referred to three radiolarian assemblages: *Eoalbaillella lilaensis* (Middle Devonian, Givetian), *Helenifore laticlavium*, and *Holoeciscus foremanae* (Late Devonian).

In southern China, in Guangxi Province (Fig. 3), Luo et al. (2002) described an Early Givetian radiolarian assemblage from the Tanhe Formation.

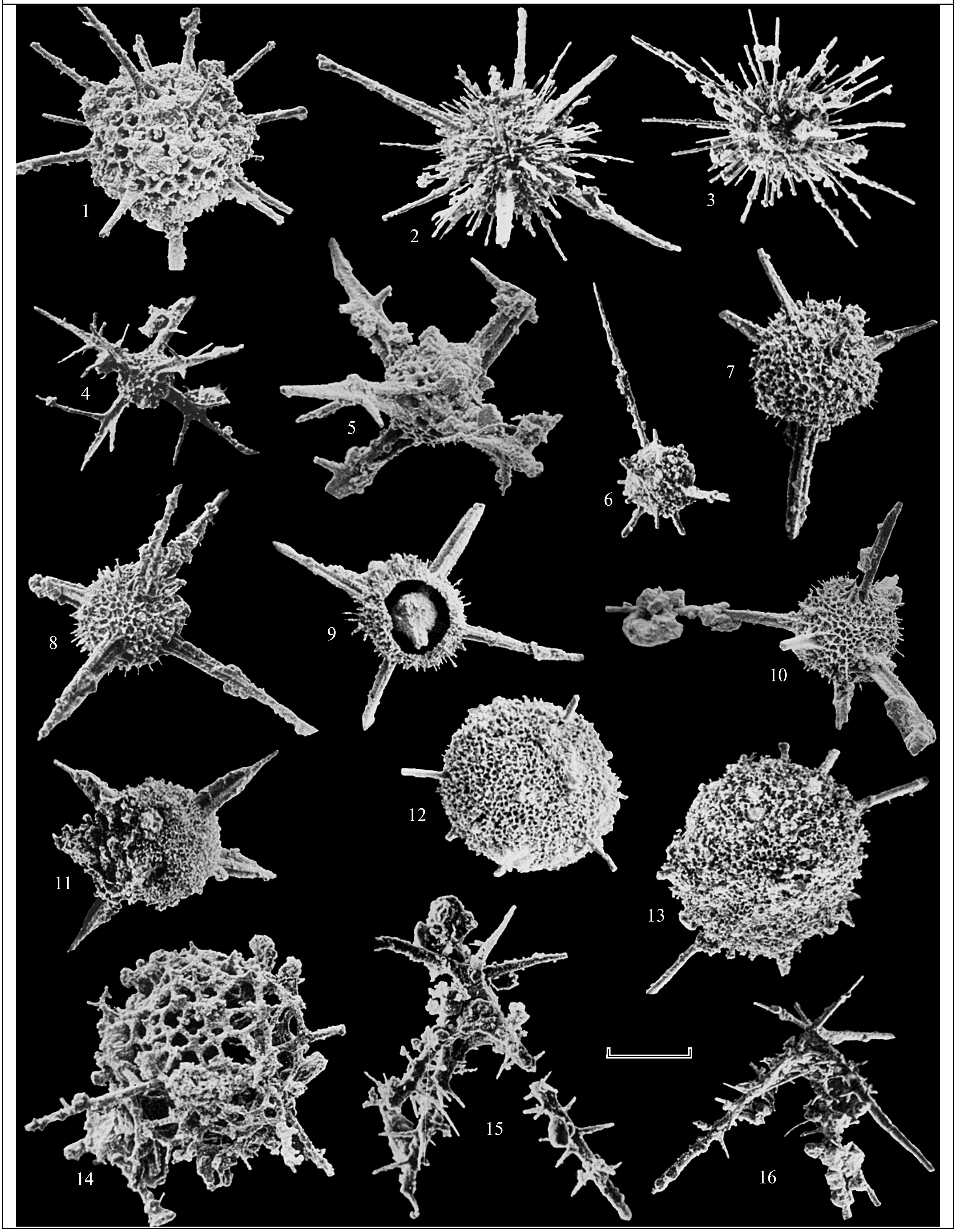
In Chiang Mai Province of northern Thailand (Fig. 3), an Eifelian–Givetian radiolarian assemblage with *Tlecerina sp.–Stigmosphaerostylus* sp. was established (Saesaengseerung et al., 2006), which is similar somewhat to the previously described radiolarian assemblages of northern Thailand (Wonganan and Caridroit, 2005) and New South Wales of Australia (Aitchison, 1988a, 1988b).

LATE DEVONIAN

The first attempt to develop zonal biostratigraphy based on radiolarians was undertaken by Holdsworth and Jones (1980a, 1980b) for the Upper Devonian–Permian of the Yukon River Basin in eastern Alaska. Based on general evolutionary patterns of spiny Aculearia, they recognized several radiolarian assemblages in this period and provided very brief characteristics of each assemblage. In so doing, Frasnian radiolarians were combined in one zonal assemblage (Pre-*Holoeciscus*), the Famennian beds are characterized by three radiolarian assemblages: *Holoeciscus*-1, *Holoeciscus*-2, and *Holoeciscus*-3.

The first integrated radiolarian biostratigraphic scale of the Paleozoic was developed by Nazarov (1981b, 1988, 1989) and, later, supplemented by studies of Nazarov and Ormiston (1985, 1986, 1990, 1993)

Plate 7



based on detailed analysis of temporal and spatial distribution of all Paleozoic radiolarians known at that time. According to the biostratigraphic scheme of Nazarov and Ormiston, the Upper Devonian is characterized by two radiolarian assemblages, *Tetrentactinia barysphaera–Ceratoikiscum famennium* (Famennian Stage) and *Polyentactinia circumretia–Bientactinosphaera egindyensis* (Frasnian Stage).

New data on biostratigraphic distribution of radiolarians of the Russian Platform, Greater Urals, and Rudny Altai (Fig. 3) allowed us to supplement the radiolarian scale for the Devonian of Russia (Table 6).

Frasnian Age

According to the Devonian biostratigraphic scheme of Nazarov and Ormiston (Nazarov, 1981b, 1988; Nazarov and Ormiston, 1985, 1990, 1993), the Frasnian Age is characterized by one assemblage, *Bientactinosphaera egindyensis–Polyentactinia circumretia*, with abundant and diverse radiolarian genera and species. Nazarov established the *Bientactinosphaera egindyensis–Polyentactinia circumretia* biostratigraphic radiolarian assemblage based on geological materials of the Egindy Formation in the section on the Aitpaika Creek in the southern marginal area of the Sakmara Zone of the Southern Urals and Northern Mugodzhary (Fig. 3) (Nazarov, 1975, 1988). In addition, Maslov and Artyushkova (2002) reported on gray, dark gray, and black cherts with radiolarians of the Mukasovian Regional Substage in the region of the village of Temyasovo on the left bank of the Sakmara River somewhat north of the southern periphery of the Sakmara Zone.

According to the data of Nazarov (1975), sherty slates and breccia of the lower part of the Egindy Formation conformably overlie clastic rocks of the Givetian Stage (Aitpaika Formation); therefore, the lowermost part of the Egindy Formation is possibly of the Late Givetian age. In the middle part of the section of the Egindy Formation, siliceous matter contains distinct carbonate lenses composed of nodules, the space between which is filled with dark gray siliceous matter, where the conodont *Palmatolepis subrecta* Miller et Young and poorly preserved radiolarians are found. On the contrary, the carbonate nodules contain a very rich and diverse radiolarian assemblage (of more than 50 species of 15 genera) and the conodonts *Palmatolepis subrecta* Miller et Young, *P. foliacea* Hinde, *P. punctata* Hinde, and *P. hassi* Müller (Nazarov, 1975, 1988; Nazarov and Ormiston, 1990, 1993), which are evidence that the host rock was accumulated in the Middle and Upper Frasnian (*punctata–linguiformis* conodont zones).

According to the data of Ivanov and Puchkov (Ivanov et al., 1983, 1984; Ivanov and Puchkov, 1984), the Aitpaika Formation includes several different Middle Devonian horizons of siliceous breccias; and limestone blocks in the Aitpaika Formation, with a rich Givetian fauna, are olistoliths, they are approximately equal in age to enclosing siliceous matrix of the formation with conodonts of the Upper Eifelian–Givetian age. Cherts of the Egindy Formation observed in the stratotype section were formed over almost the entire Frasnian Age and replaced at the very beginning of the Famennian by graywacke sandstones of the Zilair Group. The Egindy Formation in the area of its distribution is subdivided into two subformations (Ivanov et al., 1983, 1984; Ivanov and Puchkov, 1984):

(1) The lower subformation is composed mostly by dark brown platy cherts and siliceous–clayey slates, enclosing the conodonts *Polygnathus dengleri* Bisch. et Zieg., *P.* cf. *dengleri* Bisch. et Zieg., *P. asymmetricus asymmetricus* Bisch. et Zieg., and *P.* ex gr. *varcus* Stauf., which are evidence of the Early Frasnian age of these rocks;

←

Explanation of Plate 7

Givetian radiolarians of the Southern Urals and western Australia; assemblage with *Spongentactinella windjanensis–Bientactinosphaera nigra*: spherical porous Sphaerellaria (1–10), spongy Spumellaria (11–14), and spiny Aculearia (15, 16).

Fig. 1. *Astroentactinia biaciculata* Nazarov, 1975, specimen GIN, no. 4354/16; scale bar, 52 μm.

Figs. 2 and 3. *Helioentactinia* cf. *polyacanthina* (Foreman, 1963): (2) specimen GIN, no. 4354/14; scale bar, 115 μm; (3) specimen GIN, no. 19656/18; scale bar, 126 μm.

Figs. 4 and 5. *Apophisisphaera hystricuosa* (Aitchison, 1993): (4) specimen GIN, no. 4354/23; scale bar, 115 μm; (5) specimen GIN, no. 9656/1; scale bar, 52 μm.

Fig. 6. *Entactinia manalloea* Foreman, 1963, specimen GIN, no. 19656/11; scale bar, 115 μm.

Fig. 7. *Radiobisphaera* cf. *assidera* (Nazarov, 1975), specimen GIN, no. 4354/27; scale bar, 115 μm.

Figs. 8 and 9. *Bientactinosphaera* cf. *cancellicula* (Foreman, 1963): (8) specimen GIN, no. 19656/3; scale bar, 126 μm; (9) specimen GIN, no. 4354/12; scale bar, 98 μm.

Fig. 10. *Bientactinosphaera* aff. *nigra* (Hinde, 1899), specimen GIN, no. 4354/23; scale bar, 126 μm.

Fig. 11. *Spongentactinella spongites* (Foreman, 1963), specimen GIN, no. 4354/21; scale bar, 115 μm.

Figs. 12 and 13. *Spongentactinella windjanensis* Nazarov, 1982: (12) specimen GIN, no. 4354/19; scale bar, 150 μm; (13) specimen GIN, no. 19656/38; scale bar, 126 μm.

Fig. 14. *Polyentactinia circumretia* Nazarov et Ormiston, 1993, specimen GIN, no. 19656/24; scale bar, 115 μm.

Figs. 15 and 16. *Palaeoscenidium cladophorum* Deflandre, 1953: (15) specimen GIN, no. 19656/12; scale bar, 52 μm; (16) specimen GIN, no. 4354/25; scale bar, 115 μm.

Middle Devonian, Givetian Stage; (1, 2, 5, 8–12, 16) Southern Urals, Aktyubinsk Region, Shuldak River, Shuldak Formation; (3, 4, 5, 7, 13–15) western Australia, Canning Basin, Gogo Formation (Nazarov et al., 1982; Nazarov, 1994, pl. XXXIII, figs. 1–7, pl. XXXIII, figs. 1–8; 1988, pl. XIII, fig. 9).

(2) The upper subformation is formed mostly of light gray, thick platy cherts and clayey–flinty slates, with the conodonts *Palmatolepis flabelliformis* Stauf., *P.* cf. *subrecta* Mill. et Young, *P. martenbergensis* Mull., and *P.* cf. *proversa* Zieg., which suggest the Middle–lowermost Upper Frasnian dating of the strata, within the Domanik and Lower Askyn formations.

Thus, geological and paleontological materials of the Southern Urals and Northern Mugodzhary confirm the Middle–Upper Frasnian age of the *Bientactinosphaera egindyensis–Polyentactinia circumretia* Assemblage (Table 6).

Radiolarians from the Egindy Formation on the Aitpaika Creek are more similar in generic and species composition and skeleton size to the radiolarian assemblage described by Foreman (1963) from the Lower Famennian, Upper Devonian (shaly Huron Member of Ohio) of North America (Nazarov, 1975, 1988).

As Middle Frasnian radiolarians of the Timan–Pechora Basin are compared with Frasnian radiolarians of other regions of the world, it is evident that this assemblage contains only individual specimens of typical Upper Frasnian species (*Bientactinosphaera aitpaiensis* (Nazarov), *B. guangxiensis* (Li et Wang), and *Polyentactinia circumretia* Nazarov et Ormiston), which occur only in the uppermost beds of the section, and the species *Cyclocarpus tubiformis* Li et Wang and *Astroentactinia stellata* Nazarov are completely absent from the assemblage (Afanasieva, 1997a, 2000a).

In addition, deposits of the Domanik Formation (Middle Frasnian) are characterized by widespread of species that appear for the first time at the end of the Middle Devonian and are known from the lower part of the Gogo Formation of western Australia (Nazarov et al., 1982): *Spongentactinella windjanensis* Nazarov, *Ornatoentactinia solita* Afanasieva, *O. spartaci* Afanasieva (*Entactinosphaera* cf. *cancellicula* Foreman, as identified by Nazarov), and *Ceratoikiscum stellatum* Aitchison. These radiolarian species are absent not only in the Famennian beds, but also in the Upper Frasnian.

The radiolarian assemblage from the Domanik Formation of the Middle Frasnian of the Timan–Pechora Basin has many species in common with the radiolarian assemblage from the upper part of the Gogo Formation of western Australia (Nazarov and Ormiston, 1983b; Aitchison, 1993): *Bientactinosphaera echinata* (Hinde), *B. grandis* (Nazarov), *B. variacanthina* (Foreman), *B. egindyensis* (Nazarov), *Radiobisphaera assidera* (Nazarov), *Ceratoikiscum delicatum* Cheng, *C. bujugum* Foreman, *Palaeoscenidium cladophorum* Deflandre, *Spongentactinella* sp. 1 (=*S. olafi* Afanasieva), *Palaeoscenidium delicatum* Aitchison, *P. phalangium* Aitchison, and others (Afanasieva, 1997a, 2000a).

Thus, the radiolarian assemblage from the Domanik Formation of the Middle Frasnian of the Timan–Pechora Basin shares some species with Early Frasnian and Late Frasnian radiolarian associations and plays a connecting role in evolutionary changes of radiolarian assemblages of the Frasnian Age.

We revised Frasnian radiolarians from the following deposits:

(1) Vetlasyansk Formation of the Upper Frasnian of the southern Timan–Pechora Basin;

(2) Egindy Formation of the Middle–Upper Frasnian of the Southern Urals and Northern Mugodzhary;

(3) Domanik Formation of the Middle Frasnian of the Southern Urals, Volga–Ural and Timan–Pechora basins;

(4) Mukasovian Regional Substage of the Middle Frasnian of the Southern Urals;

(5) Middle–Upper Devonian of the Rudny Altai;

(6) Ust'-Yarenga Formation of the Lower Frasnian of the Timan–Pechora Basin;

(7) Lower part of the Gogo Formation of the Canning Basin of western Australia, corresponding to the Lower Frasnian.

As a result of original studies and revision of the previously reported data, we have recognized seven radiolarian assemblages within the Frasnian Stage (Table 6):

- *Polyentactinia circumretia–Bientactinosphaera egindyensis* for the Middle and Upper Frasnian of the Southern Urals and Northern Mugodzhary and Upper Frasnian of the Rudny Altai (Nazarov, 1975, 1988; Afanasieva et al., 2008, 2009; Afanasieva and Amon, 2009a);
- *Bientactinosphaera pittmani–Russirad kazintsovae* for the Upper Frasnian of the Timan–Pechora Basin and the eastern slope of the Middle Urals (Afanasieva and Amon, this work);
- *Radiobisphaera domanicensis–Radiobisphaera menneri* for the Middle Frasnian (Domanik Formation) of the western slope of the Southern Urals and Volga–Ural Basin (Afanasieva and Amon, this work);
- *Moskovistella allbororum–Ceratoikiscum ukhtensis* for the Middle Frasnian (Domanik Formation) of the Timan–Pechora Basin and Rudny Altai (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 2001; Afanasieva et al., 2008, 2009);
- *Primaritripus chuvashovi* for the Middle Frasnian of the Southern Urals (Afanasieva and Amon, 2009a);
- *Helenifore gogoense–Retisphaera concinna* for the Lower Frasnian of Australia (Afanasieva and Aitchison, 2001);
- *Palaeodiscaleksus punctus–Astroentactinia biaciculata* for the Lower Frasnian of the Timan–Pechora Basin (Afanasieva and Amon, this work).

Early Frasnian

A break in sedimentation at the Middle–Late Devonian boundary in the Russian Platform separates two large cycles corresponding to the time of Frasnian and Famennian sedimentation separated by a large unconformity (erosion), which was caused by rearrangement of the entire structural pattern of the platform (Tikhomirov, 1995).

The maximum transgression of the Ural Sea on the Russian Platform occurred in the Frasnian Age. As compared with the Givetian Age, the area of normal marine sedimentation in the northeastern Russian Platform considerably expanded in the Frasnian. During the Early Frasnian, within most of the platform, terrigenous deposits accumulated in the continental and coastal–continental conditions, which were replaced at the end of the Early Frasnian by coastal and shallow marine conditions (Tikhii, 1975) (Fig. 12a).

Early Frasnian radiolarians of the Volga–Ural basin and Middle Urals. Individual poorly preserved Early Frasnian radiolarians were recorded for the first time by Bykova (1955) in the Volga–Ural Basin near the village of Aksubaevo (Figs. 3, 8, 12a).

A few members of the "Ural" Radiolarian Assemblage were described by Bykova (1955) from the Lower Frasnian beds of the Bolshaya Arsha River Basin in the Middle Urals (Figs. 3, 8, 12a, 13): *Borisella radiata* (Antropov), *Trochodiscus concavutas* Vissarionova, and *T. elegans* (Vissarionova).

In the Volga–Ural Basin, near the towns of Tuimazy and Sterlibashevo of western Bashkortostan, the following forms have been recorded: individual *Astroentactinia* cf. *stellata* Nazarov, *Trochodiscus elegans* (Vissarionova), and *T. parva* (Bykova); and near the village of Aksubaevo in Tatarstan and in the vicinity of the town of Syzran, *Astroentactinia* cf. *stellata* Nazarov, *Trochodiscus elegans* (Vissarionova), and *T. parva* (Bykova) (Fig. 11; Table 5).

Early Frasnian assemblage with Helenifore gogoense–Retisphaera concinna. Aitchison (1993) and Won (1997a, 1997b) described in detail a rich radiolarian assemblage consisting of 125 species and subspecies of 32 genera from carbonate nodules of the lower part of the Gogo Formation (bottom of the Frasnian Stage) of the Canning Basin, western Australia (Fig. 3). The correlation of this radiolarian assemblage with the conodont scale (*lower to middle asymmetricus* Zone) allowed the establishment of the radiolarian assemblage with *Helenifore gogoense–Spongentactinia concinna*, which is characteristic of the Lower Frasnian.

The analysis of the taxonomic composition of the radiolarian assemblage of western Australia in comparison with the radiolarian association from the Domanik Formation of the Timan–Pechora Basin allowed Afanasieva and Aitchison (2001) to establish a biostratigraphic assemblage with *Helenifore gogoense–Retisphaera concinna* (Pl. 8, figs. 21–31), which is characteristic of the Lower Frasnian and corresponds to the *lower to middle asymmetricus* Conodont Zone.

The Early Frasnian radiolarian assemblage from the Gogo Formation is distinguished by many (33 species) representatives of spiny radiolarians of the families Ceratoikiscidae and Palaeoscenidiidae (Pl. 8, figs. 21–26).

The most typical forms of this assemblage which are only typical of the Lower Frasnian are *Paleotripus gogoense* Aitchison, *Ceratoikiscum torale* Aitchison, *C. spiculatum* Aitchison, *Palaeoscenidium venustum* Aitchison, *Secuicollacta araneam* Aitchison, and *Entactinia proceraspina* Aitchison (Pl. 8, figs. 21, 23–25, 28, 29).

Typical species of the radiolarian assemblage from the Lower Frasnian Gogo Formation are *Ceratoikiscum echinatum* Aitchison, *Helenifore gogoense* Aitchison, *Entactinia hystricuosa* Aitchison, and *Retisphaera concinna* (Aitchison) (Pl. 8, figs. 22, 26, 30, 31).

Among the Early Frasnian radiolarians described, species characteristic of the Middle Frasnian or Late Frasnian radiolarian assemblages have not been recorded, but Middle Devonian species are present, including *Bientactinosphaera aculeatissima* (Aitchison), *Helenifore laticlavium* Nazarov et Ormiston, and *Helioentactinia stellaepolus* Aitchison.

Early Frasnian assemblage with Palaeodiscaleksus punctus–Astroentactinia biaciculata. Early Frasnian radiolarians were established for the first time by Afanasieva (2000a) in the deposits of the northern and southern Timan–Pechora Basin; they are represented by 11 species of eight genera (Figs. 3, 12a, 14; Fig. 6b, I, X.

The Early Frasnian radiolarian assemblage of the northern Timan–Pechora Basin (Fig. 6b, X; Fig. 15; Table 7) is characterized by the appearance in deposits of the external shelf of abundant, but uniform discoidal radiolarians (two species of two genera), *Palaeodiscaleksus punctus* (Hinde) and *Palaeotripus patella* (Hinde) (Pl. 9, figs. 10–12).

In the southern Timan–Pechora Basin, the radiolarian assemblage is more diverse, but less abundant. Radiolarians from the Ust'-Yarenga Formation on the Chut River are represented by nine species of six genera (Figs. 6c, 14, 15; Table 7; Pl. 9, figs. 1–9), including *Astroentactinia biaciculata* Nazarov, *A. paronae* (Hinde), *Borisella bykovae* Afanasieva, *B. maksimovae* Afanasieva, *Entactinia patorovaria* Afanasieva, *E. bogdanovi* Afanasieva, *Meschedea crassicortex* Won, *Moskovistella deorsiacus* (Nazarov et Ormiston), and *Ceratoikiscum spinosiarcuatum* Foreman (Afanasieva, 2000a).

The presence of small Early Frasnian radiolarians in the southern Timan–Pechora Basin and, particularly, the taxonomic homogeneity of abundant discoidal radiolarians in the northern part of the basin is probably accounted for by unfavorable for radiolarians shallow-water conditions of the paleosea.

The radiolarian assemblages considered allowed us to establish a new biostraton, beds with *Palaeodiscale-*

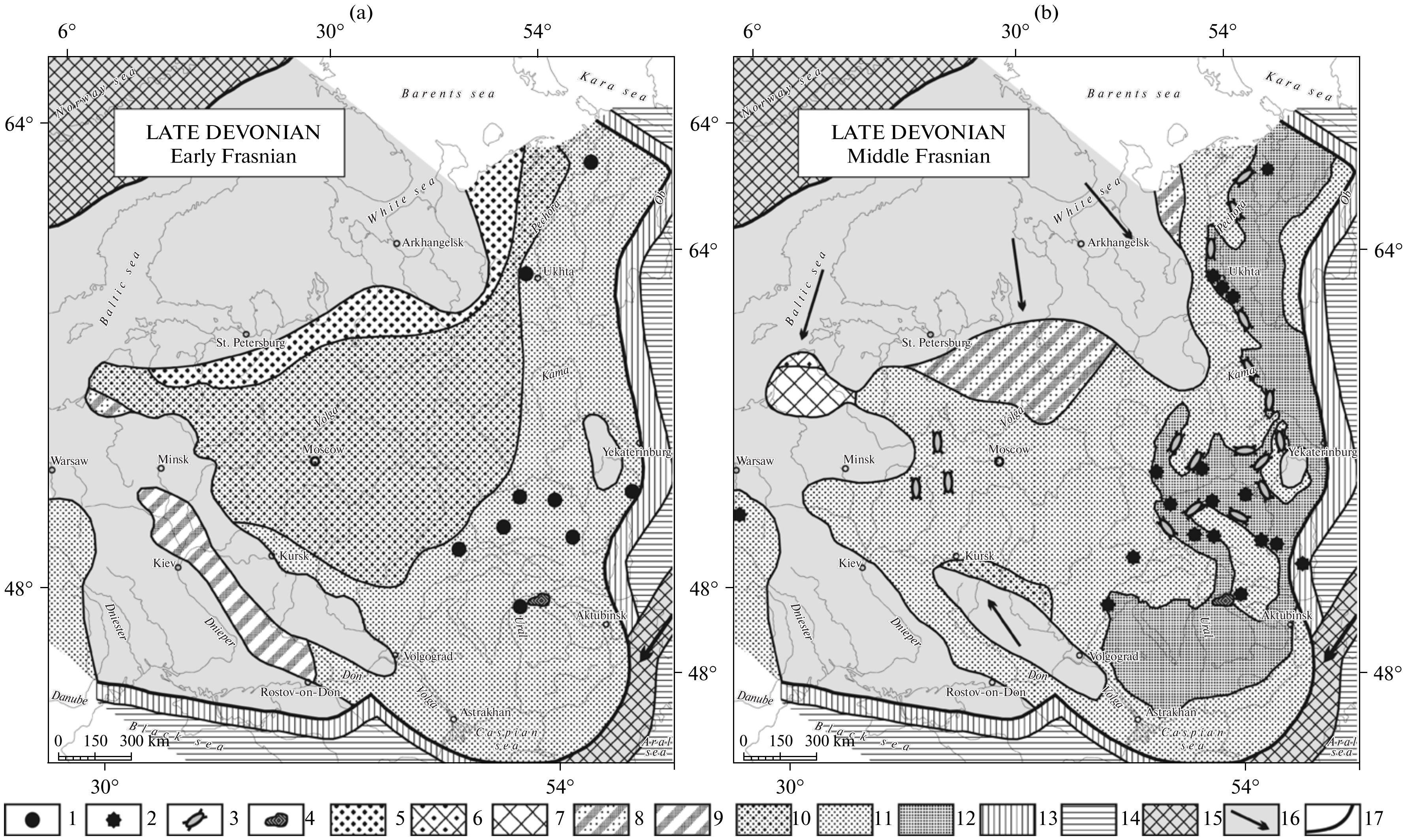


Fig. 12. Paleobiogeographic scheme for the (a) Early and (b) Middle Frasnian of the Russian Platform and Greater Urals and radiolarian localities: (1, 2) radiolarian localities: (1) Early Frasnian and (2) Middle Frasnian; (3) paleoreefs; (4) Karachaganak bioherm; (5) continental fluvial plains; (6, 7) sea with increased salinity: (6) coastal region, (7) shallow internal shelf; (8, 9) sea with low salinity: (8) coastal region, (9) internal shelf; (10–14) sea with normal salinity: (10) coastal region, (11) internal shelf, (12) external shelf, (13) continental slope, (14) paleocean bottom; (15) active fold belts; (16) main directions of transportation of clastic material from land; and (17) boundary of the Russian Platform. Paleobiogeographic schemes are based on the data of Tikhomirov (1967, 1995), Maksimova (1975), Tikhii (1975), Sorokin (1978), Menner et al. (1991), Trokhova (1991), Belyaeva et al. (1998), Racki (1992, 1997), Rodionova et al. (1995), Menner et al. (1996), Nikishin et al. (1996) Yunusov et al. (1997).

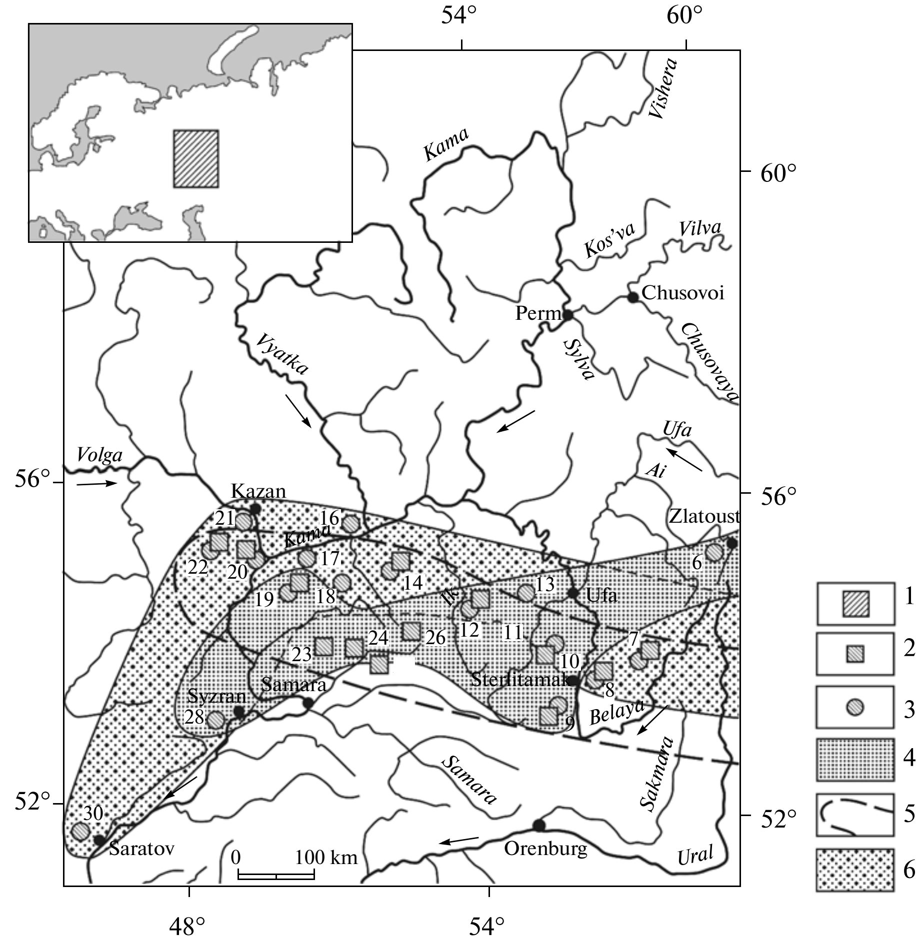


Fig. 13. Geographical ranges of radiolarians on the western slope of the Southern Urals and in the Volga–Ural Basin in the Early and Middle Frasnian, Late Devonian. Designations: (1) working area, (2) radiolarian assemblage with *Radiobisphaera domanicensis–Radiobisphaera menneri* from the Domanik Formation of the Middle Frasnian, (3) "Ural" Radiolarian Assemblage of the Devonian, (4) Early Frasnian, (5) Middle Frasnian, Domanik Time, (6) Middle Frasnian, Mendym Time. For radiolarian localities (after Bykova, 1955), see Fig. 7.

ksus punctus–Astroentactinia biaciculata, which corresponds to the middle and upper subformations of the Ust'-Yarenga Formation of the Lower Frasnian (Tables 6, 8). The new radiolarian biostraton corresponds to the *Komioceras schtuckenbergi, Timanites keyserlingi*, and *Hoeninghausia nalivkini* ammonoid zones and the *late falsilovalis–transitans* conodont zones (Table 8).

Middle Frasnian

At the beginning of the Middle Frasnian, a marine transgression began, which expanded from the vast Ural Paleocean. It gradually covered increasing area and formed marginal epicontinental seas, such as the Timan–Pechora Sea. In the Middle Frasnian, the marine transgression three times penetrated into the Russian Platform and, in the Domanik Time, it reached a maximum, so that most of the platform was occupied by the sea (Fig. 12b). Only the Baltic Syneclise had a semi-isolated gulf of the intraplatform sea with increased salinity (Tikhii, 1975).

The first Middle Frasnian radiolarians were described by Bykova (1955) in thin sections of siliceous–carbonate rocks of the Domanik Formation of the Southern Urals and Volga–Ural Basin (Figs. 3, 11, 12b, 13, 16).

The presence of abundant radiolarians in the stratotype of the Domanik Formation on the Domanik River in the Ukhtinskii District of the Timan–Pechora Basin (Figs. 3, 6c, 12b) was reported for the first time by Kushnareva (1959). The first figures of Domanik radiolarians in thin sections of limestones (without determination or description) in the stratotype of the Domanik Formation on the Domanik River of the Ukhtinskii District of the Timan–Pechora Basin (Figs. 6c, 12b, 17) were published by Maksimova (1970), and preliminary identification of some of these radiolarians (without descriptions) was performed by Nazarov (1975, 1988). Judging from photographs of thin sections (Maksimova, 1970), these radiolarians belong to the Middle Frasnian Domanik Assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis* (Afanasieva,

Plate 8

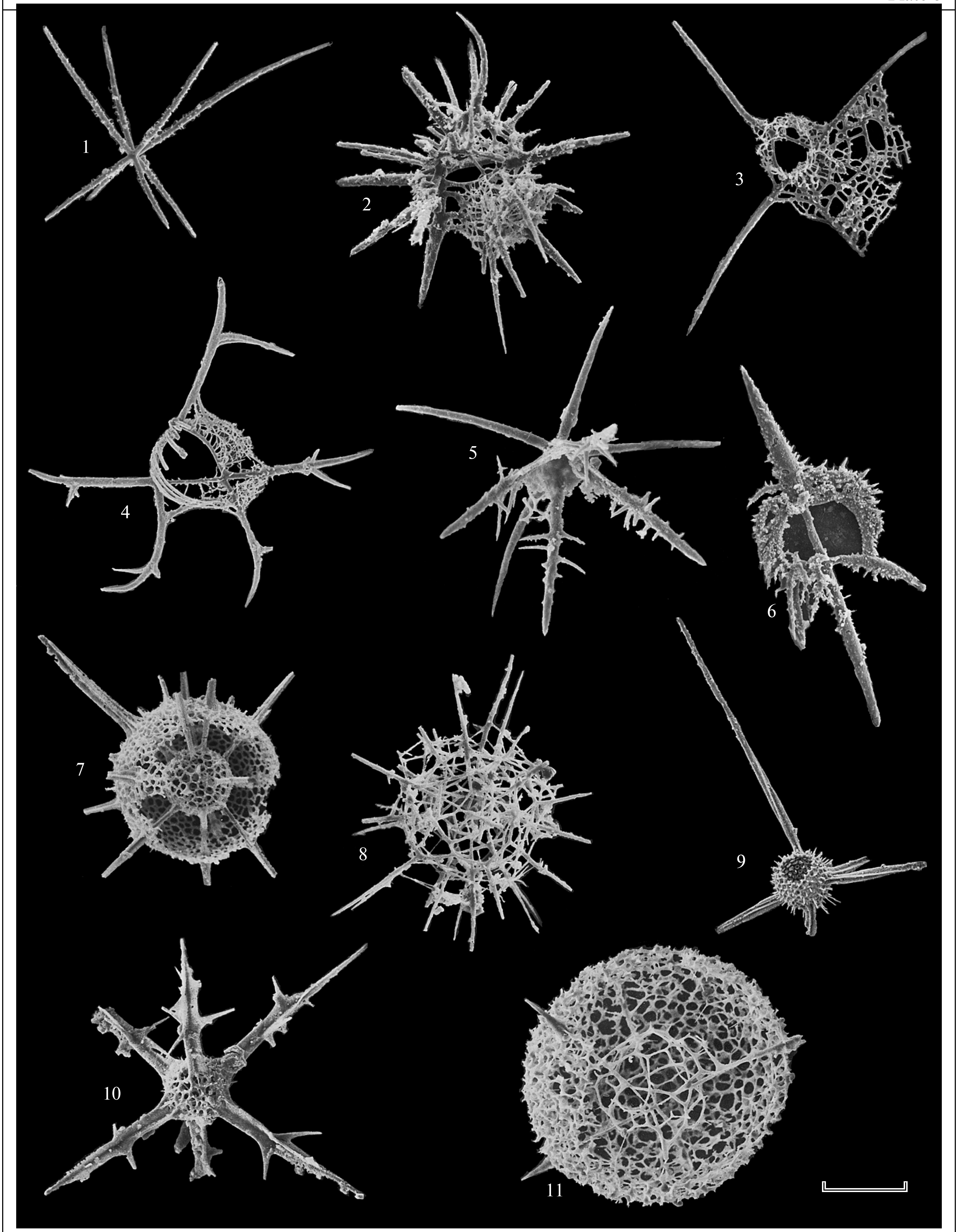


Table 8. Biostratigraphic zones based on conodonts, ammonoids, and radiolarians in the Frasnian Stage of the Timan–Pechora Basin

System	Series	Stage	Substage	Formation, Subformation, Unit		Biostratigraphic zones			
						Conodont	Ammonoidea	Radiolaria	
						Ziegler and Sandberg, 1996	Becker et al., 2000	Afanasieva, 1997a, 2000a; Afanasieva and Amon, this study	
Devonian	Upper	Frasnian	Upper	Sedyu		*linguiformis*	?		
				Lyaiol	IV	*rhenana* late	*Manticoceras lyaiolense*	*Bientactinosphaera pittmani – Russirad kazintsovae*	
					III	early			
					II		*Virginoceras ljaschenkoae*		?
					I		?		
			Middle	Domanik	Upper	*jamieae* *hassi* late	*Nordiceras timanicum = Manticoceras ammon*	*Moskovistella allbororum – Ceratoikiscum ukhtensis*	Rdm-3
					Middle	early			Rdm-2
					Lower	*punctata*	*Probeloceras domaniscense*		Rdm-1
			Lower	Ust'-Yarega	Upper	*transitans*	*Komioceras schtuckenbergi*	Beds with *Palaeodiscaleksus punctus – Astroentactinia biaciculata*	
					Middle	*falsilovalis* late	*Timanites keyselingi* *Hoeninghausia nalivkini*		
					Lower		?		

1997a, 2000a) and include *Astroentactinia biaciculata* Nazarov, *A. crassata* Nazarov, *Bientactinosphaera* spp., *B. grandis* (Nazarov), *Entactinia patorovaria* Afanasieva, *Helioentactinia polyacanthina* (Foreman), and *Radiobisphaera domanicensis* (Bykova) (Fig. 17).

The richest assemblages of Middle Frasnian radiolarians were investigated by Afanasieva (1997a, 2000a) and Afanasieva and Mikhailova (2001) in the Domanik Formation of the southern Timan–Pechora Basin (Figs. 3, 6c, 12b, 14, 15). The Domanik deposits are particularly interesting because there radiolarians conserved in carbonate nodules among siliceous differences of rocks.

To date, we have established a new Middle Frasnian radiolarian locality on Argagan Mountain (Fig. 1, X) of the Southern Urals (Afanasieva and Amon, 2009a) (Figs. 3, 12b).

Middle Frasnian assemblage with Radiobisphaera domanicensis–Radiobisphaera menneri. The first Middle Frasnian radiolarians were described by Bykova (1955) in thin sections from siliceous–carbonate rocks of the Domanik Formation of the Southern

Explanation of Plate 8

Early Frasnian radiolarians of western Australia; radiolarian assemblage with *Helenifore gogoense–Spongentactinia concinna*.

Fig. 1. *Paleotripus gogoense* Aitchison, 1993, specimen no. GSWA-F43981; scale bar, 86 μm.

Fig. 2. *Ceratoikiscum echinatum* Aitchison, 1993, specimen no. GSWA-F44019; scale bar, 71 μm.

Fig. 3. *Ceratoikiscum torale* Aitchison, 1993, specimen no. GSWA-F44022; scale bar, 89 μm.

Fig. 4. *Ceratoikiscum spiculatum* Aitchison, 1993, specimen no. GSWA-F43991; scale bar, 115 μm.

Fig. 5. *Palaeoscenidium venustum* Aitchison, 1993, specimen no. GSWA-F43965; scale bar, 58 μm.

Fig. 6. *Helenifore gogoense* Aitchison, 1993, specimen no. GSWA-F44025; scale bar, 68 μm.

Fig. 7. *Helioentactinia stellaepolus* Aitchison, 1993, specimen no. GSWA-F44081; scale bar, 71 μm.

Fig. 8. *Secuicollacta araneam* Aitchison, 1993, specimen no. GSWA-F44079; scale bar, 42 μm.

Fig. 9. *Entactinia proceraspina* Aitchison, 1993, specimen no. GSWA-F44069; scale bar, 150 μm.

Fig. 10. *Apophisisphaera hystricuosa* (Aitchison, 1993), specimen no. GSWA-F44063; scale bar, 63 μm.

Fig. 11. *Retisphaera concinna* (Aitchison, 1993), specimen no. GSWA-F44057; scale bar, 59 μm.

Upper Devonian, Lower Frasnian Substage; western Australia, Canning Basin, Gogo Formation (after Afanasieva and Aitchison, 2000).

Plate 9

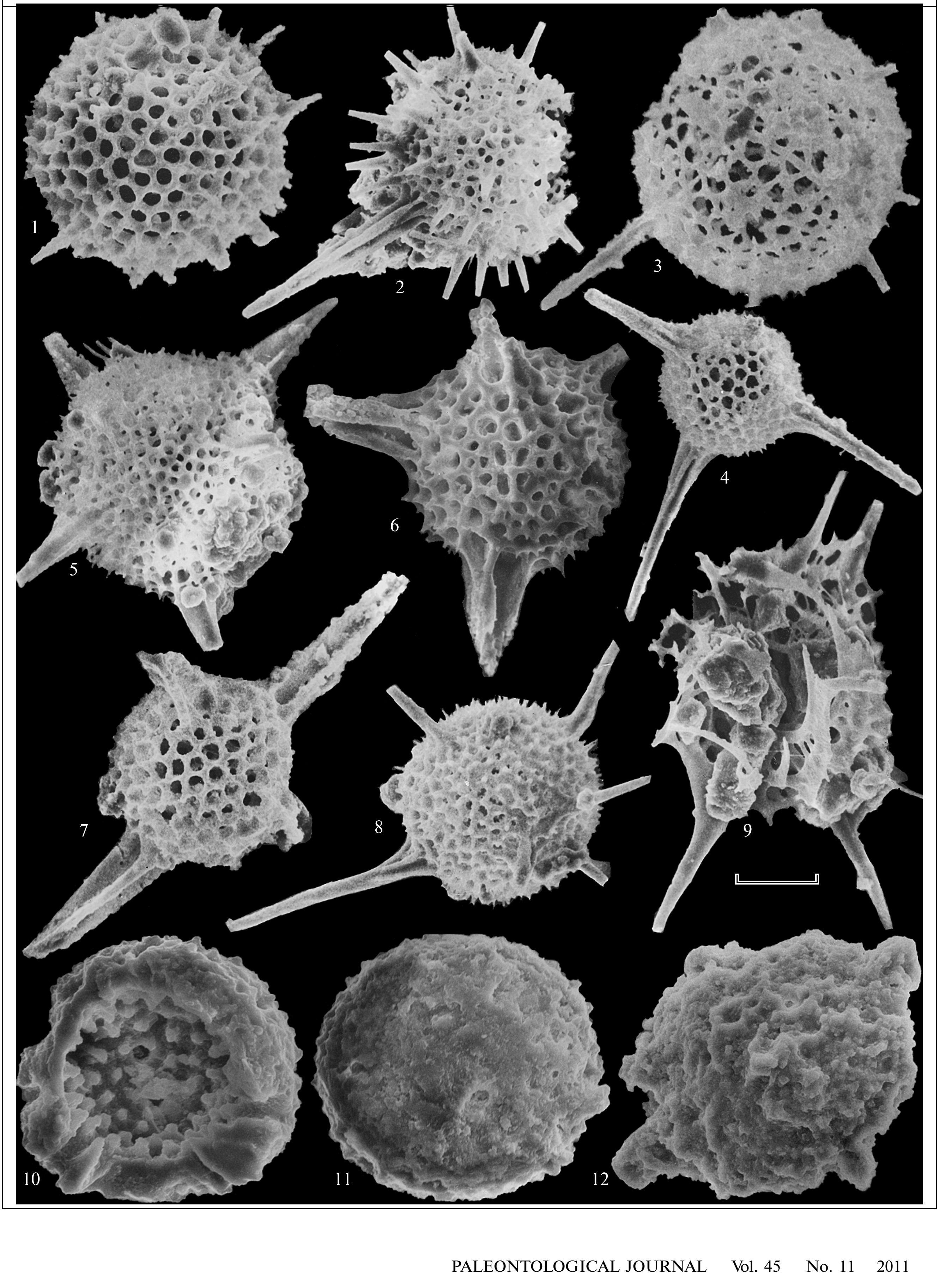


Table 9. Unification of the taxonomic composition of radiolarians from the Middle Frasnian Domanik Formation of the Southern Urals and Volga–Ural Basin

Bykova, 1955	Afanasieva and Amon, 2010d, 2010e
Acanthosphaera australis Hinde, 1899	*Astroentactinia* cf. *stellata* Nazarov, 1975
Amphibrachium (?) sp.	*Gedauia* (?) sp.
Cenosphaera scitula Hinde, 1899	*Astroentactinia* cf. *crassata* Nazarov, 1975
Dorysphaera domanicensis Bykova, 1955	*Radiobisphaera domanicensis* (Bykova, 1955)
Plagiocantha nana Bykova, 1955	*Palacantholithus nana* (Bykova, 1955)
Plagoniscus ex gr. *simplex* Hinde, 1899	*Palacantholithus* ex gr. *simplex* (Hinde, 1899)
Plagoniscus(?) sp.	*Palaeothalomnus* cf. *quadriramosum* (Foreman, 1963)
Staurodruppa nucula Hinde, 1899	*Staurodruppa nucula* Hinde, 1899
Staurolonche davidi Hinde, 1899	*Bientactinosphaera* cf. *grandis* (Nazarov, 1975)
Trilonche vetusta Hinde, 1899	*Bientactinosphaera* cf. *variacanthina* (Foreman, 1963)
Xiphosphaera echinatum (Hinde, 1899)	*Radiobisphaera* cf. *menneri* Afanasieva, 2000

Urals and Volga–Ural Basin (western Bashkortostan, Tatarstan, Samara Region) (Fig. 8). In some parts of the section, radiolarians form mass accumulations, although they are mostly poorly preserved, so that the matter contains only rounded empty holes, with traces of spines deviating from them. At the same time, Bykova (1955, pls. XX–XXIII) determined and described some radiolarians, including *Acanthosphaera australis* Hinde, *Amphibrachium* (?) sp., *Cenosphaera scitula* Hinde, *Dorysphaera domanicensis* Bykova, *Plagiocantha nana* Bykova, *Plagoniscus* ex gr. *simplex* Hinde, *Plagoniscus (?)* sp., *Staurodruppa nucula* Hinde, *Staurolonche davidi* Hinde, *Trilonche vetusta* Hinde, and *Xiphosphaera echinatum* (Hinde). In doing so, Bykova (1955, p. 91) remarks that "radiolarian community from the Domanik beds of these areas was undoubtedly much richer than the association described."

A revision of radiolarians from the Domanik Formation of the Southern Urals and Volga–Ural Basin has shown that they are similar to Domanik radiolarians from the southern Timan–Pechora Basin (Afanasieva, 2000a); hereinafter, they are considered according to the modern classification of radiolarians (Afanasieva et al., 2005d; Afanasieva and Amon, 2006a, 2010d, 2010e) (Table 9) as follows: *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Bientactinosphaera* cf. *grandis* (Nazarov), *B.* cf. *variacanthina* (Foreman), *Gedauia* (?) sp., *Palacantholithus nana* (Bykova), *P. simplex* (Hinde), *Palaeothalomnus* cf. *quadriramosum* (Foreman), *Radiobisphaera domanicensis* (Bykova), *R. echinatum* (Hinde), *R.* cf. *menneri* Afanasieva, and *Staurodruppa nucula* Hinde.

In the Southern Urals, in the Sikaza and Ryauzyak river basins (Figs. 11, 13), bituminous limestones of the Domanik Formation have yielded only one radiolarian species, *Astroentactinia* cf. *stellata* Nazarov.

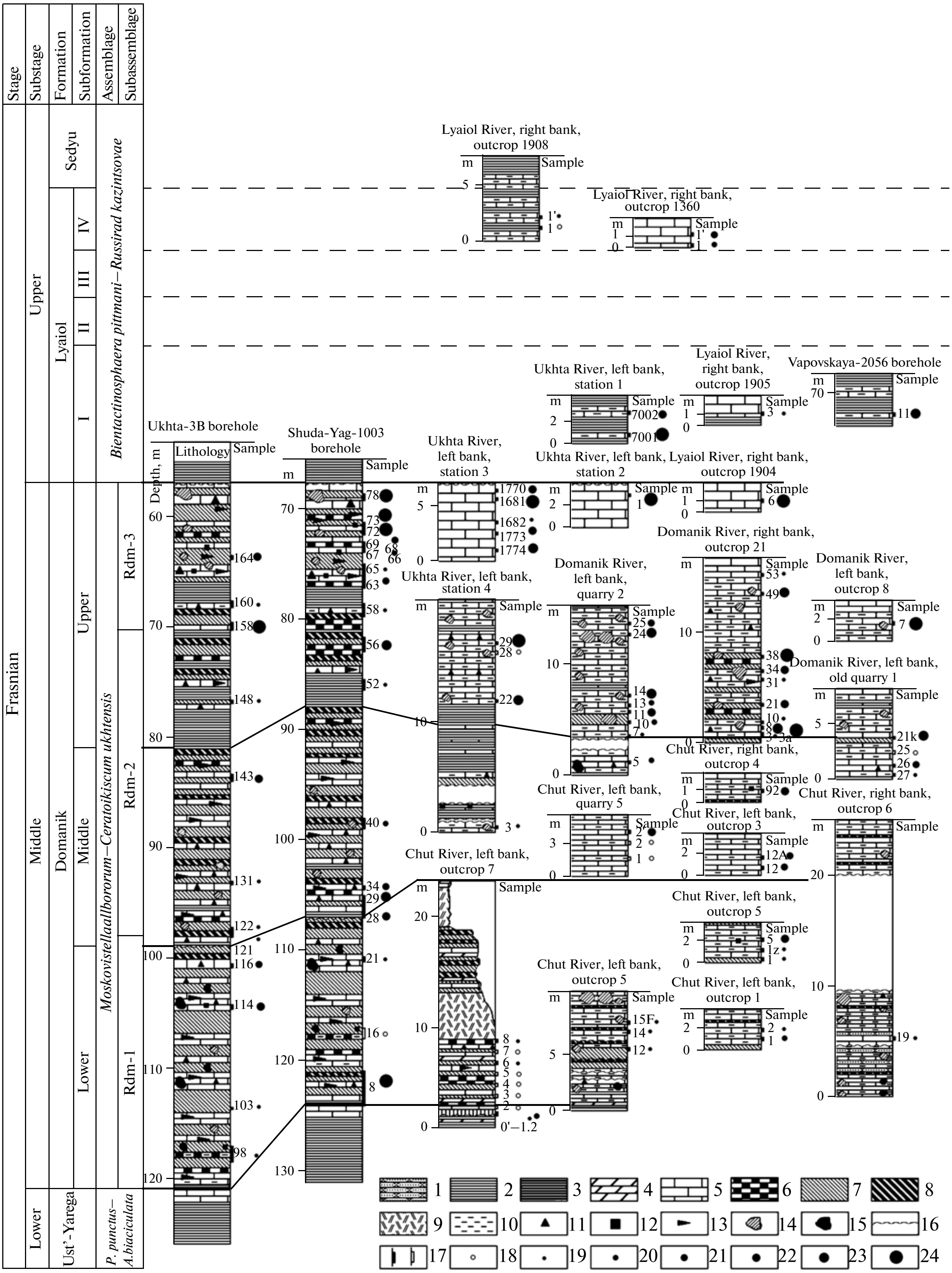
In western Bashkortostan, radiolarian accumulation occur in the Domanik beds near the town of Tuimazy and villages of Sterlibashevo and Elatminki (Figs. 11, 13). A locality near the town of Tuimazy has yielded *Astroentactinia* cf. *stellata* Nazarov, *Bientactinosphaera* cf. *grandis* (Nazarov), *B.* cf. *variacanthina* (Foreman), and *Palacantholithus simplex* (Hinde); and in the Domanik section near the village of Sterlibashevo, only one species, *Astroentactinia* cf. *stellata* Nazarov (Fig. 16) has been recorded.

Explanation of Plate 9

Early Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Palaeodiscaleksus punctus–Astroentactinia biaciculata*: spherical porous Sphaerellaria (1–4, 6–8), spongy Spumellaria (5), spiny Aculearia (9), and discoidal Stauraxonaria (10–12).

Fig. 1. *Astroentactinia biaciculata* Nazarov, 1975, specimen PIN, no. 5311/12316; scale bar, 37 μm.
Fig. 2. *Astroentactinia paronae* (Hinde, 1899), specimen PIN, no. 5311/12321; scale bar, 40 μm.
Fig. 3. *Borisella bykovae* Afanasieva, 2000, specimen PIN, no. 5311/12313; scale bar, 33 μm.
Fig. 4. *Borisella maksimovae* Afanasieva, 2000, specimen PIN, no. 5311/12326; scale bar, 56 μm.
Fig. 5. *Meschedea crassicortex* Won, 1997, specimen PIN, no. 5311/12319; scale bar, 33 μm.
Fig. 6. *Entactinia patorovaria* Afanasieva, 2000, specimen PIN, no. 5311/12323; scale bar, 40 μm.
Fig. 7. *Entactinia bogdanovi* Afanasieva, 2000, specimen PIN, no. 5311/12327; scale bar, 33 μm.
Fig. 8. *Moskovistella deorsiacus* (Nazarov et Ormiston, 1993), specimen PIN, no. 5311/12310; scale bar, 43 μm.
Fig. 9. *Ceratoikiscum spinosiarcuatum* Foreman, 1963, specimen PIN, no. 5311/12322; scale bar, 33 μm.
Figs. 10 and 11. *Palaeodiscaleksus punctus* (Hinde, 1899): (10) specimen PIN, no. 5311/12608; scale bar, 26 μm; (11) specimen PIN, no. 5311/12615; scale bar, 35 μm.
Fig. 12. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5311/12604; scale bar, 33 μm.

Upper Devonian, Lower Frasnian Substage; Timan–Pechora Basin: (1–9) Chut River, outcrop 7, sample 1,2b; (10–12) borehole Zapadnaya Vissertynskaya-1 (3601–3616 m of depth), sample K-447d-90.


Stage
Substage
Formation
Subformation
Assemblage
Subassemblage
Frasnian
Upper
Middle
Lower
Sedyu
Lyaiol
Domanik
Ust'-Yarega
IV
III
II
I
Upper
Middle
Lower
Bientactinosphaera pittmani–Russirad kazintsovae
Moskovistellaallbororum–Ceratoikiscum ukhtensis
P. punctus–A.biaciculata
Rdm-3
Rdm-2
Rdm-1
Ukhta-3B borehole
Depth, m
Lithology
Sample
Shuda-Yag-1003 borehole
Ukhta River, left bank, station 3
Ukhta River, left bank, station 4
Ukhta River, left bank, station 1
Ukhta River, left bank, station 2
Lyaiol River, right bank, outcrop 1908
Lyaiol River, right bank, outcrop 1360
Lyaiol River, right bank, outcrop 1905
Lyaiol River, right bank, outcrop 1904
Vapovskaya-2056 borehole
Domanik River, left bank, quarry 2
Domanik River, right bank, outcrop 21
Domanik River, left bank, outcrop 8
Domanik River, left bank, old quarry 1
Chut River, right bank, outcrop 4
Chut River, left bank, quarry 5
Chut River, left bank, outcrop 3
Chut River, right bank, outcrop 6
Chut River, left bank, outcrop 7
Chut River, left bank, outcrop 5
Chut River, left bank, outcrop 1
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In Tatarstan, dark bituminous siliceous limestones of the Domanik beds near the villages of Cheremshan, Aktash, and Kamskoe Ust'e (Figs. 11, 13) have yielded radiolarians, which formed in places mass accumulations (Bykova, 1955). However, well-preserved radiolarians are rare in the Domanik beds near the village of Kamskoe Ust'e. It turned out that the fine lattice of their skeletons is composed of pyrite, which replaced silica, making them black and well distinguished against a background of brownish matter (Fig. 16): *Astroentactinia* cf. *crassata* Nazarov, *Bientactinosphaera* cf. *grandis* (Nazarov), *B.* cf. *variacanthina* (Foreman), *Gedauia* (?) sp., *Palacantholithus simplex* (Hinde), *Radiobisphaera domanicensis* (Bykova), and *Staurodruppa nucula* Hinde.

In the Domanik beds of the Samara Region, on the Baitugan River and near the villages of Krasnovka, Radaevka, and Sernovodsk (Figs. 11, 13), siliceous limestones contain mass accumulations of very poorly preserved radiolarians. At the same time, these beds have yielded the most diverse radiolarian assemblage (Fig. 16), including *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Bientactinosphaera* cf. *grandis* (Nazarov), *B.* cf. *variacanthina* (Foreman), *Gedauia* (?) sp., *Palacantholithus simplex* (Hinde), *P. nana* (Bykova), *Palaeothalomnus* cf. *quadriramosum* (Foreman), *Radiobisphaera domanicensis* (Bykova), *R.* cf. *menneri* Afanasieva, and *Staurodruppa nucula* Hinde.

The analysis of distribution of radiolarians from siliceous–carbonate rocks of the Domanik Formation of the Southern Urals and Volga–Ural Basin in comparison with radiolarian assemblages from the Domanik beds of the Timan–Pechora Basin allowed us to establish for the Domanik Formation an assemblage with *Radiobisphaera domanicensis–Radiobisphaera menneri* (Table 6). The geographical range of this assemblage is the western slope of the Southern Urals and Volga–Ural Basin (western Bashkortostan, Tatarstan, and the Samara Region).

"Ural" radiolarian assemblage of the Middle Frasnian. The Domanik beds of the Middle Frasnian of the Volga–Ural Basin usually lack members of the "Ural" Radiolarian Assemblage (Bykova, 1955). In western Bashkortostan, very rare *Astroentactinia* have been recorded in thin sections of limestones. In Tatarstan, foraminifers occur in dark bituminous limestones of the Domanik Formation with an admixture of fragmentary gray limestones. The same is observed near the village of Cheremshan. Fragments of gray limestone enclosed in limestone of the Domanik type have yielded *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, and *Trochodiscus elegans* var. *subsphaera* (Vissarionova) (Figs. 11, 13; Table 5).

However, in the overlying Middle Frasnian Mendym Formation, small radiolarians of the "Ural" Assemblage are usually diverse and more widespread than in the Givetian and Lower Frasnian (Bykova, 1955) (Figs. 11, 13; Table 5).

Middle Frasnian Mendym radiolarians of the "Ural" Assemblage are represented in the Southern Urals in the Sikaza and Ryauzyak river basins by only one species, *Astroentactinia* cf. *stellata* Nazarov.

In limestones of the Mendym beds of western Bashkortostan near the town of Tuimazy and villages of Kargaly and Elatminki, three species of the "Ural" Radiolarian Assemblage have been recorded, i.e., *Astroentactinia* cf. *stellata* Nazarov, *A.* cf. *biaciculata* Nazarov, and *Entactinia tuberculata* (Lipina).

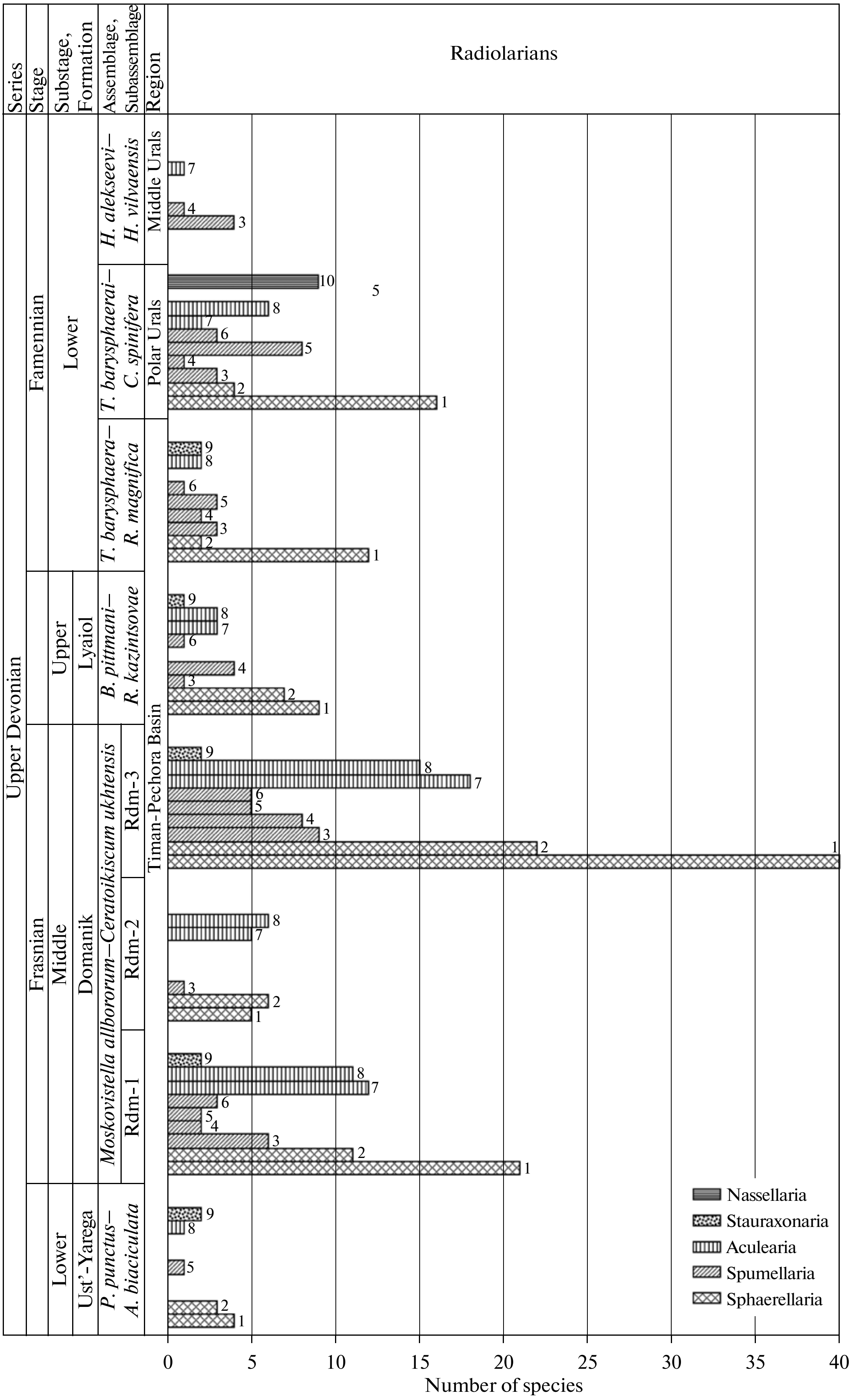
The microfauna from the Mendym beds of Tatarstan in the vicinity of Aksubaevo, Aktash, Verkhnii Uslon, Kamskoe Ust'e, Staroe Romashkino, Shugurovo, and Yanga-Aul is more diverse and represented by *Astroentactinia* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia tuberculata* (Lipina), *E. paulis* (Bykova), *Trochodiscus elegans* (Vissarionova), *T. elegans* var. *subsphaera* (Vissarionova), *T. concavutas* Vissarionova, and *T. parva* (Bykova).

Near the town of Syzran, *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, and *Trochodiscus parva* (Bykova) have been recorded. Individual *Trochodiscus parva* (Bykova) occur near the village of Teplovka of the Saratov Region.

Middle Frasnian assemblage with Moskovistella allbororum–Ceratoikiscum ukhtensis. The study of radiolarians from a complete section of the Domanik Formation based on boreholes and outcrops in the Ukhtinskii District of the Timan–Pechora Basin (Figs. 6c, 12b, 14) allowed Afanasieva (1997a, 2000a) to reveal for the first time a radiolarian assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis* (Tables 6, 8). The stratotype of the new assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis* is the section of borehole Shuda-Yag-1003 (Table 10).

The Middle Frasnian radiolarian assemblage is extremely diversity, including 129 species of 32 genera (Fig. 15; Tables 7, 10). Typical species of this assemblage are *Moskovistella allbororum* Afanasieva, *Radiobisphaera menneri* Afanasieva, *Spongentactinella olafi* Afanasieva, and *Ceratoikiscum ukhtensis* Afanasieva; its distinctive features are species with well-developed apophyses and many spiny taxa.

Fig. 14. Correlation of deposits of the Frasnian Stage in the Timan–Pechora Basin: (1) sandstone, (2) clay, (3) claystone, (4) marl, (5) limestone, (6) cherty limestone, (7) flinty slate, (8) massive flint, (9) talus; (10) clayey matter, (11) silicification, (12) pyrite, (13) bituminosity; (14–15) nodules: (14) carbonate, (15) siliceous; (16) erosion surface, (17) sample no.: (a) with radiolarians and (b) without radiolarians; (18–24) distribution of radiolarians over the section (specimen per g of matter): (18) absent, (19) individual (1–5 specimens), (20) rare (10–15 specimens), (21) often (20–40 specimens), (22) frequent (50–100 specimens), (23) very frequent (200–500 specimens), (24) extremely frequent (>1000 specimens).


Series
Stage
Substage, Formation
Assemblage, Subassemblage
Region
Radiolarians
Upper Devonian
Famennian
Lower
Upper
Lyaiol
Frasnian
Middle
Domanik
Lower
Ust'-Yarega
H. alekseevi–H. vilvaensis
Middle Urals
T. barysphaerai–C. spinifera
Polar Urals
T. barysphaera–R. magnifica
B. pittmani–R. kazintsovae
Moskovistella allbororum–Ceratoikiscum ukhtensis
Rdm-3
Rdm-2
Rdm-1
P. punctus–A. biaciculata
Timan-Pechora Basin
7
4
3
10
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7
6
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3
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9
8
5
2
1
Nassellaria
Stauraxonaria
Aculearia
Spumellaria
Sphaerellaria
0
5
10
15
20
25
30
35
40
Number of species

The assemblage is dominated by *Bientactinosphaera grandis* (Nazarov), *B. variacanthina* (Foreman), *B. symphypora* (Foreman), *Astroentactinia paronae* (Hinde), *A. biaciculata* Nazarov, *Spongentactinella veles* (Foreman), *Polyentactinia kossistekensis* Nazarov, *Palaeoscenidium cladophorum* Deflandre, *Ceratoikiscum delicatum* Cheng, *C. spinosum* Cheng, *C. planistellare* Foreman, *C. bujugum* Foreman, and *Palacantholithus stellatus* Deflandre.

The most typical members of the assemblage which are characteristic of the Middle Frasnian are probably *Moskovistella victorialis* Afanasieva, *M. khaini* Afanasieva, *Bientactinosphaera morozovi* Afanasieva, *Polyentactinia zhamoidai* Afanasieva, *Borisella bykovae* Afanasieva, *Ornatoentactinia solita* Afanasieva, and *Nazarovites bioculus* Afanasieva.

The correlation of this radiolarian assemblage with the standard zones of ammonoids (*Ponticeras domanicense–Nordiceras timanicum*) and conodonts (*punctata–early rhenana*) suggests that the assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis* belongs to the Middle Frasnian (Afanasieva, 2000a; Afanasieva and Mikhailova, 2001) (Table 8).

A detailed analysis of Middle Frasnian radiolarians of the Timan–Pechora Basin allowed the recognition within the assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis* of three radiolarian subassemblages (lower Rdm-1, middle Rdm-2, and upper Rdm-3), which differ quantitatively and qualitatively in radiolarian composition (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 2001) (Tables 6, 8).

Rdm-1 subassemblage. The biostratigraphic position of the Rdm-1 Subassemblage corresponds to the *Ponticeras domanicense* Ammonoid Zone and the lower part of the *Nordiceras timanicum* Zone as well as to the *punctata* Conodont Zone and the lower part of the *early hassi* Zone (Table 8). The subassemblage is characterized by a relatively low abundance (from 100 to 1000 specimens per 1 g of matter) and includes 70 species of 23 genera (Fig. 15; Tables 7, 10).

Spherical porous representatives of the class Sphaerellaria comprise 32 species of eight genera, with the prevalence of the genera *Bientactinosphaera* (eight species), *Astroentactinia* (six species), *Ornatoentactinia* (five species), and *Moskovistella* (four species) (Pl. 10, figs. 1–8).

Spherical spongy and latticed radiolarians of the class Spumellaria are represented by 13 species of eight genera, among which only *Haplentactinia* (four species) and *Polyentactinia* (two species) are distinguished (Pl. 10, figs. 9–11).

Spiny radiolarians of the class Aculearia are represented by 23 species of five genera, with the dominance of the genera *Ceratoikiscum* (ten species), *Palaeoscenidium* (six species), and *Nazarovites* (four species) (Pl. 10, figs. 12–18).

Discoidal radiolarians of the class Stauraxonaria are only represented by two species of two genera, *Palaeodiscaleksus punctus* (Hinde) and *Primaritripus patella* (Hinde) (Pl. 10, figs. 19–21).

Typical species of the Rdm-1 Subassemblage are *Helioentactinia gudymovae* Afanasieva and *Nazarovites aprelevkensis* Afanasieva, which occur mostly at the bottom of the Domanik section (Pl. 10, figs. 4, 18).

The most typical species determining the general appearance of the association are *Astroentactinia tantilla* Nazarov, *A. vishnevskayae* Afanasieva, *Ceratoikiscum avimexpectans* Deflandre, *Nazarovites mikhailovae* Afanasieva, and *Palaeoscenidium scaurum* Afanasieva (Pl. 10, figs. 1, 2, 12, 14, 17). At the same time, the following forms are also widespread: *Astroentactinia tikhomirovi* Afanasieva, *Bientactinosphaera morozovi* Afanasieva, *Entactinia bogdanovi* Afanasieva, *Radiobisphaera menneri* Afanasieva, *Tetragregnon quadrispinosa* (Foreman), *Ceratoikiscum spinosiarcuatum* Foreman, *C.?* cf. *vimenum* Nazarov et Ormiston, and *Palaeoscenidium tabernaculum* Aitchison (Pl. 10, figs. 3, 5, 7, 8, 11, 13, 15, 16).

In the Lower Domanik, individual *Bientactinosphaera conglobata* (Nazarov), *Polyentactinia kossistekensis* Nazarov, and *Russirad kazintsovae* Afanasieva occur (Pl. 10, figs. 6, 9, 10), which flourised in the Late Domanik and Early Frasnian.

Borisella mediforma (Won), *Haplentactinia labyrinthica* (Aitchison), *Helioentactinia gudymovae* Afanasieva, and *Magnentactinia fragilis* Won are confined to the Lower Domanik (Table 7).

Rdm-2 subassemblage. The biostratigraphic position of the Rdm-2 Subassemblage corresponds to the middle part of the *Nordiceras timanicum* Ammonoid Zone and to the upper part of the *early hassi* Conodont Zone and the *late hassi* Conodont Zone (Tables 6, 8) and shows a decrease in the abundance of radiolarians in deposits (from 20–40 to individual specimens per 1 g of matter) and extremely low species diversity, 23 species of 11 genera (Fig. 15; Tables 7, 10).

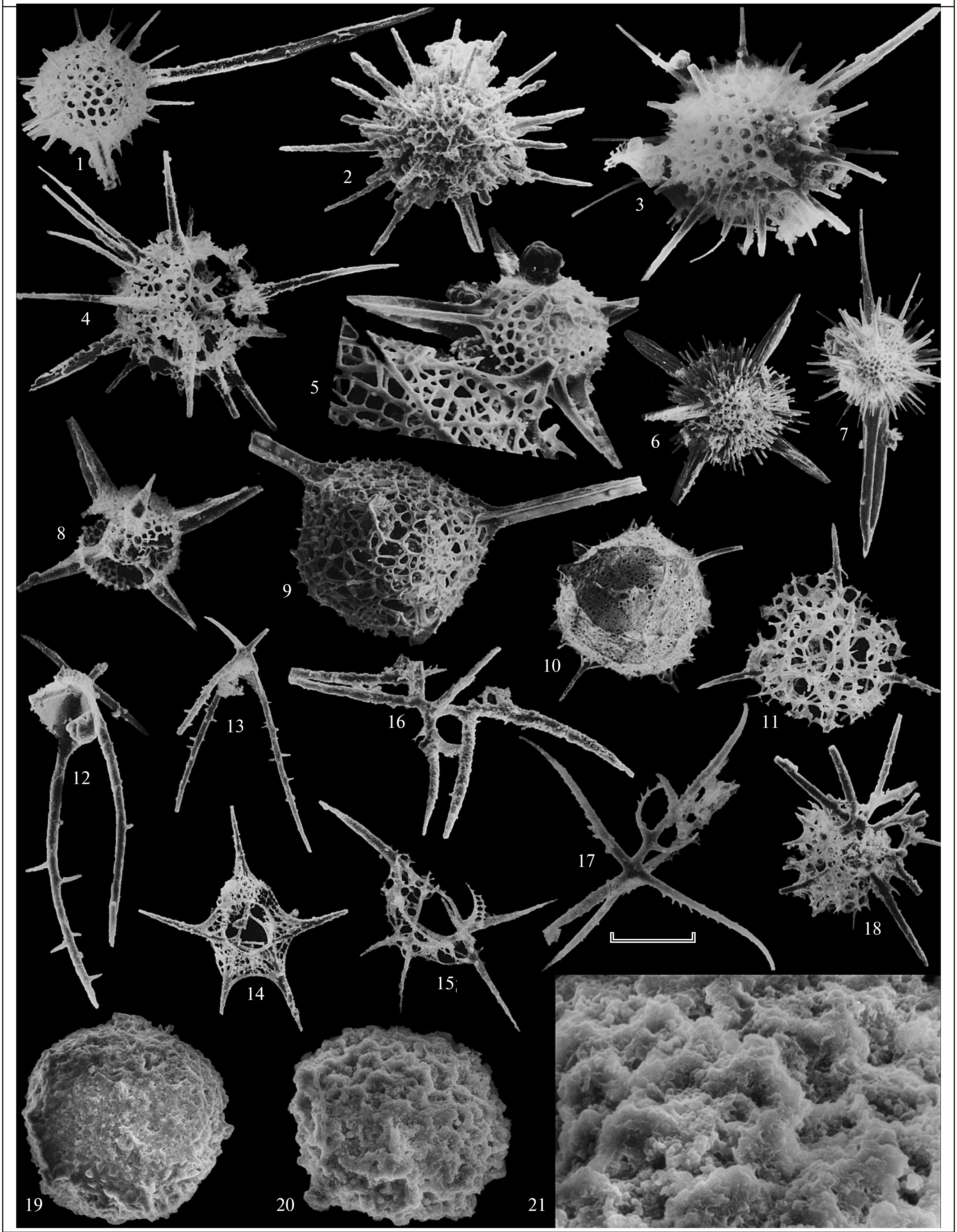
Spherical porous members of the class Sphaerellaria comprise 11 species of five genera, with the prevalence of the genera *Moskovistella* (five species) and *Bientactinosphaera* (three species) (Pl. 11, figs. 1–5).

Spherical latticed radiolarians of the class Spumellaria are only represented by one species, *Retientactinosphaera clavata* Afanasieva (Pl. 11, fig. 6) (Afanasieva, 2011).

Spiny radiolarians of the class Aculearia are represented by 11 species of five genera; five species belong to the genus *Ceratoikiscum*. Among spiny Aculearia,

Fig. 15. Radiolarians of the Upper Devonian of the Timan–Pechora Basin, Polar and Middle Urals: (1–2) Sphaerellaria: (1) family Entactiniidae and (2) family Astroentactiniidae; (3–6) Spumellaria: (ily Haplentactiniidae, (4) family Polyentactiniidae, (5) family Spongentactiniidae, and (6) family Spongopolyentactiniidae; (7, 8) Aculearia: (7) order Fasciculata, (8) order Triangulata; (9) Stauraxonaria: order Palaeodiscata; and (10) Nassellaria: order Pylomariata.

Plate 10



species of which prevail in number in each particular point of the section, it is impossible to recognize typical species of the assemblage. It is only possible to indicate several species which are most frequent in the Middle Domanik Beds, i.e., *Palacantholithus stellatus* Deflandre, *Circulaforma delicata* Cheng, *Ceratoikiscum stellatum* Aitchison, and *C. planistellare* Foreman (Pl. 11, figs. 7–10).

Typical radiolarian species of the Rdm-2 Subassemblage are *Moskovistella mira* Afanasieva, which occurs only in this subformation, and *Ceratoikiscum stellatum* Aitchison, known in the Middle Frasnian (Table 7; Pl. 11, figs. 3, 8).

Among radiolarians of the Rdm-2 Subassemblage, the species *Bientactinosphaera symphypora* (Foreman), *Entactinia bifida* Afanasieva, *Moskovistella octoradiata* Afanasieva, *M. sincera* Afanasieva, and *Retientactinosphaera clavata* Afanasieva (Pl. 11, figs. 1, 2, 4–6) appear for the first time.

Rdm-3 Subassemblage. The biostratigraphic position of the Rdm-3 Subassemblage corresponds to the upper part of the *Nordiceras timanicum* Ammonoid Zone and *jamieae* Conodont Zone and bottom of the *rhenana* Conodont Zone (Table 8). The Rdm-3 Subassemblage displays a sharp increase in the total aboundance of radiolarians (more than 1000 specimens per 1 g of matter) and very high species diversity, 124 species of 31 genera (Fig. 15; Tables 7, 10).

Spherical porous radiolarians of the class Sphaerellaria (Pl. 12) distinctly dominate the Late Domanik Assemblage, comprising 62 species of nine genera, the most important of which are *Bientactinosphaera* (16 species) and *Moskovistella* (11 species). In addition, a significant role is played by the genera *Entactinia* (eight species), *Astroentactinia* (seven species), *Borisella* (six species), and *Ornatoentactinia* (six species).

Species diversity of spherical spongy and latticed radiolarians of the class Spumellaria (Pl. 13, figs. 1–7) is somewhat lower, 27 species of 12 genera, including the most diverse genera *Polyentactinia* (seven species), *Haplentactinia* (six species), and *Spongentactinella* (four species).

Spiny radiolarians of the class Aculearia are represented by 33 species of eight genera, with the most diverse genera *Ceratoikiscum* (14 species) and *Palaeoscenidium* (six species) (Pl. 13, figs. 9–19).

Discoidal radiolarians of the class Stauraxonaria include members of only two species of two genera: *Primaritripus patella* (Hinde) and *Palaeodiscaleksus punctus* (Hinde) (Pl. 13, fig. 8).

Typical species of the Rdm-3 Subassemblage are *Moskovistella allbororum* Afanasieva, *M. khaini* Afanasieva, *Radiobisphaera menneri* Afanasieva (Pl. 12, figs. 3, 4, 17), and species that appear for the first time at the end of the Domanik Time: *Astroentactinia rusaevi* Afanasieva, *Borisella mariae* Afanasieva, *Bientactinosphaera guangxiensis* (Li et Wang), *Entactinia micula* Foreman (Pl. 12, figs. 1, 9, 11, 15), *Palaeothalomnus timokhini* Afanasieva, and *P. arrhinia* (Foreman) (Pl. 13, figs. 17, 19).

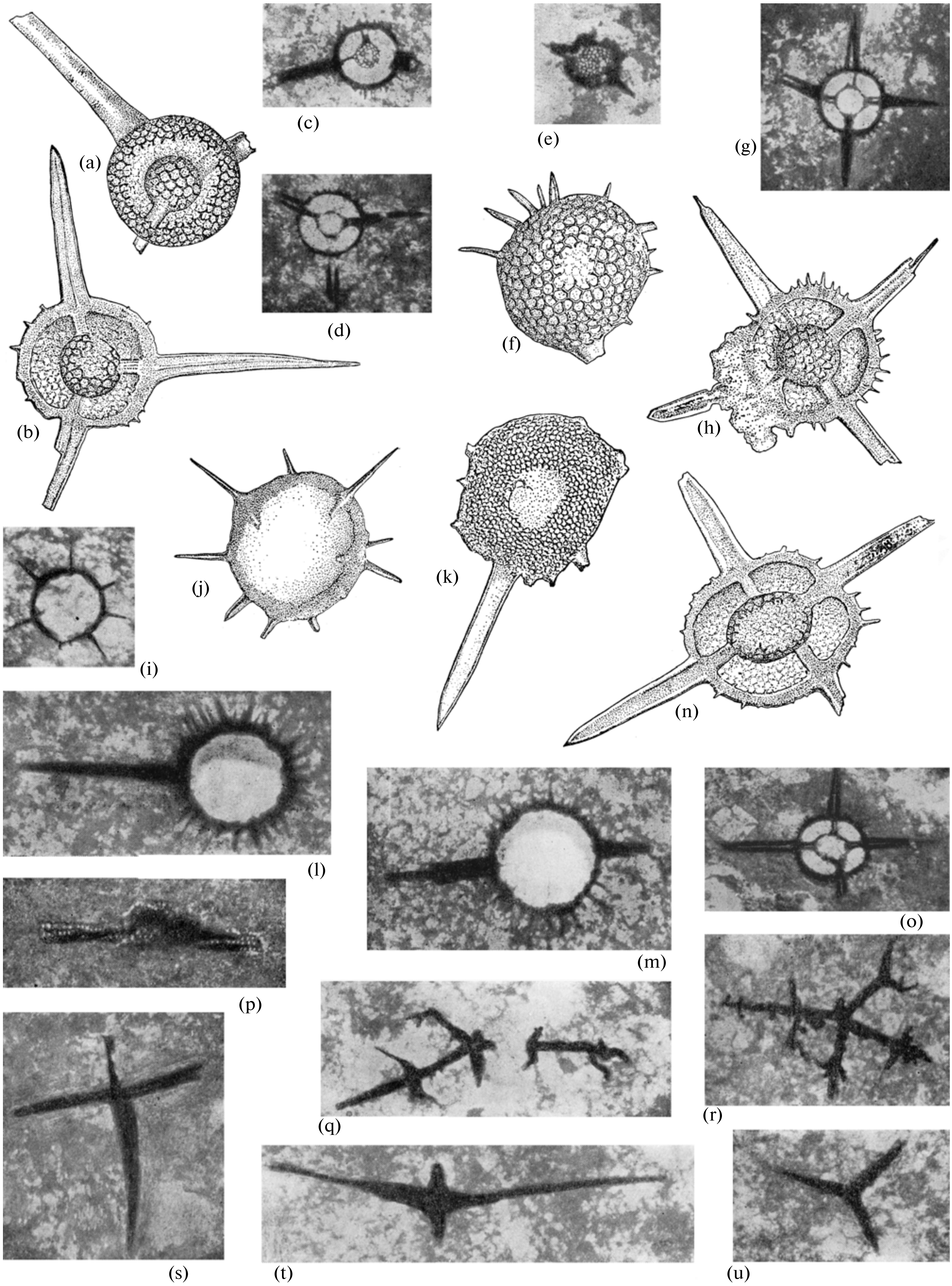
Predominant distribution in these beds is shown by the spherical radiolarians *Bientactinosphaera miletenkoi* Afanasieva, *Borisella bykovae* Afanasieva, *B. maksimovae* Afanasieva, *Moskovistella rozanovi* Afanasieva, *M. victorialis* Afanasieva, *Ornatoentactinia*

Explanation of Plate 10

Middle Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis*, Rdm-1 Subassemblage: spherical porous Sphaerellaria (1–8), latticed (9, 10) and spongy (11) Spumellaria, spiny Aculearia (12–18) and discoidal Stauraxonaria (19–21).

Fig. 1. *Astroentactinia vishnevskayae* Afanasieva, 2000, specimen PIN, no. 5311/04134; scale bar, 59 μm.
Fig. 2. *Astroentactinia tantilla* Nazarov, 1975, specimen PIN, no. 5311/11901; scale bar, 63 μm.
Fig. 3. *Astroentactinia tikhomirovi* Afanasieva, 2000, specimen PIN, no. 5311/04108; scale bar, 56 μm.
Fig. 4. *Helioentactinia gudymovae* Afanasieva, 2000, specimen PIN, no. 5311/10507; scale bar, 43 μm.
Fig. 5. *Entactinia bogdanovi* Afanasieva, 2000, specimen PIN, no. 5311/04419; scale bar, 33 μm.
Fig. 6. *Bientactinosphaera conglobata* (Nazarov, 1975), specimen PIN, no. 5311/04404; scale bar, 125 μm.
Fig. 7. *Radiobisphaera menneri* Afanasieva, 2000, specimen PIN, no. 5311/04010; scale bar, 89 μm.
Fig. 8. *Bientactinosphaera morozovi* Afanasieva, 2000, specimen PIN, no. 5311/04122; scale bar, 43 μm.
Fig. 9. *Russirad kazintsovae* Afanasieva, 2000, specimen PIN, no. 5311/04524; scale bar, 68 μm.
Fig. 10. *Polyentactinia kossistekensis* Nazarov, 1975, specimen PIN, no. 5311/04003; scale bar, 89 μm.
Fig. 11. *Tetragregnon quadrispinosa* (Foreman, 1963), specimen PIN, no. 5311/04202; scale bar, 43 μm.
Fig. 12. *Palaeoscenidium scaurum* Afanasieva, 2000, specimen PIN, no. 5311/04304; scale bar, 43 μm.
Fig. 13. *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 5311/04027; scale bar, 89 μm.
Fig. 14. *Ceratoikiscum avimexpectans* Deflandre, 1953, specimen PIN, no. 5311/04021; scale bar, 89 μm.
Fig. 15. *Ceratoikiscum spinosiarcuatum* Foreman, 1963, specimen PIN, no. 5311/04031; scale bar, 43 μm.
Fig. 16. *Ceratoikiscum?* cf. *vimenum* Nazarov et Ormiston, 1983, specimen PIN, no. 5311/04303; scale bar, 43 μm.
Fig. 17. *Nazarovites mikhailovae* Afanasieva, 2000, specimen PIN, no. 5311/10306; scale bar, 43 μm.
Fig. 18. *Nazarovites aprelevkensis* Afanasieva, 2000, specimen PIN, no. 5311/04411; scale bar, 59 μm.
Fig. 19. *Palaeodiscaleksus punctus* (Hinde, 1899): specimen PIN, no. 5311/12334; scale bar, 68 μm.
Figs. 20 and 21. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5311/12330: (20) scale bar, 42 μm; (21) fragment, scale bar, 12 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin, borehole Shuda-Yag-1003: (1, 3, 7, 8, 10, 13, 14, 16, 17) sample 8 (120.9–124.0 m of depth); (2, 4, 11, 12, 15) sample 28 (106–107 m of depth); (5, 6, 9, 18) sample 29 (105–106 m of depth); (19–21) Chut River, outcrop 7, sample 4.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solita Afanasieva, (Pl. 12, figs. 5–8, 10, 13), *Retientactinosphaera clavata* Afanasieva, *Haplentactinia alekseevi* Afanasieva, *H. barskovi* Afanasieva, *Polyentactinia zhamoidai* Afanasieva, and *Spongentactinella olafi* Afanasieva (Pl. 13, figs. 1, 3–7); spiny taxa are dominated by *Ceratoikiscum ukhtensis* Afanasieva, *C. araneosum* Afanasieva, *Nazarovites bioculus* Afanasieva, *N. pinnula* Afanasieva, and *Palaeoscenidium tabernaculum* Aitchison (Pl. 13, figs. 9–11, 13, 16).

Typical species of the upper part of the Domanik section are radiolarians that were recorded for the first time in the Middle Devonian and flourished at the end of the Domanik Time: *Radiobisphaera assidera* (Nazarov), *Ornatoentactinia spartaci* Afanasieva (Pl. 12, figs. 12, 18), and *Spongentactinella windjanensis* Nazarov (Pl. 13, fig. 2).

The first occurrence in the Late Domanik and subsequent wide distribution is characteristic of radiolarians which flourished in the Late Frasnian–Famennian, i.e., *Astroentactinia paronae* (Hinde), *Entactinia paula* Foreman (Pl. 12, figs. 2, 14), *Ceratoikiscum incomptum* Nazarov, *C. goodbodyi* Cheng, *C. simplum* Cheng, and *Palaeothalomnus quadriramosum* (Foreman) (Pl. 13, figs. 12, 14, 15, 18).

In the Domanik Time, the last occurrence of the species *Ceratoikiscum?* cf. *vimenum* Nazarov et Ormiston (Pl. 10, fig. 16) is recorded; it appeared for the first time in the Lower Frasnian of the Gogo Formation (Nazarov and Ormiston, 1983b).

Middle Frasnian assemblage with Primaritripus chuvashovi. On the southern slope of Argagan Mountain of the Southern Urals in Bashkiria (near the village of Sultantemirovo, south of the town of Baimak), in gray layered cherts of the Mukasovian Regional Substage, we established a new Middle Frasnian radiolarian locality (Fig. 1, X). The Middle Frasnian age of its beds is revealed based on the presence of imprints of the conodont *Palmatolepis punctata* (Hinde) (Maslov and Artyushkova, 2002).

The Middle Frasnian radiolarian assemblage of the Southern Urals is represented by 14 species of eight genera (Table 2).

Spherical porous radiolarians of the class Sphaerellaria comprise five species of four genera (Pl. 14, figs. 1–5): *Astroentactinia tenuis* (Furutani), *Bientactinosphaera pittmani* (Hinde), *B. vetusta* (Hinde), *Radiobisphaera domanicensis* (Bykova), and *Radiobisphaera rozanovi* Afanasieva et Amon.

Spiny radiolarians of the class Aculearia are represented by the species *Palacantholithus stellatus* Deflandre (Pl. 14, fig. 6).

Discoidal radiolarians of the class Stauraxonaria are represented by eight species of three genera: *Palaeodiscaleksus cribrarius* (Hinde), *P. punctus* (Hinde), *P. tumefactus* Afanasieva et Amon, *Primaritripus patella* (Hinde), *P. buribayensis* Afanasieva et Amon, *P. chuvashovi* Afanasieva et Amon, *P. kariukmasensis* Afanasieva et Amon, and *Trochodiscus planatus* Hinde (Pl. 14, figs. 7–19).

The Middle Frasnian radiolarian assemblage is still dominated by discoidal radiolarians (about 70% of the total number of individuals); this was characteristic of shallow water areas of the eastern Russian Platform in the Early and Middle Devonian of the Southern Urals (Afanasieva and Amon, 2008b, 2009a) and shallow marine conditions in the Early Frasnian of the Timan–Pechora Basin (Afanasieva, 2000a).

We regard the Middle Frasnian radiolarian association according to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006) as a characteristic assemblage of a new biostraton, beds with *Primaritripus chuvashovi* (Table 6), which corresponds to the lower part of the Middle Frasnian, the *punctata* Conodont Zone.

The new Late Devonian Middle Frasnian biostraton of radiolarians (Table 6) occurs and is valid within the Southern Urals and Northern Mugodzhary and corresponds in stratigraphic position to the lower part of the Rdm-1 Subassemblage of the *Moskovistella allbororum–Ceratoikiscum ukhtensis* radiolarian assemblage of the Timan–Pechora Basin (Afanasieva and Amon, 2009a).

Middle–Late Frasnian assemblage with Polyentactinia circumretia–Bientactinosphaera egindyensis. Radiolarians of the Middle–Late Frasnian assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis* was established for the first time, investigated, and described by Nazarov (1973, 1975, 1988) in

←

Fig. 16. The first radiolarians from the Domanik Formation of the Middle Frasnian of the Volga–Ural Basin, described by E.V. Bykova (1955): (a–d) *Bientactinosphaera* cf. *variacanthina* (Foreman, 1963), with distinct meshed internal spherical shell: (a, b) reconstruction, ×330: (a) Bykova, 1955, pl. XX, fig. 1; (b) pl. XXI, fig. 2; (c, d) skeleton section, ×100: (c) pl. XXII, fig. 3; (d) pl. XXII, fig. 2; (e, f) *Astroentactinia* cf. *crassata* Nazarov, 1975, meshed external surface of the skeleton is seen: (e) skeleton section, ×100, pl. XXII, fig. 7; (f) reconstruction, ×330, pl. XX, fig. 3; (g, h) *Bientactinosphaera* cf. *grandis* (Nazarov, 1975): (g) skeleton section, with cavities inside spines, ×100, pl. XXII, fig. 1; (h) reconstruction, with meshed internal spherical shell, ×330, pl. XX, fig. 4; (i, j) *Astroentactinia* cf. *stellata* Nazarov, 1975: (i) skeleton section, ×100, pl. XXIII, fig. 2; (j) reconstruction, ×330, pl. XXI, fig. 1; (k) *Radiobisphaera domanicensis* (Bykova, 1955), reconstruction, ×330, pl. XX, fig. 2; (l, m) *Radiobisphaera* cf. *menneri* Afanasieva, skeleton section, ×100: (l) pl. XXII, fig. 5; (m) pl. XXII, fig. 4; (n, o) *Staurodruppa nucula* Hinde, 1899: (n) reconstruction, with internal and outer shells in section, ×330, pl. XXI, fig. 3, (o) skeleton section, ×100, pl. XXII, fig. 6; (p) *Gedauia* (?) sp., skeleton section, ×100, pl. XXIII, fig. 8; (q, r) *Palaeothalomnus* cf. *quadriramosum* (Foreman, 1963), skeleton section, ×100: (q) pl. XXIII, fig. 6; (r) pl. XXIII, fig. 7; (s, t) *Palacantholithus* ex gr. *simplex* (Hinde, 1899), skeleton section, ×100: (s) pl. XXIII, fig. 3; (t) pl. XXIII, fig. 4; (u) *Palacantholithus nana* (Bykova, 1955), skeleton section, ×100, pl. XXIII, fig. 5. Radiolarian localities: (a–h, k, n–p, s) Tatarstan: (a, c, d, h, k, p, s) village of Kamskoe Ust'e, (b, e, f, n, o) village of Krasnovka; (i, j) western Bashkortostan, village of Sterlibashevo; (l, m, q, r, t, u) Samara Region, village of Radaevka.

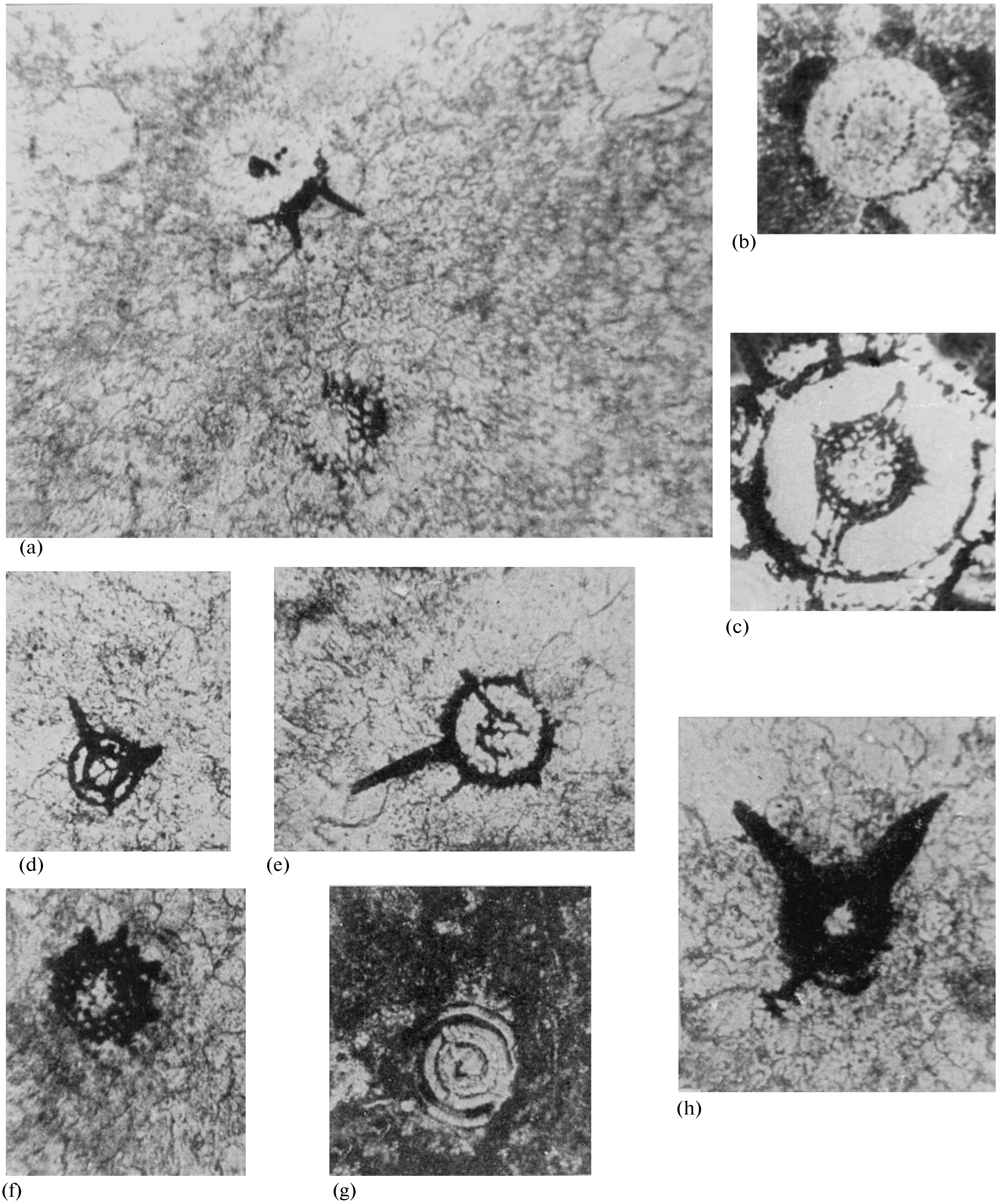


Fig. 17. The first radiolarians from the Domanik Formation of the Middle Frasnian of the Timan–Pechora Basin: (a–h) photographs of thin sections with radiolarians (after Maksimova, 1970, pl. 5, ×160), Ukhtinskii District of the Timan–Pechora Basin: (a) *Astroentactinia* cf. *crassata* Nazarov, 1975, *A.* cf. *biaciculata* Nazarov, 1975, *Bientactinosphaera* spp.; (b) *Helioentactinia* cf. *polyacanthina* (Foreman, 1963); (c, d) *Bientactinosphaera* cf. *grandis* (Nazarov, 1975); (e) *Radiobisphaera* cf. *domanicensis* (Bykova, 1955); (f) *Astroentactinia* cf. *biaciculata* Nazarov, 1975; (g) *Bientactinosphaera* spp.; and (h) *Entactinia* cf. *patorovaria* Afanasieva, 2000.

the stratotypic section of the Egindy Formation on the Aitpaika Creek (Fig. 1, XIV) in the southern marginal area of the Sakmara Zone of the Southern Urals and Northern Mugodzhary (Fig. 3; Table 6). According to the data of Nazarov (1975, 1988), the Middle–Late Frasnian radiolarian assemblage includes members of more than 50 species of 15 genera (Pls. 15, 16).

The assemblage is characterized by the prevalence of spherical porous Sphaerellaria; it is dominated by the genera *Bientactinosphaera* (three species) (Pl. 15, figs. 1–4; Pl. 16, figs. 11–13), with two shells and three-bladed spines, and *Astroentactinia* (five species) (Pl. 16, figs. 1–8), with one shell and conical and three-bladed spines.

Spherical spongy radiolarians of the class Spumellaria are only represented by the genus *Spongentactinia*, with short three-bladed spines (Pl. 16, figs. 9, 10).

Latticed and reticulate members of the class Spumellaria are more abundant and diverse, with the most prominent genera *Haplentactinia, Retentactinia,* and *Polyentactinia* (Pl. 15, figs. 5, 6, 9–14).

Among spiny radiolarians of the class Aculearia, the first typical Ceratoikiscidae appeared (Pl. 15, figs. 7, 8).

Typical species of the assemblage are *Polyentactinia circumretia* Nazarov et Ormiston, *P. kossistekensis* Nazarov, *Astroentactinia stellata* Nazarov, *A. crassata* Nazarov, *A. paronae* (Hinde), *Bientactinosphaera aitpaiensis* (Nazarov), *B. egindyensis* (Nazarov), *B. grandis* (Nazarov), and *Ceratoikiscum rectum* Nazarov.

The lower boundary of the radiolarian assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis*, in opinion of Nazarov (1988), is established tentatively, marked by the occurrence of *Bientactinosphaera egindyensis* (Nazarov), *B. aitpaiensis* (Nazarov), *Polyentactinia kossistekensis* Nazarov, *P. circumretia* Nazarov et Ormiston, and *Astroentactinia stellata* Nazarov.

The age of this assemblage in deposits of the Sakmara Zone of the Southern Urals and Northern Mugodzhary is within the Middle–Late Frasnian in the combined Domanik and Mendym formations on the Ural Scale and, probably, with addition of the bottom of the Askyn Formation. At present, this is the limit of accuracy in the determination of the stratigraphical position of the assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis* in the Southern Urals and Northern Mugodzhary; and it is impossible now to date it more precisely.

Late Frasnian

At the beginning of the Late Frasnian, after a break in sedimentation, a new transgression from the east began. At that time, in the western Moscow Syneclise, general outline of a lagoon was formed, which was periodically salinated and continued to the end of the Devonian Time. Connection with the Baltic Syneclise was finally broken; a lagoon with increased salinity was formed there. At the end of the Late Frasnian Age, there was general regression of the sea. At the end of the Frasnian, a in the sea level significantly decreased and the platform was almost completely dried (Tikhii, 1975) (Fig. 18a).

Late Frasnian radiolarians were investigated by Nazarov (1988) in a section on the Unya River in the Evtropiny Noski locality on the western slope of the Northern Urals (Figs. 3; 6b, II). Radiolarians were found in a 60-m-thick member of siliceous–clayey shales and siltstones with limestone interbeds, which are referred based on conodonts to the upper part of the Frasnian Stage, the *Palmatolepis gigas* Zone (which is correlated with the *rhenana–linguiformis* zones) (Puchkov, 1979a, 1979b; Nazarov, 1988). The radiolarian assemblage includes *Moskovistella allbororum* Afanasieva (*Entactinia additiva?* according to Nazarov, 1988), *Entactinia* cf. *dissora* Nazarov, *Bientactinosphaera* cf. *grandis* (Nazarov), *B.* aff. *cancellicula* (Foreman), *Polyentactinia* sp., and *Astroentactinia* sp.

In a section of the Egindy Formation on the Aitpaika Creek (Fig. 1, XIV), in the Sakmara Zone of the Southern Urals and Northern Mugodzhary, Nazarov (1975, 1988) established for the first time and described a radiolarian assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis*, which occurs in the Middle and Upper Frasnian (Fig. 3; Table 6).

On the eastern slope of the Middle Urals (Fig. 3), in the Rezh Structural–Facies Zone (Fig. 1, III, IV), Amon and Korovko (1992; Amon, 1995a; Korovko et al., 1999) found Late Frasnian radiolarians.

Frasnian radiolarians were recorded in thin sections from organogenic–detrital beds of the northern marginal area of the Caspian Depression (Figs. 3, 12a, 12b, 18a). Frasnian radiolarians of the incipient Karachaganak bioherm display a more diverse assemblage than in the Givetian Age, including six species of five genera. The radiolarian assemblage includes four species of three genera of spherical porous Sphaerellaria: *Astroentactinia biaciculata* Nazarov, *Bientactinosphaera variacanthina* (Foreman), *Entactinia* cf. *micula* Foreman, and *Entactinia* sp. and two species of two genera of spherical spongy Spumellaria, *Polyentactinia* sp. and *Spongentactinella veles* (Foreman) (Afanasieva, 1987, 2000a).

Late Frasnian radiolarians are known in the southern Timan–Pechora Basin (Afanasieva, 2000a) (Figs. 3, 6c).

Bykova (1955) indicated that the diverse “Ural” Radiolarian Assemblage was most widespread in the Late Frasnian of the Volga–Ural Basin of the Northern and Southern Urals (Figs. 11, 19).

Late Frasnian assemblage with Bientactinosphaera pittmani–Russirad kazintsovae. Upper Frasnian radiolarians were recorded for the first time by Afanasieva (2000a) in the southern Timan–Pechora Basin (Figs. 3, 6c, 14), in the Lyaiol Formation, which directly overlies the Domanik Formation of the Middle Frasnian. Shallow-water deposits of the Sedyu

Table 10. Distribution of radiolarians in the Middle Frasnian Domanik Formation of borehole Shuda-Yag-1003 of the Timan–Pechora Basin (after Afanasieva, 2000a)

Borehole Shuda-Yag-1003, depth in meters	120.9–124.0	106.0–107.0	105.0–106.0	104.1–104.6	98.0–99.0	81.6–83.0	75.0–77.3		73.5–74.0	73.3–73.5		73.0–73.3	71.9–72.4	71.4–71.9	68.9–69.3
Radiolarians per gram of rock	≥500	50–100	≥200	20–40	10–15	≥200	20–40	1–5	≥200	1–5	>1000	20–40	>1000	>1000	>1000
Paleoclimatic coefficient	1.17	1	3.25	0.57	0.67	1	0.67	1	0.8	0.5	1.19	1.57	2.86	2	2.25
Species diversity of spherical (S)/spiny (A) radiolarians D_3fr_2: 77/32	21/18	14/14	26/8	4/7	2/3	7/7	2/3	2/2	4/5	1/2	19/16	11/7	40/14	32/16	27/12
	Rdm-1: 42/23			Rdm-2: 12/10							Rdm-3: 73/30				
Ceratoikiscum spinosiarcuatum Foreman, 1963	▨														
Borisella mediforma (Won, 1997)	▨	▨													
Helioentactinia gudymovae Afanasieva, 2000	▨	▨													
Palaeoscenidium phalangium Aitchison, 1993	▨										▨				
Nazarovites mikhailovae Afanasieva, 2000	▨	▨										▨			
Borisella bykovae Afanasieva, 2000	▨	▨											▨		
Ceratoikiscum avimexpectans Deflandre, 1953	▨										▨		▨		
Ceratoikiscum goodbodyi Cheng, 1986	▨										▨		▨		
Polyentactinia zhamoidai Afanasieva, 2000	▨		▨								▨		▨		
Moskovistella rozanovi Afanasieva, 2000	▨												▨	▨	
Somphoentactinia gavrilovi Afanasieva, 2000	▨												▨	▨	
Palaeoscenidium delicatum Aitchison, 1993	▨													▨	
Astroentactinia vishnevskayae Afanasieva, 2000	▨	▨												▨	
Astroentactinia tikhomirovi Afanasieva, 2000	▨	▨												▨	
Ceratoikiscum delicatum Cheng, 1986	▨	▨	▨								▨		▨	▨	
Polyentactinia kossistekensis Nazarov, 1975	▨		▨								▨	▨	▨	▨	
Palaeoscenidium tabernaculum Aitchison, 1993	▨										▨		▨	▨	▨
Bientactinosphaera variacanthina (Foreman, 1963)	▨		▨								▨		▨	▨	▨
Ceratoikiscum spinosum Cheng, 1986	▨	▨									▨	▨	▨	▨	▨
Ornatoentactinia solita Afanasieva, 2000	▨		▨									▨		▨	▨
Spongentactinella veles (Foreman, 1963)	▨												▨		▨
Astroentactinia crassata Nazarov, 1975	▨		▨										▨	▨	▨
Spongentactinella olafi Afanasieva, 2000	▨		▨										▨	▨	▨
Astroentactinia paronae (Hinde, 1899)	▨	▨	▨										▨	▨	▨
Haplentactinia alekseevi Afanasieva, 2000	▨	▨												▨	▨
Russirad kazintsovae Afanasieva, 2000	▨		▨												▨
Palaeoscenidium scaurum Afanasieva, 2000	▨	▨	▨												▨
Ceratoikiscum planistellare Foreman, 1963	▨			▨					▨		▨			▨	
Radiobisphaera menneri Afanasieva, 2000	▨			▨			▨		▨		▨		▨	▨	
Ceratoikiscum stellatum Aitchison, 1993	▨	▨	▨	▨		▨			▨				▨	▨	
Palaeoscenidium robustum Aitchison, 1993	▨					▨							▨	▨	▨
Bientactinosphaera morozovi Afanasieva, 2000	▨					▨		▨				▨	▨	▨	▨
Moskovistella khaini Afanasieva, 2000	▨					▨					▨		▨	▨	▨
Nazarovites pinnula Afanasieva, 2000	▨	▨				▨	▨	▨			▨	▨		▨	▨
Bientactinosphaera grandis (Nazarov, 1975)	▨		▨		▨	▨			▨	▨			▨	▨	▨
Ceratoikiscum ukhtensis Afanasieva, 2000	▨	▨	▨			▨					▨	▨	▨		▨

Table 10. (Contd.)

Borehole Shuda-Yag-1003, depth in meters	120.9–124.0	106.0–107.0	105.0–106.0	104.1–104.6	98.0–99.0	81.6–83.0	75.0–77.3		73.5–74.0	73.3–73.5		73.0–73.3	71.9–72.4	71.4–71.9	68.9–69.3
Radiolarians per gram of rock	≥500	50–100	≥200	20–40	10–15	≥200	20–40	1–5	≥200	1–5	>1000	20–40	>1000	>1000	>1000
Paleoclimatic coefficient	1.17	1	3.25	0.57	0.67	1	0.67	1	0.8	0.5	1.19	1.57	2.86	2	2.25
Species diversity of spherical (S)/spiny (A) radiolarians D_3fr_2: 77/32	21/18	14/14	26/8	4/7	2/3	7/7	2/3	2/2	4/5	1/2	19/16	11/7	40/14	32/16	27/12
	Rdm-1: 42/23			Rdm-2: 12/10							Rdm-3: 73/30				
Nazarovites bioculus Afanasieva, 2000	▨	▨	▨	▨							▨		▨	▨	▨
Palaeoscenidium cladophorum Deflandre, 1953	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨
Palacantholithus stellatus Deflandre, 1953	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨
Astroentactinia tantilla Nazarov, 1975		▨													
Ceratoikiscum? cf. *vimenum* Nazarov, Ormiston, 1983		▨													
Entactinia patorovaria Afanasieva, 2000		▨										▨			
Ceratoikiscum robustum Aitchison, 1993		▨											▨		
Tetragregnon quadrispinosa (Foreman, 1963)		▨												▨	
Borisella maksimovae Afanasieva, 2000		▨											▨	▨	▨
Palacantholithus curvativus Afanasieva, 2000		▨													▨
Ornatoentactinia agarkovi Afanasieva, 2000		▨	▨								▨				
Bientactinosphaera australis (Aitchison, 1993)		▨	▨										▨		
Moskovistella victorialis Afanasieva, 2000		▨	▨										▨		▨
Circulaforma delicata Cheng, 1986		▨		▨	▨	▨					▨	▨	▨		▨
Nazarovites aprelevkensis Afanasieva, 2000			▨								▨				
Retisphaera exquisita (Aitchison, 1993)			▨								▨				
Bientactinosphaera maslakovae Afanasieva, 2000			▨									▨			
Bientactinosphaera conglobata (Nazarov, 1975)			▨									▨	▨		
Haplentactinia bornazi Afanasieva, 2000			▨										▨		
Ornatoentactinia spartaci Afanasieva, 2000			▨										▨	▨	
Radiobisphaera assidera (Nazarov, 1975)			▨										▨	▨	
Ornatoentactinia beljaevorum Afanasieva, 2000			▨										▨	▨	
Ornatoentactinia spinisica Afanasieva, 2000			▨											▨	
Bientactinosphaera pinica Afanasieva, 2000			▨									▨	▨	▨	▨
Bientactinosphaera hystricosa (Foreman, 1963)			▨										▨		▨
Haplentactinia barskovi Afanasieva, 2000			▨										▨		▨
Entactinia bogdanovi Afanasieva, 2000			▨												▨
Moskovistella allbororum Afanasieva, 2000			▨	▨					▨		▨		▨		▨
Astroentactinia biaciculata Nazarov, 1975			▨		▨	▨	▨					▨		▨	▨
Moskovistella octoradiata Afanasieva, 2000				▨							▨				
Entactinia bifida Afanasieva, 2000				▨									▨		
Ceratoikiscum incomptum Nazarov, 1975				▨		▨			▨					▨	
Retientactinosphaera clavata Afanasieva, 2011						▨							▨	▨	
Moskovistella sincera Afanasieva, 2000						▨							▨		
Bientactinosphaera symphypora (Foreman, 1963)						▨								▨	
Moskovistella mira Afanasieva, 2000								▨	▨						

Table 10. (Contd.)

Borehole Shuda-Yag-1003, depth in meters	120.9–124.0	106.0–107.0	105.0–106.0	104.1–104.6	98.0–99.0	81.6–83.0	75.0–77.3		73.5–74.0	73.3–73.5		73.0–73.3	71.9–72.4	71.4–71.9	68.9–69.3
Radiolarians per gram of rock	≥500	50–100	≥200	20–40	10–15	≥200	20–40	1–5	≥200	1–5	>1000	20–40	>1000	>1000	>1000
Paleoclimatic coefficient	1.17	1	3.25	0.57	0.67	1	0.67	1	0.8	0.5	1.19	1.57	2.86	2	2.25
Species diversity of spherical (S)/spiny (A) radiolarians D_3fr_2: 77/32	21/18	14/14	26/8	4/7	2/3	7/7	2/3	2/2	4/5	1/2	19/16	11/7	40/14	32/16	27/12
	Rdm-1: 42/23			Rdm-2: 12/10							Rdm-3: 73/30				
Helioentactinia polyacanthina (Foreman, 1963)											■				
Helioentactinia perjucunda Nazarov et Ormiston, 1983											■				
Haplentactinia aperticuva (Aitchison, 1993)											■				
Borisella pantosompha (Foreman, 1963)											■				
Entactinia crustescens Foreman, 1963											■		■		
Borisella mariae Afanasieva, 2000											■		■		
Ornatoentactinia klevtsovae Afanasieva, 2000											■			■	
Ceratoikiscum simplum Cheng, 1986											■			■	
Palaeothalomnus arrhinia (Foreman, 1963)											■				■
Astroentactinia rusaevi Afanasieva, 2000											■				■
Bientactinosphaera miletenkoi Afanasieva, 2000											■	■	■	■	
Polyentactinia craticulata Foreman, 1963												■			
Ceratoikiscum bujugum Foreman, 1963												■		■	
Entactinia micula Foreman, 1963												■	■	■	■
Bientactinosphaera cancellicula (Foreman, 1963)													■		■
Apophysisphaera profundisculus (Aitchison, 1993)													■		
Helioentactinia aster Aitchison, 1993													■		
Moskovistella baccata Afanasieva, 2000													■		
Cancellosphaera varia (Won, 1997)													■		
Borisella primitiva Afanasieva, 2000													■		
Spongentactinella windjanensis Nazarov, 1982													■		
Bissylentactinia? cf. *rudicula* Nazarov, 1975													■		
Bientactinosphaera inusitata (Foreman, 1963)													■	■	
Meschedea crassicortex Won, 1997														■	
Moskovistella lucet Afanasieva, 2000														■	
Ceratoikiscum araneosum Afanasieva, 2000														■	
Retentactinia kelleri Afanasieva, 2000														■	
Palaeothalomnus timokhini Afanasieva, 2000														■	
Palaeothalomnus quadriramosum (Foreman, 1963)														■	
Entactinia paula Foreman, 1963														■	
Entactinia diversita Nazarov, 1973														■	■
Bientactinosphaera guangxiensis (Li et Wang, 1991)															■
Haplentactinia kuzminae Afanasieva et Amon, sp. nov.															■
Moskovistella additiva (Foreman, 1963)															■
Palhindeolithus ambiguus Deflandre, 1973															■
Radiobisphaera domanicensis (Bykova, 1955)															■
Retentactinia longa Won, 1997															■

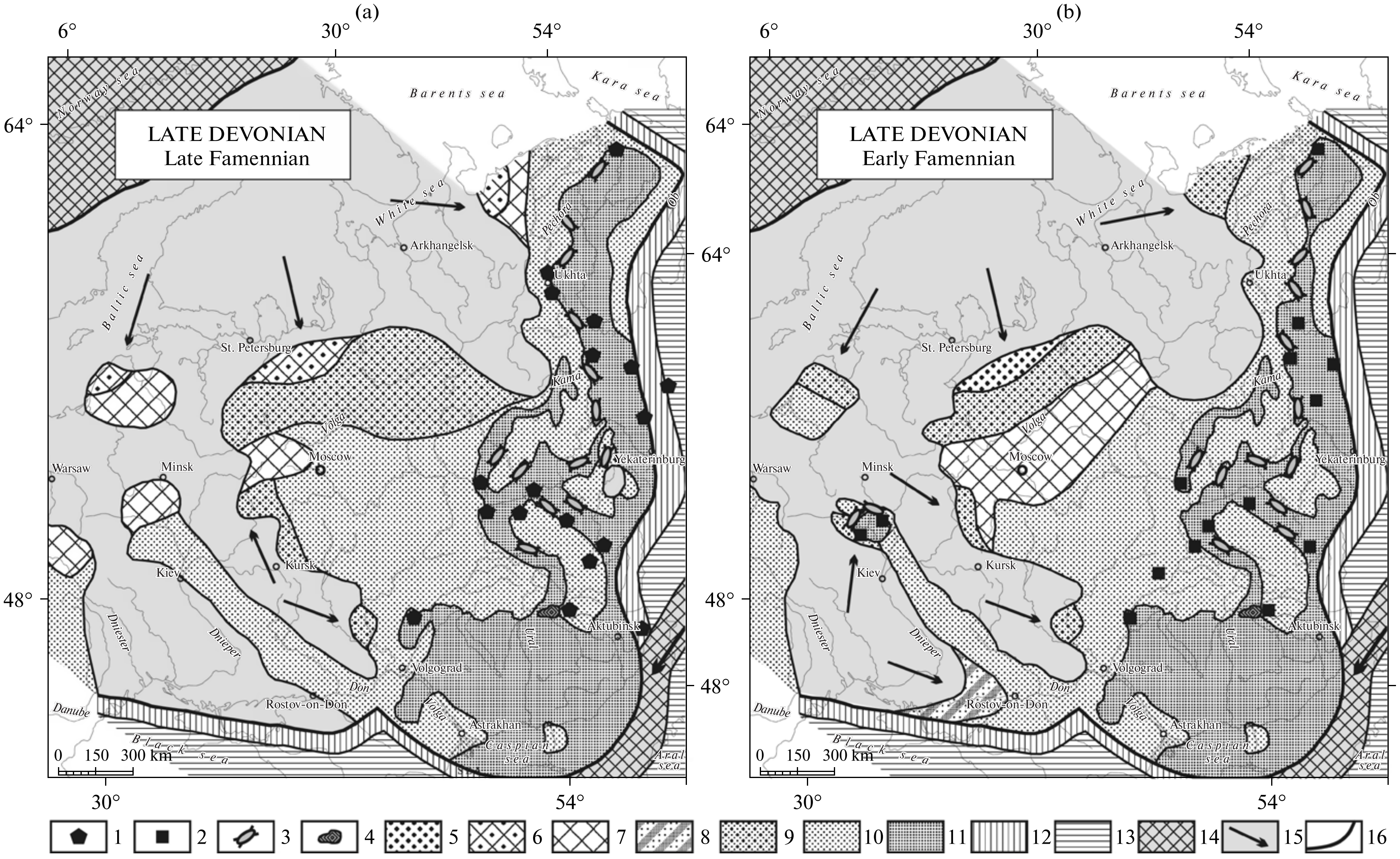
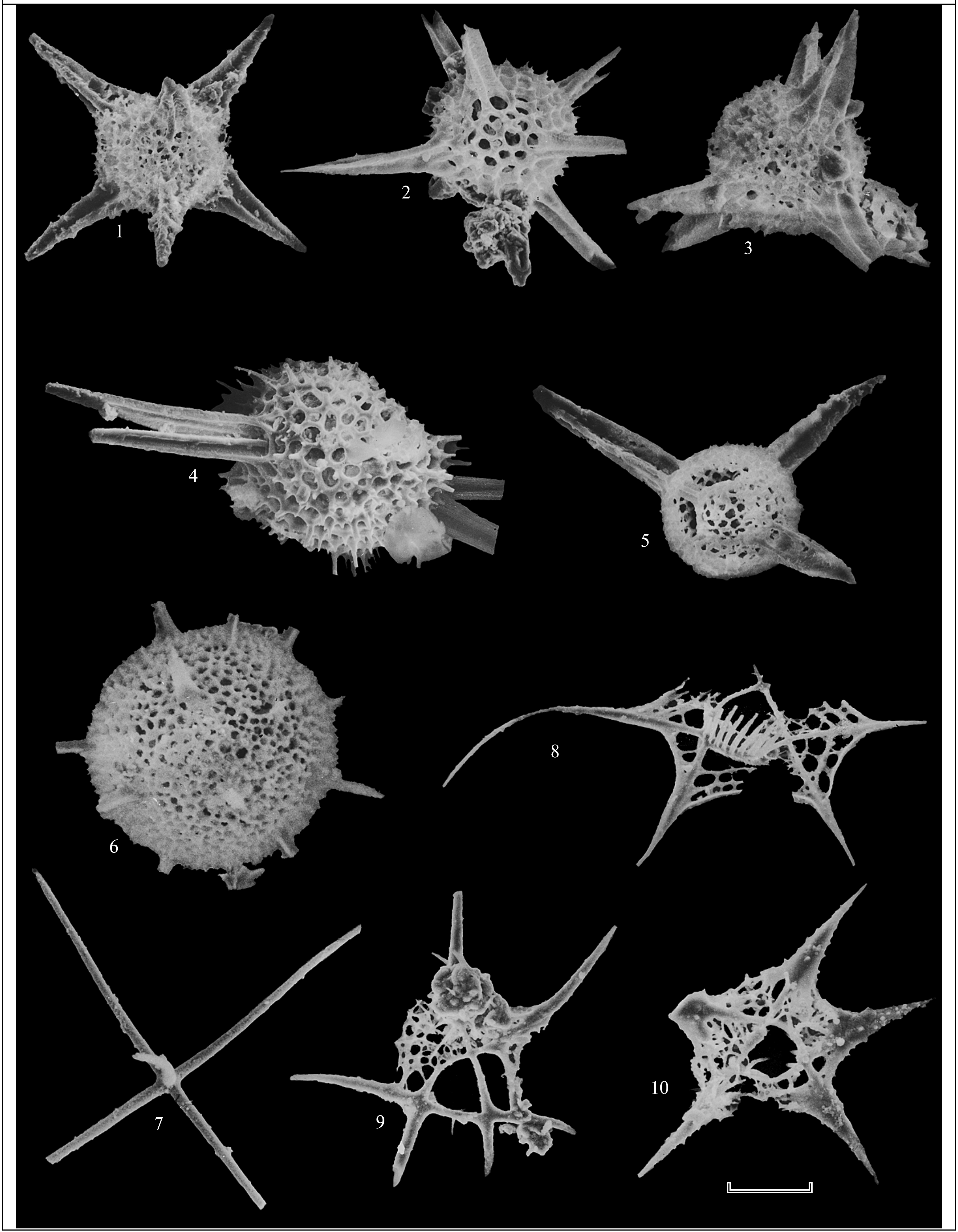


Fig. 18. Paleobiogeographic scheme of the Late Frasnian (a) and Early Famennian (b) of the Russian Platform and Greater Urals and radiolarian localities: (1, 2) radiolarian localities: (1) Late Frasnian and (2) Early Famennian; (3) paleoreefs; (4) Karachaganak bioherm; (5) continental fluvial plains; (6, 7) sea with increased salinity: (6) coastal region, (7) shallow internal shelf; (8) sea with low salinity; (9–13) sea with normal salinity: (9) coastal region, (10) internal shelf, (11) external shelf, (12) continental slope, (13) paleocean bottom; (14) active fold belt; (15) main directions of transportation of clastic material from land; (16) boundary of the Russian Platform. Paleobiogeographic schemes are based on the data of Tikhomirov (1967, 1995), Tikhii (1975), Sorokin (1978) Menner et al. (1991, 1996), Trokhova (1991), Belyaeva et al. (1998), Racki (1992, 1997), Rodionova et al. (1995), Nikishin et al. (1996), Pushkin (1997), and Yunusov et al. (1997).

Plate 11



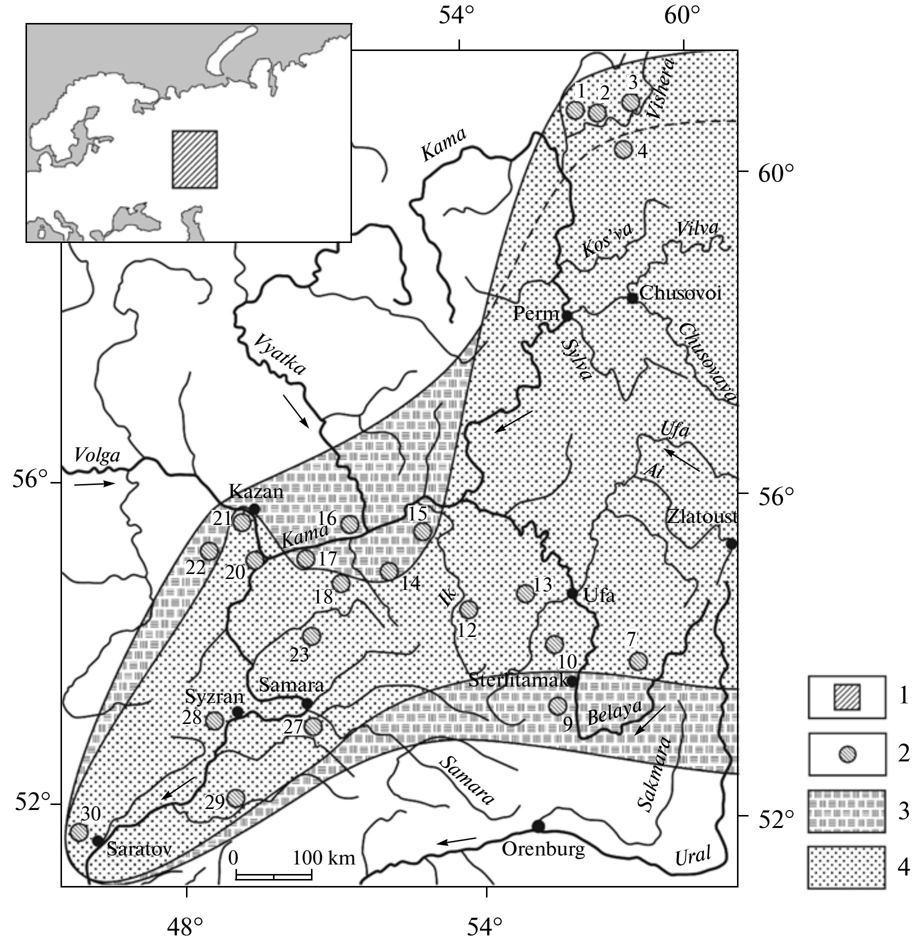


Fig. 19. Geographical ranges of radiolarians on the western slope of the Southern Urals and in the Volga–Ural Basin in the Late Frasnian and Famennian of the Late Devonian. Designations: (1) working area, (2) "Ural" Radiolarian Assemblage of the Devonian, (3) Late Frasnian, and (4) Famennian. For radiolarian localities (after Bykova, 1955), see Fig. 7.

Formation of the Upper Frasnian, which overlie the Lyaiol Formation, lack radiolarians (Table 8).

The Late Frasnian radiolarian assemblage of the Timan–Pechora Basin is relatively diverse, including 29 species of 15 genera (Fig. 15; Table 7). At the same time, the first (lower) member of the Lyaiol Formation includes almost all radiolarians of the Late Frasnian assemblage, 28 species of 14 genera.

Spherical porous radiolarians of the class Sphaerellaria comprise 16 species of seven genera (Pl. 17; Pl. 18, figs. 7, 8), with the dominance of the genera *Bientactinosphaera* (five species) and *Moskovistella* (five species).

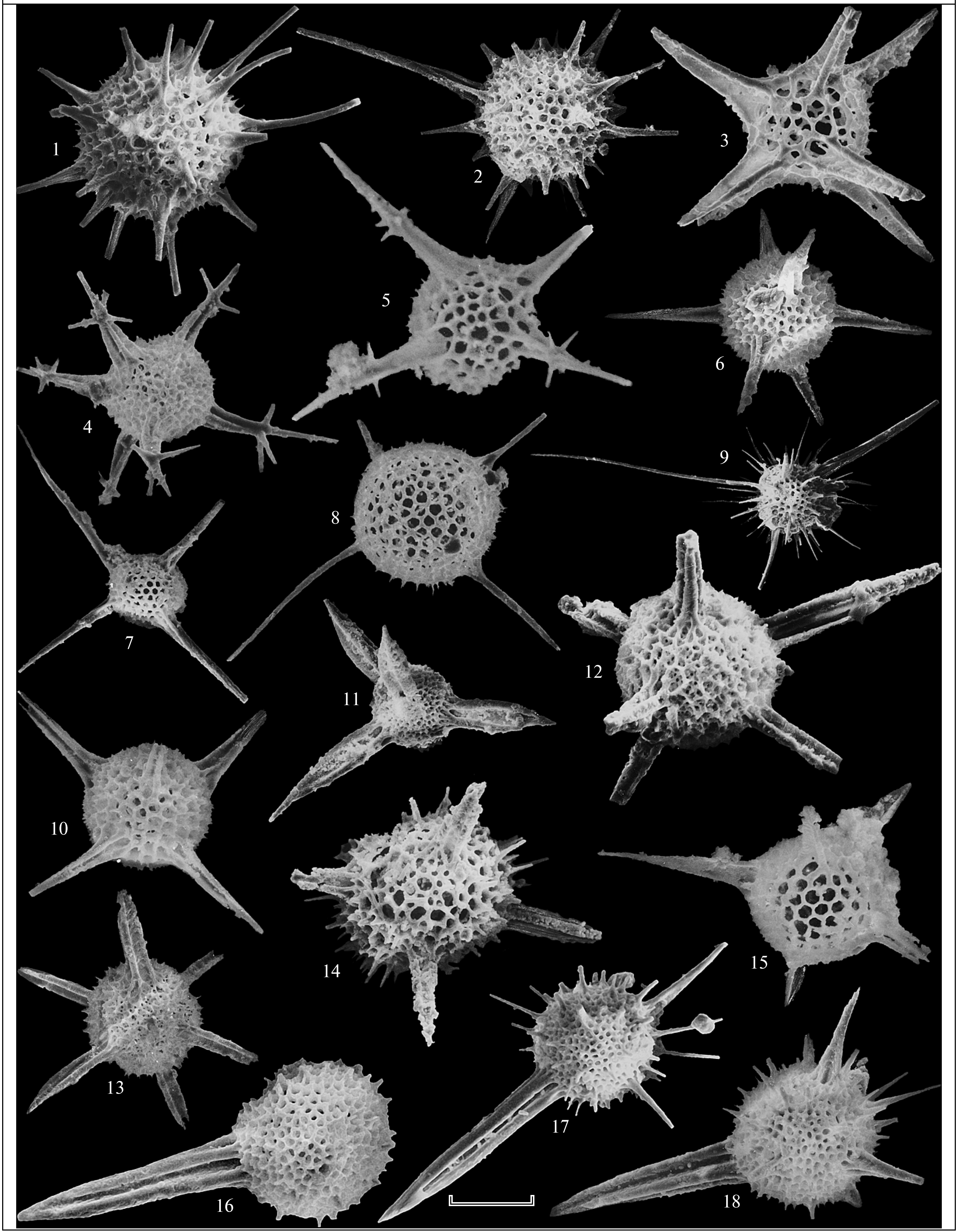
Explanation of Plate 11

Middle Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis*, Rdm-2 Subassemblage: spherical porous Sphaerellaria (1–5), spongy Spumellaria (6), and spiny Aculearia (7–10).

Fig. 1. *Moskovistella sincera* Afanasieva, 2000, specimen PIN, no. 5311/04609; scale bar, 43 μm.
Fig. 2. *Moskovistella octoradiata* Afanasieva, 2000, specimen PIN, no. 5311/04601; scale bar, 43 μm.
Fig. 3. *Moskovistella mira* Afanasieva, 2000, specimen PIN, no. 5311/04633; scale bar, 33 μm.
Fig. 4. *Entactinia bifida* Afanasieva, 2000, specimen PIN, no. 5311/04604; scale bar, 59 μm.
Fig. 5. *Bientactinosphaera symphypora* (Foreman, 1963), specimen PIN, no. 5311/04608; scale bar, 43 μm.
Fig. 6. *Retientactinosphaera clavata* Afanasieva, 2011, specimen PIN, no. 5311/04621; scale bar, 37 μm.
Fig. 7. *Palacantholithus stellatus* Deflandre, 1973, specimen PIN, no. 5311/04529; scale bar, 89 μm.
Fig. 8. *Ceratoikiscum stellatum* Aitchison, 1993, specimen PIN, no. 5311/04536; scale bar, 59 μm.
Fig. 9. *Circulaforma delicata* Cheng, 1986, specimen PIN, no. 5311/04602; scale bar, 59 μm.
Fig. 10. *Ceratoikiscum planistellare* Foreman, 1963, specimen PIN, no. 5311/04533; scale bar, 43 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin, borehole Shuda-Yag-1003: (1, 5, 6) sample 56 (81.6–83.0 m of depth); (2, 4, 7, 8, 9, 10) sample 34 (104.1–104.6 m of depth); (3) sample 65 (75.0–77.3 m of depth).

Plate 12



Spherical spongy and latticed members of the class Spumellaria are represented by six species of three genera (Pl. 18, figs. 1–6), among which the genus *Polyentactinia* (four species) is most representative.

Spiny radiolarians of the class Aculearia are represented by six species of four genera (Pl. 18, figs. 9–13), with the prevalence of the genus *Ceratoikiscum* (three species).

The second and third members of the Lyaiol Formation lack radiolarians (Fig. 15; Table 7).

The fourth member has yielded an impoverished radiolarian assemblage, represented by rare spherical *Bientactinosphaera variacanthina* (Foreman), *Entactinia* sp., and *Astroentactinia* sp. and spiny *Palacantholithus stellatus* Deflandre.

In the upper beds of the fourth member, radiolarians are represented by individual spherical *Entactinia* sp. and discoidal *Palaeodiscaleksus punctus* (Hinde) and *Primaritripus patella* (Hinde); this is probably evidence of the beginning of a new shallowing of the paleobasin (Pl. 18, figs. 14, 15).

On the western slope of the Northern Urals, in a section on the Unya River in the Evtropiny Noski locality (Fig. 6b, II), a mixed Frasnian and Famennian radiolarian assemblage has been recorded (Nazarov, 1988).

The assemblage includes taxa known from the Frasnian and Famennian stages: *Astroentactinia* sp., *Bientactinosphaera* aff. *cancellicula* (Foreman), *B.* cf. *grandis* (Nazarov), *Entactinia* cf. *dissora* Nazarov, *Moskovistella allbororum* Afanasieva, and *Polyentactinia* sp. as well as the species *Tetrentactinia barysphaera* Foreman, which is only characteristic of the Famennian.

The Late Frasnian radiolarian assemblage of the Timan–Pechora Basin is characterized by the presence of abundant spherical taxa with two differently directed main spines: *Bientactinosphaera egindyensis* (Nazarov), *B. obtusa* (Hinde), and *B. pittmani* (Hinde) (Pl. 17, figs. 3–5). The assemblage is distinguished by frequent occurrences of porous *Borisella maksimovae* Afanasieva, with six long narrow rod-shaped spines (Pl. 18, fig. 8), and abundant *Russirad kazintsovae* Afanasieva, with a latticed skeleton (Pl. 18, fig. 5).

In addition, the Late Frasnian radiolarian assemblage of the Timan–Pechora Basin includes relatively frequent *Bientactinosphaera variacanthina* (Foreman) (Pl. 17, fig. 2), *Polyentactinia kossistekensis* Nazarov, and *P. rudihispida* Nazarov et Ormiston (Pl. 18, figs. 1, 4).

Radiolarians of the Late Frasnian of the eastern slope of the Middle Urals

“Sokharevo” section. The study of radiolarians in thin sections allowed the revelation of distribution of the Late Frasnian assemblage with *Bientactinosphaera pittmani–Russirad kazintsovae* in the carbonate strata of the Upper Devonian of the eastern slope of the Middle Urals (Tables 6, 11). We have recorded radiolarians in Upper Frasnian limestones of the type section “Sokharevo” (Fig. 1, II), which is situated on the left and right banks of the Rezh River in the Sverdlovsk Region near the village of Sokharevo (Anfimov and Chuvashov, 2008).

The Late Frasnian radiolarian assemblage of the “Sokharevo” section includes 27 species of 13 genera (Table 11): *Adamasirad* cf. *cathedrarius* (Afanasieva), *Adamasirad* sp., *Archocyrtium* cf. *riedeli* Deflandre, *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *paronae* (Hinde), *Astroentactinia* sp., *Bientactinosphaera* cf. *pinica* Afanasieva, *B.* cf. *egindyensis* (Nazarov), *B.* cf. *grandis* (Nazarov), *B.* cf. *pittmani* (Hinde), *Bientactinosphaera* sp., *Entactinia* cf. *bella* Afanasieva et Amon, sp. nov., *Moskovistella* cf. *additiva* (Foreman), *M.* cf. *khaini* Afanasieva, *Palaeodiscaleksus* cf. *punctus*

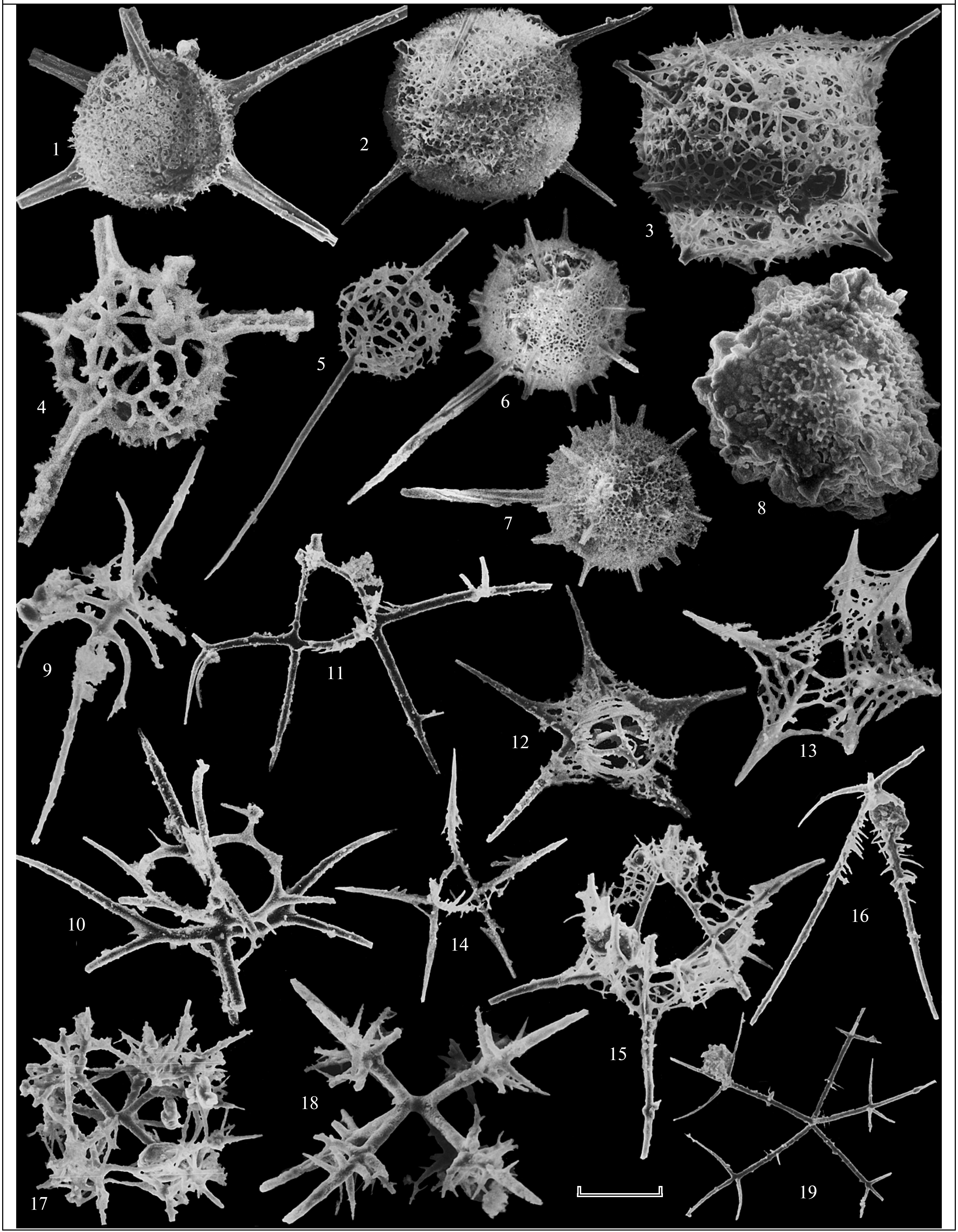
Explanation of Plate 12

Middle Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis*, Rdm-3 Subassemblage: spherical porous Sphaerellaria.

Fig. 1. *Astroentactinia rusaevi* Afanasieva, 2000, specimen PIN, no. 5311/04726; scale bar, 43 μm.
Fig. 2. *Astroentactinia paronae* (Hinde, 1899), specimen PIN, no. 5311/08627; scale bar, 59 μm.
Fig. 3. *Moskovistella khaini* Afanasieva, 2000, specimen PIN, no. 5311/04727; scale bar, 33 μm.
Fig. 4. *Moskovistella allbororum* Afanasieva, 2000, specimen PIN, no. 5311/09512; scale bar, 56 μm.
Fig. 5. *Moskovistella victorialis* Afanasieva, 2000, specimen PIN, no. 5311/09628; scale bar, 43 μm.
Fig. 6. *Moskovistella rozanovi* Afanasieva, 2000, specimen PIN, no. 5311/05132; scale bar, 43 μm.
Fig. 7. *Borisella maksimovae* Afanasieva, 2000, specimen PIN, no. 5311/04919; scale bar, 83 μm.
Fig. 8. *Borisella bykovae* Afanasieva, 2000, specimen PIN, no. 5311/09537; scale bar, 43 μm.
Fig. 9. *Borisella mariae* Afanasieva, 2000, specimen PIN, no. 5311/04708; scale bar, 133 μm.
Fig. 10. *Bientactinosphaera miletenkoi* Afanasieva, 2000, specimen PIN, no. 5311/08831; scale bar, 43 μm.
Fig. 11. *Bientactinosphaera guangxiensis* (Li et Wang, 1991), specimen PIN, no. 5311/04928; scale bar, 79 μm.
Fig. 12. *Ornatoentactinia spartaci* Afanasieva, 2000, specimen PIN, no. 5311/09705; scale bar, 40 μm.
Fig. 13. *Ornatoentactinia solita* Afanasieva, 2000, specimen PIN, no. 5311/08804; scale bar, 59 μm.
Fig. 14. *Entactinia paula* Foreman, 1963, specimen PIN, no. 5311/09627; scale bar, 59 μm.
Fig. 15. *Entactinia micula* Foreman, 1963, specimen PIN, no. 5311/04834; scale bar, 33 μm.
Fig. 16. *Radiobisphaera domanicensis* (Bykova, 1955), specimen PIN, no. 5311/13330; scale bar, 43 μm.
Fig. 17. *Radiobisphaera menneri* Afanasieva, 2000, specimen PIN, no. 5311/04714; scale bar, 59 μm.
Fig. 18. *Radiobisphaera assidera* (Nazarov, 1975), specimen PIN, no. 5311/08821; scale bar, 56 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin: borehole Shuda-Yag-1003: (1, 3, 9, 17) sample 68 (73.0–73.3 m of depth); (2, 6) sample 72 (71.9–72.4 m of depth); (7, 11) sample 78 (68.9–69.3 m of depth); (10, 13, 18) sample 73 (71.4–71.9 m of depth); (15) sample 69 (73.0–73.3 m of depth); (4, 5, 8, 12, 14) Lyaiol River, outcrop 1904, sample 6; (16) Ukhta River, point 4, sample 22.

Plate 13



(Hinde), *P.* cf. *tumefactus* Afanasieva et Amon, *Palaeodiscaleksus* sp., *Palaeoscenidium* sp., *Polyentactinia* cf. *circumretia* Nazarov et Ormiston, *P.* cf. *kossistekensis* Nazarov, *P.* cf. *propinqua* Nazarov, *Polyentactinia* sp., *Radiobisphaera* cf. *rozanovi* Afanasieva et Amon, *Radiobisphaera* sp., *Russirad* cf. *kazintsovae* Afanasieva, *Spongentactinella* cf. *veles* (Foreman), and *Spongentactinia* cf. *fungosa* Nazarov.

Spherical porous radiolarians of the class Sphaerellaria are represented by 13 species of five genera (Pl. 19, figs. 1–8), with the most diverse genera *Bientactinosphaera* (five species) and *Astroentactinia* (three species).

Spherical spongy and latticed members of the class Spumellaria comprise nine species of five genera (Pl. 19, figs. 9–18), including latticed members of the genus *Polyentactinia* (four species) and many spongy *Spongentactinia* and *Spongentactinella*.

Discoidal radiolarians of the class Stauraxonaria are represented by three species of the genus *Palaeodiscaleksus* (Pl. 19, figs. 20, 21).

Radiolarians with pylome from the order Pylomariata are represented by the species *Archocyrtium* cf. *riedeli* Deflandre (Pl. 19, fig. 19).

Spiny radiolarians of the class Aculearia are very few and problematic; this is probably connected with poor preservation in thin sections. These taxa are tentatively assigned to the genus *Palaeoscenidium*.

The radiolarian assemblage of the "Sokharevo" section is almost identical in taxonomic composition to the association from the Timan–Pechora Basin. The main distinction of the Sokharevo Radiolarian Assemblage is the dominance of spherical spongy and latticed Spumellaria, among which the genera *Russirad* and *Polyentactinia* are particularly notable. Another distinctive feature of the Sokharevo Assemblage is a small number of spiny taxa of only one genus, *Palaeoscenidium*, whereas the Timan–Pechora Basin has yielded more diverse spiny radiolarians of four genera, *Ceratoikiscum, Palacantholithus, Palaeoscenidium*, and *Palaeothalomnus*. And, finally, the third distinctive feature of the "Sokharevo" section is the appearance of the first spongy radiolarians of the genera *Adamasirad* and radiolarians with pylome *Archocyrtium* of the order Pylomariata, which are only known in the Timan–Pechora Basin and Polar Urals since the Early Famennian.

Boroukhino tectonic plate. In addition to the "Sokharevo" section, Late Frasnian radiolarians were recorded by Amon and Korovko (1992; Amon, 1995a; Korovko et al., 1999) in the Boroukhino Tectonic Plate of the Rezh Structural–Formational Zone, which was open by boreholes P-21, P-31 (Fig. 1, III, IV). The assemblage is represented by 14 species of seven genera (Table 11): *Astroentactinia* cf. *robusta* (Hinde), *Astroentactinia* sp., *Bientactinosphaera* cf. *pittmani* (Hinde), *B.* cf. *vetusta* (Hinde), *Bientactinosphaera* sp., *Ceratoikiscum* sp., *Entactinia* cf. *bella* Afanasieva et Amon, sp. nov., *E.* cf. *diversita* Nazarov, *Entactinia* sp., *Haplentactinia* sp., *Polyentactinia* cf. *circumretia* Nazarov et Ormiston, *P.* cf. *propinqua* Nazarov, *Polyentactinia* sp., and *Spongentactinia* cf. *fungosa* Nazarov.

Spherical porous radiolarians of the class Sphaerellaria are represented by eight species of three genera, among which the genera *Bientactinosphaera* (three species) and *Entactinia* (three species) are particularly notable.

Spherical spongy and latticed members of the class Spumellaria comprise five species of three genera, among which the genus *Polyentactinia* (three species) is particularly notable.

Spiny radiolarians of the class Aculearia are very few and probably belong to the genus *Ceratoikiscum*.

Explanation of Plate 13

Middle Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Moskovistella allbororum–Ceratoikiscum ukhtensis*, Rdm-3 Subassemblage: spherical spongy (1, 2) and latticed (3–7) Spumellaria, discoidal Stauraxonaria (8), and spiny Aculearia (9–19).

Fig. 1. *Spongentactinella olafi* Afanasieva, 2000, specimen PIN, no. 5311/08514; scale bar, 89 μm.
Fig. 2. *Spongentactinella windjanensis* Nazarov, 1982, specimen PIN, no. 5311/08515; scale bar, 89 μm.
Fig. 3. *Polyentactinia zhamoidai* Afanasieva, 2000, specimen PIN, no. 5311/04722; scale bar, 43 μm.
Fig. 4. *Haplentactinia barskovi* Afanasieva, 2000, specimen PIN, no. 5311/08609; scale bar, 33 μm.
Fig. 5. *Haplentactinia alekseevi* Afanasieva, 2000, specimen PIN, no. 5311/09621; scale bar, 59 μm.
Figs. 6 and 7. *Retientactinosphaera clavata* Afanasieva, 2011: (6) specimen PIN, no. 5311/08728; scale bar, 63 μm; (7) specimen PIN, no. 5311/08625; scale bar, 67 μm.
Fig. 8. *Palaeodiscaleksus punctus* (Hinde, 1899), specimen PIN, no. 5311/12429; scale bar, 43 μm.
Fig. 9. *Nazarovites pinnula* Afanasieva, 2000, specimen PIN, no. 5311/09508; scale bar, 43 μm.
Fig. 10. *Nazarovites bioculus* Afanasieva, 2000, specimen PIN, no. 5311/09834; scale bar, 56 μm.
Fig. 11. *Ceratoikiscum ukhtensis* Afanasieva, 2000, specimen PIN, no. 5311/09835; scale bar, 59 μm.
Fig. 12. *Ceratoikiscum goodbodyi* Cheng, 1986, specimen PIN, no. 5311/08520; scale bar, 59 μm.
Fig. 13. *Ceratoikiscum araneosum* Afanasieva, 2000, specimen PIN, no. 5311/08706; scale bar, 63 μm.
Fig. 14. *Ceratoikiscum incomptum* Nazarov, 1975, specimen PIN, no. 5311/08811; scale bar, 83 μm.
Fig. 15. *Ceratoikiscum simplum* Cheng, 1986, specimen PIN, no. 5311/04810; scale bar, 59 μm.
Fig. 16. *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 5311/04807; scale bar, 89 μm.
Fig. 17. *Palaeothalomnus timokhini* Afanasieva, 2000, specimen PIN, no. 5311/08713; scale bar, 56 μm.
Fig. 18. *Palaeothalomnus quadriramosum* (Foreman, 1963), specimen PIN, no. 5311/08721; scale bar, 56 μm.
Fig. 19. *Palaeothalomnus arrhinia* (Foreman, 1963), specimen PIN, no. 5311/09504; scale bar, 98 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin: borehole Shuda-Yag-1003: (1, 2, 4, 7, 12) sample 72 (71.9–72.4 m of depth); (3, 15, 16) sample 68 (73.5–73.3 m of depth); (6, 13, 14, 17, 18) sample 73 (71.4–71.9 m of depth); (5, 9–11, 19) Lyaiol River, outcrop 1904, sample 6; (8) Domanik River, quarry 2, sample 25.

Table 11. Stratigraphic distribution of Late Devonian radiolarians of the eastern slope of the Middle Urals

System	Devonian		
Series	Upper		
Stage	Frasnian		Famennian
Substage	Upper		Lower
Formation	Askyn		Makarov
Biostraton	*Bientactinosphaera pittmani – Russirad kazintsovae*		*Tetrentactinia barysphaera – Ceratoikiscum famennium*
Location Radiolarians	Sokharevo	Boroukhino Tectonic Plate	
Adamasirad cf. *cathedrarius* (Afanasieva, 2000)	■		
Adamasirad sp.	■		
Archocyrtium cf. *riedeli* Deflandre, 1960	■		
Astroentactinia cf. *paronae* (Hinde, 1899)	■		
Bientactinosphaera cf. *egindyensis* (Nazarov, 1975)	■		
Bientactinosphaera cf. *grandis* (Nazarov, 1975)	■		
Bientactinosphaera cf. cf. *pinica* Afanasieva, 2000	■		
Moskovistella cf. *additiva* (Foreman, 1963)	■		
Moskovistella cf. *khaini* Afanasieva, 2000	■		
Palaeodiscaleksus cf. *punctus* (Hinde, 1899)	■		
Palaeodiscaleksus cf. *tumefactus* Afanasieva et Amon, 2008	■		
Palaeodiscaleksus sp.	■		
Palaeoscenidium sp.	■		
Polyentactinia cf. *kossistekensis* Nazarov, 1975	■		
Radiobisphaera cf. *rozanovi* Afanasieva et Amon, 2009	■		
Radiobisphaera sp.	■		
Russirad cf. *kazintsovae* Afanasieva, 2000	■		
Spongentactinella cf. *veles* (Foreman, 1963)	■		
Bientactinosphaera cf. *pittmani* (Hinde, 1899)	■	■	
Polyentactinia cf. *circumretia* Nazarov et Ormiston, 1993	■	■	
Polyentactinia cf. *propinqua* Nazarov, 1975	■	■	
Spongentactinia cf. *fungosa* Nazarov, 1975	■	■	
Astroentactinia cf. *biaciculata* Nazarov, 1975	■		■
Astroentactinia sp.	■	■	■
Bientactinosphaera sp.	■	■	■
Entactinia cf. *bella* Afanasieva et Amon, sp. nov.	■	■	■
Polyentactinia sp.	■	■	■
Astroentactinia cf. *robusta* (Hinde, 1899)		■	
Bientactinosphaera cf. *vetusta* (Hinde, 1899)		■	
Entactinia cf. *diversita* Nazarov, 1973		■	
Ceratoikiscum sp.		■	■
Entactinia sp.		■	■
Haplentactinia sp.		■	■
Entactinia cf. *paula* Foreman, 1963			■
Bientactinosphaera cf. *pulcherima* (Nazarov et Ormiston, 1990)			■
Haplentactinia cf. *flagellifera* Nazarov et Ormiston, 1993			■
Haplentactinia cf. *rhinophyusa* Foreman, 1963			■
Helioentactinia sp.			■
Polyentactinia cf. *rudihipsida* (Nazarov et Ormiston, 1993)			■
Polyentactinia cf. *suave* (Nazarov, 1977)			■
Radiobisphaera cf. *palimbola* (Foreman, 1963)			■
Somphoentactinia cf. *somphozona* (Foreman, 1963)			■
Spongentactinia cf. *nupera* Nazarov, 1981			■
Spongentactinia sp.			■
Tetrentactinia cf. *barysphaera* Foreman, 1963			■
Tetrentactinia sp.			■

The radiolarian assemblage corresponds in stratigraphical position to the *upper rhenana* Conodont Zone of the standard scale (Bikbaev and Snigireva, 2002).

Thus, according to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006), the Upper Frasnian radiolarian association is a new characteristic biostratigraphic assemblage with *Bientactinosphaera pittmani–Russirad kazintsovae*, which corresponds to the Upper Frasnian, the *rhenana* Conodont Zone and *Manticoceras lyaiolense* and *Virginoceras ljaschenkoae* ammonoid zones (Table 8).

The new Late Devonian Upper Frasnian radiolarian biostraton (Tables 6, 8) occurs and is valid within the Timan–Pechora Basin (Afanasieva, 2000a; Afanasieva and Mikhailova, 2001) and on the eastern slope of the Middle Urals.

“Ural” radiolarian assemblage of the Late Frasnian. The diverse “Ural” Radiolarian Assemblage is most widespread in the Late Frasnian (Bykova, 1955) (Figs. 18a, 19).

In the Northern Urals, in the Yaz’va River Basin, there are many radiolarians, including *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *B. radiata* (Antropov), *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. subvasta* (Bykova), *E. tuberculata* (Lipina), and *Trochodiscus concavutas* Vissarionova. Dolomitized limestones on the Sikaza River of the Southern Urals contain only *Astroentactinia* cf. *stellata* Nazarov and *Entactinia paulis* (Bykova) (Figs. 11, 19; Table 5).

In Upper Frasnian carbonate sections of western Bashkortostan, near the towns of Sterlibashevo and Tuimazy and villages of Kargaly and Elatminki, radiolarians are abundant, including *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. parva* (Bykova), *T. elegans* (Vissarionova), and *T. elegans* var. *subsphaera* (Vissarionova) (Figs. 11, 19; Table 5).

In the Samara Region near the town of Syzran and villages of Berezovka and Krasnovka, Upper Frasnian limestones have yielded many *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), and *T. elegans* var. *subsphaera* (Vissarionova) (Figs. 9o, 11, 19; Table 5).

Upper Frasnian radiolarians of the “Ural” Assemblage of the Saratov Region, in the vicinity of the town of Pugachev and the village of Teplovka, are represented by many *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), *T. elegans* var. *subsphaera* (Vissarionova), and *T. parva* (Bykova).

The most diverse and abundant “Ural” Radiolarian Assemblage occurs in the Upper Frasnian beds of Tatarstan near the town of Aznakaevo and villages of Aktash, Verkhnii Uslon, Kamskoe Ust’e, Staroe Romashkino, Cheremshan, Shugurovo, and Yanga-Aul: *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *B. radiata* (Antropov), *Entactinia subvasta* (Bykova), *E. dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E.* cf. *faveolata* Nazarov, *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus elegans* (Vissarionova), *T. elegans* var. *subsphaera* (Vissarionova), and *T. parva* (Bykova) (Figs. 9k, 9m, 9n, 11, 19; Table 5).

Geographical distribution of Frasnian radiolarians

Beyond the Ural Mountains and eastern Russian Platform, the distribution of Frasnian radiolarians was established by Nazarov (1975, 1988) in red jaspers of the northern slope of the Alai Mountains, Kyrgyzstan; in siliceous greenish gray and violet siltstones and jaspers of condensed sections of ophiolitic formation of the Chara Zone of eastern Kazakhstan (Fig. 3).

In North America, Early Frasnian radiolarians are recorded in terrigenous shaly strata of the Canol Shale of northern Canada (*Polygnathus asymmetrica* Conodont Zone, Early Frasnian) (Fig. 3) (Holdsworth, 1977; Holdsworth et al., 1978). In limestone interbeds among siliceous shales, siltstones, and claystones, there were many radiolarians, including *Entactinia additiva, Bientactinosphaera grandis, Astroentactinia stellata, A. biaciculata, Polyentactinia propinqua, Ceratoikiscarn* cf. *bujagum*, etc. In generic and partly species composition, the assemblage is in general very similar to radiolarian associations of the Egindy Formation of the Southern Urals and the Domanik Formation of the Ukhtinskii District of the Timan–Pechora Basin (Nazarov, 1988, 1989).

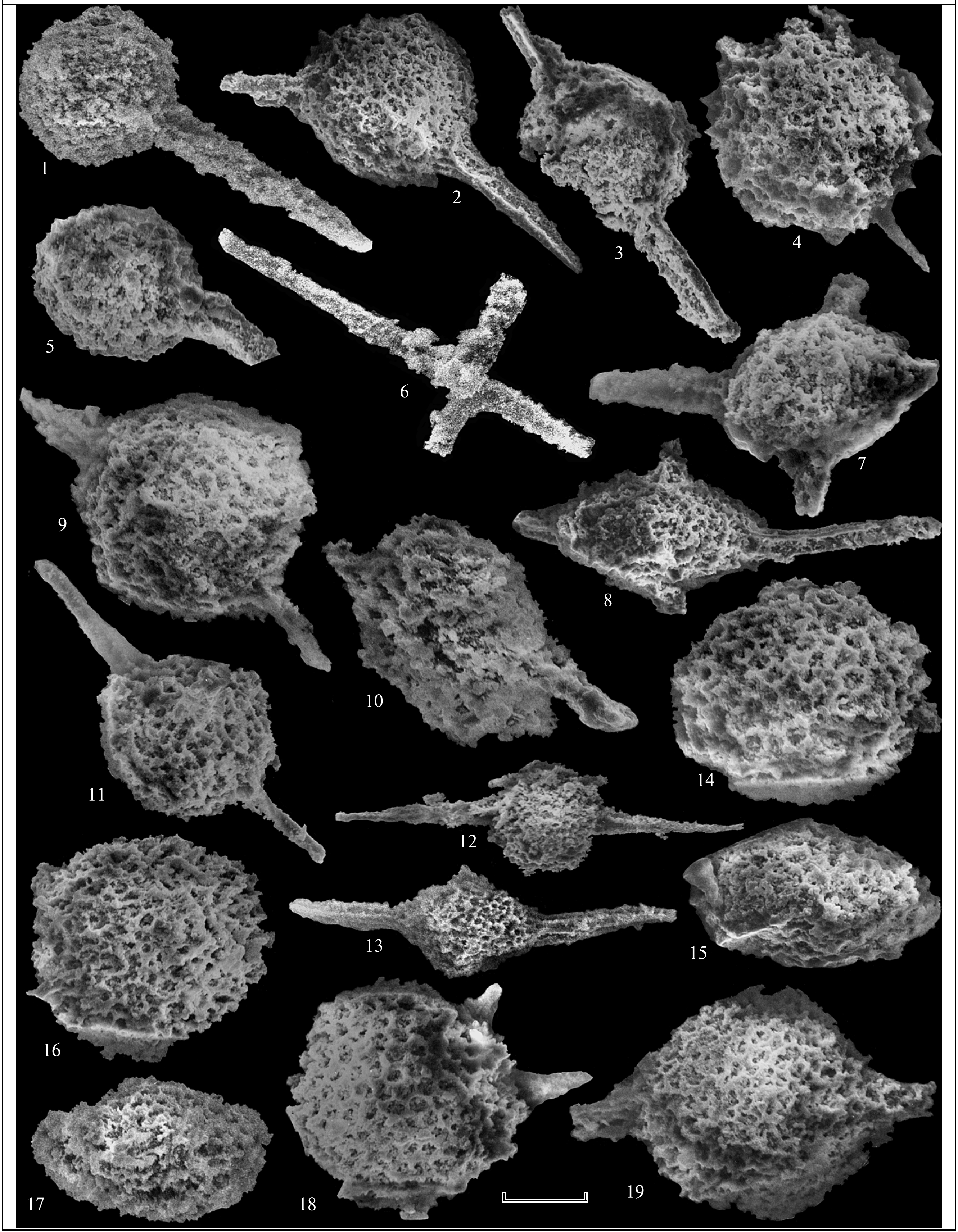
When developing the first zonal biostratigraphy based on radiolarians, Holdsworth and Jones (1980a, 1980b) combined Frasnian radiolarians of eastern Alaska (Fig. 3) into one zonal assemblage, Pre-*Holoeciscus*.

Nazarov and Ormiston (Nazarov et al., 1982; Nazarov and Ormiston, 1983b) described for the first time a Frasnian radiolarian assemblage (19 species) of the Canning Basin of western Australia (Fig. 3) from a carbonate nodule of the upper part of the Gogo Formation, which is represented by clayey-shaly beds with interbeds, lenses, and nodules of limestones. Later, Aitchison (1993) described mostly spiny radiolarians (57 species) from the lower part of the Gogo Formation (Frasnian Stage) of the Canning Basin and, subsequently, Won (1997a, 1997b) described 84 species and subspecies mostly of spherical radiolarians.

Ishiga et al. (1987) established a Frasnian radiolarian assemblage in clayey-shale beds of the Hastings Block, New England Fold Belt of eastern Australia (Fig. 3).

Li and Wang (1991) were the first to describe Frasnian radiolarians of southern China (Fig. 3) from siliceous rocks of the Liukiang Formation in east-south-

Plate 14



east of Guangxi Province. They include *Bientactinosphaera egindyensis* (Nazarov) and *B. aitpaiensis* (Nazarov), which are characteristic of the Frasnian Stage of the Southern Urals; in addition, the researchers established the species *B. guangxiensis* (Li et Wang) and *Cyclocarpus tubiformis* Li et Wang. Subsequently, Wang et al. (2000, 2003) described very diverse Middle–Late Devonian radiolarians of southern China from Yunnan, Guizhou, Guangxi, and Hunan provinces (Fig. 3) and established three radiolarian assemblages: *Eoalbaillella lilaensis* (Middle Devonian), *Helenifore laticlavium* (Late Devonian, Frasnian), and *Holoeciscus foremanae* (Late Devonian, Famennian).

In the western marginal area of the Russian Platform, in eastern Poland (Fig. 3), Vishnevskaya et al. (1997, 2002) established a Frasnian radiolarian assemblage, including 20 species of seven genera of spherical radiolarians. The radiolarian assemblage is extremely impoverished compared with the rich radiolarian association of the Timan–Pechora Basin and lacks spiny species. This is likely connected with conditions of the internal shelf, whereas radiolarians of the southern Timan–Pechora Basin dwelt under conditions of the external shelf of the ancient sea.

Boundy-Sanders et al. (1999) described radiolarians and spicules of sponges from deposits of northern spurs of the Shoshone Mountain Range, Nevada, North America (Fig. 3); it is dated Late Frasnian based on co-occurrence with conodonts of the *late rhenana* Zone. A relatively diverse radiolarian assemblage includes *Ceratoikiscum, Paleoscenidium*, spherical radiolarians, and members of a new genus, *Durahelenifore*.

Kurihara et al. (2006) have investigated the development of the Early Frasnian assemblage in the rhythmically stratified Silurian–Devonian red cherts of the Erdenetsogt Formation in the Hangai–Hentii Mountains of central Mongolia (Fig. 3). The authors emphasized the deepwater character of cherts, which completely lack terrigenous clastic matter and have abundant spherical radiolarians (radiolarites?), indicated that the study of radiolarians enables a better understanding of geological history of Central Asia. In their opinion, the data on radiolarians provide additional evidence for the fact that subduction–accretion processes in the oceanic plate of the Paleopacific played a significant role in the evolution of the Central Asiatic Orogenic Belt.

As Wonganan and Caridroit (2005) reported, an almost complete analogue of the Australian *Trilonche minax* Zone (Early Frasnian) is revealed in banded cherts of a complex accretion complex in Chiang Mai Province of northern Thailand (Fig. 3).

A somewhat different picture of radiolarian-based Devonian biostratigraphy has been proposed by Saesaengseerung et al. (2006). The working area Chiang Dao is in Chiang Mai Province of northern Thailand. The strongly condensed 30-m-thick section with radiolarians is composed of pale green and gray thin-layer cherts interbedding with thin films of clayey shales. The beds containing radiolarians overlie black siliceous clayey slates with Early Devonian graptolites. The section is divided into four zones based on radiolarians (from below upwards):

(1) The *Tlecerina* sp.–*Stigmosphaerostylus* sp. Zone (Eifelian–Givetian) resembles somewhat previously described radiolarians of northern Thailand (Wonganan and Caridroit, 2005) and eastern Australia (Aitchison, 1988a, 1988b);

(2) Three zones: *Trilonche vetusta, Astroentactinia* sp., and *Spongentactinella* sp. are dated Frasnian and resemble the previously described radiolarians of northern Thailand (Wonganan and Caridroit, 2005), western Australia (Nazarov et al., 1982; Nazarov and Ormiston, 1983b), and Southern China (Wang et al., 2003).

Explanation of Plate 14

Middle Frasnian radiolarians of the Southern Urals; assemblage with *Primaritripus chuvashovi*: spherical porous Sphaerellaria (1–5), spiny Aculearia (6), and discoidal Stauraxonaria (7–19).

Fig. 1. *Radiobisphaera domanicensis* (Bykova, 1955), specimen PIN, no. 5247/14815; scale bar, 37 μm.

Fig. 2. *Bientactinosphaera pittmani* (Hinde, 1899), specimen PIN, no. 5247/14731; scale bar, 59 μm.

Fig. 3. *Bientactinosphaera vetusta* (Hinde, 1899), specimen PIN, no. 5247/14730; scale bar, 55 μm.

Fig. 4. *Astroentactinia tenuis* (Furutani, 1990), specimen PIN, no. 5247/14818; scale bar, 37 μm.

Fig. 5. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009, specimen PIN, no. 5247/14713; scale bar, 37 μm.

Fig. 6. *Palacantholithus stellatus* Deflandre, 1973, specimen PIN, no. 5247/14811; scale bar, 32 μm.

Figs. 7 and 8. *Primaritripus kariukmasensis* Afanasieva et Amon, 2009: (7) holotype PIN, no. 5247/14729; scale bar, 33 μm; (8) specimen PIN, no. 5247/14610, lateral view; scale bar, 56 μm.

Figs. 9 and 10. *Primaritripus buribayensis* Afanasieva et Amon, 2008: (9) specimen PIN, no. 5247/14714; scale bar, 32 μm; (10) specimen PIN, no. 5247/14728, lateral view; scale bar, 30 μm.

Figs. 11–13. *Primaritripus chuvashovi* Afanasieva et Amon, 2008: (11) specimen PIN, no. 5247/14721; scale bar, 33 μm; (12) specimen PIN, no. 5247/14632; scale bar, 56 μm; (13) specimen PIN, no. 5247/14702, lateral view; scale bar, 56 μm.

Figs. 14 and 15. *Palaeodiscaleksus cribrarius* (Hinde, 1899): (14) specimen PIN, no. 5247/14720; scale bar, 32 μm; (15) specimen PIN, no. 5247/14616, lateral view; scale bar, 33 μm.

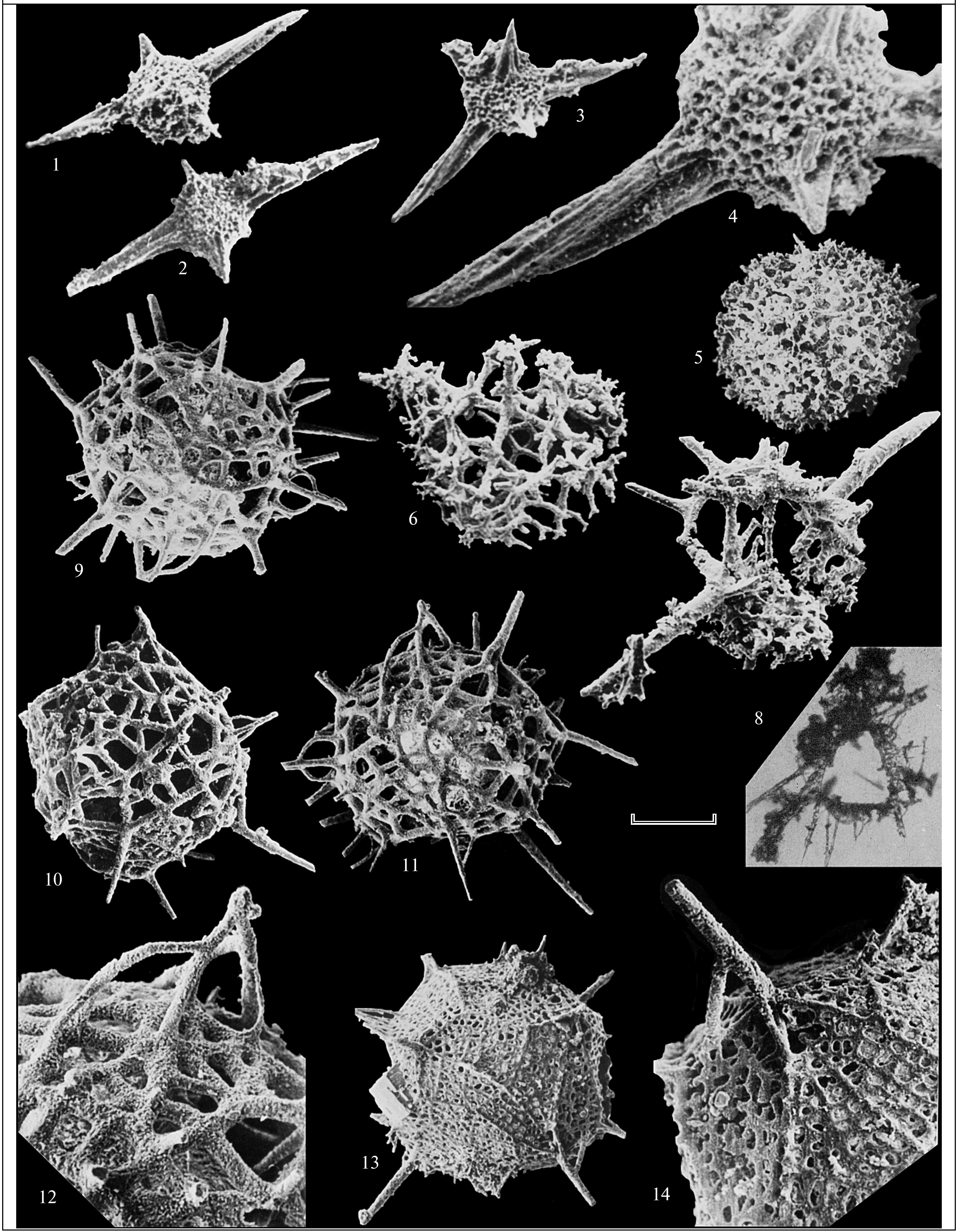
Figs. 16 and 17. *Palaeodiscaleksus tumefactus* Afanasieva et Amon, 2008: (16) specimen PIN, no. 5247/14724; scale bar, 37 μm; (17) specimen PIN, no. 5247/14705, lateral view; scale bar, 33 μm.

Fig. 18. *Trochodiscus planatus* Hinde, 1899, specimen PIN, no. 5247/14620; scale bar, 33 μm.

Fig. 19. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5247/14704; scale bar, 37 μm.

Upper Devonian, Middle Frasnian Substage; Southern Urals, section on Argagan Mountain near the village of Sultantimirovo, sample 0434/3156-1.

Plate 15



Famennian Age

After a break in sedimentation at the Frasnian–Famennian boundary, the Ural Sea penetrated again into the Russian Platform, particularly, in its central and northern areas. In the early part of the Famennian Age, the marine basin significantly expanded, marking the onset of a new transgressive–regressive cycle of sedimentation. However, the Moscow and Baltic syneclises were still separated by the Latvian saddle; they were not connected (Fig. 18b). At the end of the Devonian Period, the Russian Platform underwent a short-term Uplift, the marine basin was reduced, its water had an increased salinity (Tikhomirov, 1967, 1995; Tikhii, 1975).

In the Famennian, the southern Greater Urals underwent a large rearrangement caused by the development of the Zilair Flysch Fault (Puchkov, 2000). The eastern wing of the fault occupied the western Mugodzhary Zone, the axial part fell on the region of the bathyal assemblages, and the western wing overlay the eastern marginal area of the shelf zone of the Russian Platform. According to the reconstruction of Puchkov (2000), the essence of this rearrangement was the fact that the Magnitogorsk Island Arch closely approached Ancient Russian Continent and collided with it in the area of the Recent Southern Urals. In the Famennian, the following structural–facies zones are recognized (from west to east): (1) shelf of the ancient part of continent; (2) flysch fault before the island arch; (3) mature volcanic arch; and (4) microcontinent. To the end of the Famennian, the process of marginal continental accretion was completed, and the border of Ancient Russian Continent displaced to the area of the Recent Turgay Depression.

In the development of radiolarians in the southern Ural Mountains at the end of the Devonian, certain features of decline and stress are recognized. This was manifested primarily in a decrease in generic and species diversity, the rate of appearance of new taxa, and in geographic ranges. At the same time, the same preferences in geographic ranges are in general retained, as under conditions of transgressions in the Early Devonian, Eifelian, Givetian, and Early Frasnian, i.e., relatively shallow-water conditions rather close to continental landmasses or groups of islands. These were primarily the Western Urals and Fore-Urals, i.e., areas adjacent to Ancient Russian Continent and microcontinents.

Famennian radiolarians of perfect preservation were investigated by Nazarov (Kruchek and Nazarov, 1977) in the Pripyat Depression and provided the basis for the establishment of a biostratigraphic assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* (Figs. 3, 20; Table 7).

Beyond the stratotypic area of the Pripyat Depression, Nazarov (1988) established a less diverse Famennian radiolarian assemblage in the upper part of the section, in a member of interbedding siliceous–clayey shales, siltstones, and limestones on the Unya River in the Evtropiny Noski locality of the Malaya Pechora allochthon of the western slope of the Northern Urals (Figs. 3; 6b, IX). This part of the section corresponds to the lower part of the Famennian, *regularis* and *crepida* conodont zones. A similar assemblage was recorded northerly, in the Lemva River Basin, in flinty slates on the Malaya Nadota River (Puchkov, 1979a, 1979b) (Fig. 6b, V).

In the southern Sakmara Zone of the Southern Urals and Northern Mugodzhary (Fig. 3), an impoverished radiolarian assemblage occurred in the Famennian. According to the data of Nazarov (1975), the assemblage comes from the uppermost part of the section of the Egindy Formation on the Aitpaika Creek (Fig. 1e, XIV) and, based on the presence of a characteristic spore assemblage, is correlated with the Elets Formation of the Lower Famennian of the Russian Platform. The data of Ivanov and Puchkov (Puchkov and Ivanov, 1982; Ivanov, 1983; Ivanov and Puchkov, 1984) suggest that this member should not be assigned to the upper part of the Egindy Formation, since it belongs to the bottom of the Zilair Formation. Thus, in the stratotypic section on the Egindy River,

Explanation of Plate 15

Middle–Late Frasnian radiolarians of the Sakmara Zone of the Southern Urals and Northern Mugodzhary; assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis*: spherical porous Sphaerellaria (1–4), spongy (5) and latticed (6, 9–14) Spumellaria, and spiny Aculearia (7, 8).

Figs. 1 and 2. *Bientactinosphaera aitpaiensis* (Nazarov, 1973): (1) specimen GIN, no. 4046/106; scale bar, 89 μm; (2) specimen GIN, no. 4046/99; scale bar, 89 μm.

Figs. 3 and 4. *Bientactinosphaera egindyensis* (Nazarov, 1975), specimen GIN, no. 4046/98: (3) scale bar, 105 μm; (4) fragment, scale bar, 35 μm.

Fig. 5. *Haplentactinia inaudita* Nazarov, 1984, specimen GIN, no. 4046/105; scale bar, 132 μm.

Fig. 6. *Retentactinia longa* Won, 1997, specimen GIN, no. 4046/108; scale bar, 54 μm.

Fig. 7. *Ceratoikiscum* cf. *rectum* Nazarov, 1975, specimen GIN, no. 4046/101; scale bar, 54 μm.

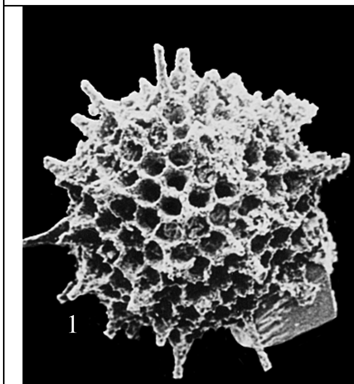
Fig. 8. *Ceratoikiscum* cf. *incomptum* Nazarov, 1975, specimen GIN, no. 48/2, in taking place light; scale bar, 46 μm.

Figs. 9–12. *Polyentactinia circumretia* Nazarov et Ormiston, 1993: (9) specimen GIN, no. 4046/121; scale bar, 86 μm; (10) specimen GIN, no. 4046/96; scale bar, 86 μm; (11) specimen GIN, no. 4046/95; scale bar, 86 μm; (12) fragment, scale bar, 30 μm.

Figs. 13 and 14. *Polyentactinia kossistekensis* Nazarov, 1975, specimen GIN, no. 4046/97: (13) scale bar, 86 μm; (14) fragment, scale bar, 33 μm.

Upper Devonian, Frasnian Stage, Egindy Formation; Northern Mugodzhary, Kazakhstan, Aktyubinsk Region, Aitpaika River (Nazarov, 1984, pl. XXXV, figs. 1–5; pl. XXXVI, figs. 1–5, 7, 8; pl. XXXVIII, fig. 7).

Plate 16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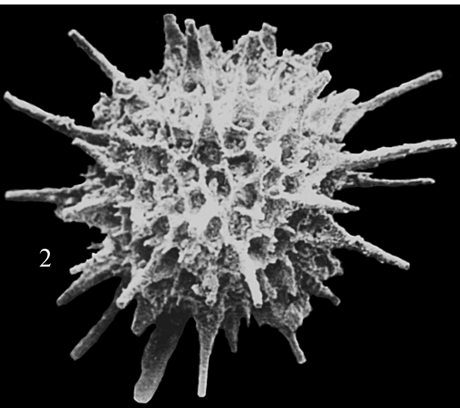
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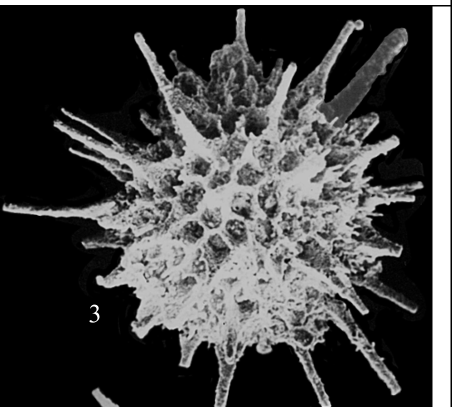
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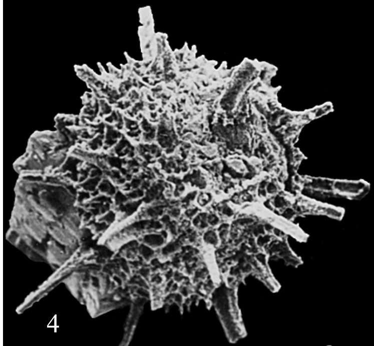
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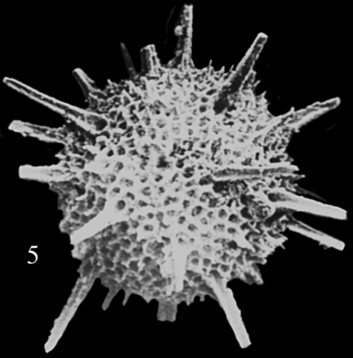
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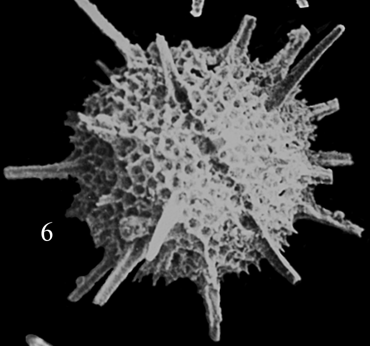
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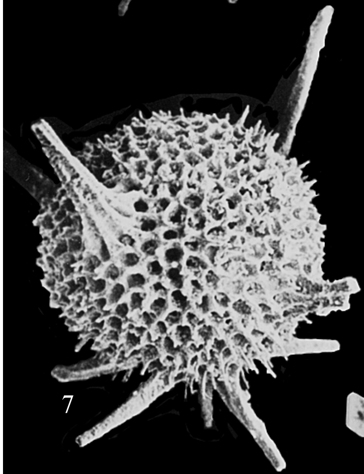
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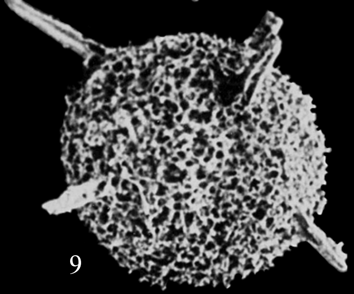
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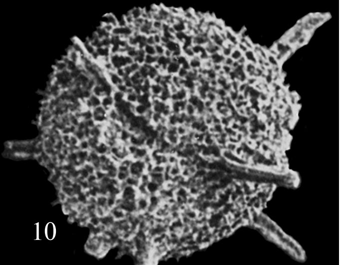
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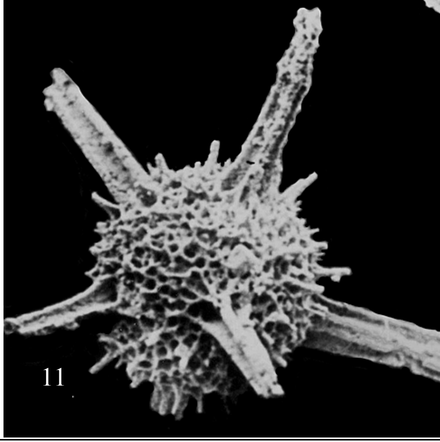
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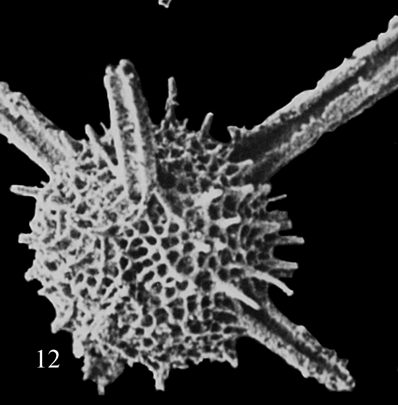
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the Egindy Formation is overlain conformably, through interbedding, by graywackes of the Zilair Formation. Interbeds of siliceous shales in graywackes of the Zilair Formation have yielded conodont assemblages with *Palmatolepis quadrantinodosalobata* Sann., *Nothognatella* sp., *Pelekysgnathus* sp., *Palmatolepis quadrantinodosalobata* Sann., *P. minuta minuta* Br. et M., *P. subperlobata* Br. et M., and *P. tenuipunctata* Sann., dated Early Famennian, lower part of the *crepida* Conodont Zone.

In the Famennian Age, the distribution of the "Ural" Radiolarian Assemblage narrowed somewhat (Bykova, 1955). It occurs in the Northern and Southern Urals and Volga–Ural Basin (Figs. 3, 19).

Famennian radiolarians have been recorded in the northern Caspian Depression in organogenic beds of the incipient Karachaganak bioherm (Figs. 3, 18b) (Afanasieva, 1987, 2000a).

Amon and Korovko (Amon and Korovko, 1992; Amon, 1995a) recorded Famennian radiolarians in the Rezh Structural–Facies Zone on the eastern slope of the Middle Urals (Figs. 1c, III, IV; 3).

Famennian radiolarians were examined by Afanasieva (2000a) in the Lemvin Zone of the Polar Urals and recorded for the first time in the region of the Saremboi–Lekkeyaga Swell of the northeastern part of the Timan–Pechora Basin (Figs. 3; 6b, XI; Table 7).

A new study and comparative analysis of Early Famennian radiolarians of the Lemvin Zone of the Polar Urals and western slope of the Middle Urals and revision of Famennian radiolarians of the Saremboi–Lekkeyaga Swell of the northeastern part of the Timan–Pechora Basin and the northern Caspian Region resulted in the establishment of five radiolarian assemblages within the Famennian Stage (Table 6):

- *Tetrentactinia barysphaera–Ceratoikiscum famennium*, Pripyat Depression, Unya River on the western slope of the Northern Urals, eastern slope of the Middle Urals, Southern Urals, and Northern Mugodzhary, (Nazarov, 1975, 1988, 1989; Kruchek and Nazarov, 1977; Amon and Korovko, 1992; Amon, 1995a);
- *Tetrentactinia barysphaera–Retientactinosphaera magnifica*, northeastern part of the Timan–Pechora Basin (Afanasieva, 2000a; Afanasieva and Amon, this work);
- *Tetrentactinia barysphaera–Caspiaza spinifera*, Lemvin Zone of the Polar Urals (Afanasieva, 2000a; Afanasieva and Amon, this work);
- *Haplentactinia alekseevi–Haplentactinia vilvaensis*, western slope of the Middle Urals (Afanasieva and Amon, this work);
- *Tetrentactinia barysphaera–Holoeciscus auceps*, northern slope of the Caspian Depression (Afanasieva, 2000a; Afanasieva and Amon, this work).

Early Famennian assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium*. The Famennian radiolarian assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* was established and examined for the first time by Nazarov (Kruchek and Nazarov, 1977; Nazarov, 1988, 1989) in the Elets Formation of the Pripyat Depression, Russian Platform, Belarus (Figs. 3, 18b, 20a). This assemblage has been recorded in (1) borehole Zapadno-Valaevskaya 1-P (3518–3629 m of depth) in the southern Pripyat Depression; (2) borehole Buinovichskaya 1-R (1670–1676 m of depth) in the central part of the Pripyat Depression; (3) boreholes Davydovskaya 27-R (3303–3336 m of depth) and Vostochno-Pervomaiskaya 1-R (3003–3006 m of depth) in the northern part of the Pripyat Depression (Fig. 20b). Radiolarians are accompanied by spicules of sponges, conodonts, plant detritus, goniatites, shells of pelecypods, gastropods, and ostracodes. The Elets Formation is dated Early Famennian based on goniatites, ostracodes, and conodonts. Conodonts include *Palmatolepis glabra glabra* Ulrich et Bassler, *P. minuta minuta* Branson et Mehl., *Polygnathus* sp., etc. (Kruchek and Nazarov, 1977).

Nazarov (Kruchek and Nazarov, 1977; Nazarov, 1988) marked a very high species diversity of the Famennian radiolarian assemblage from the Pripyat Depression, which includes 43 species of 22 genera (Table 7).

←

Explanation of Plate 16

Middle–Late Frasnian radiolarians of the Sakmara Zone of the Southern Urals and Northern Mugodzhary, assemblage with *Polyentactinia circumretia–Bientactinosphaera egindyensis*: spherical porous Sphaerellaria (1–8, 11–13) and spongy Spumellaria (9, 10).

Fig. 1. *Astroentactinia biaciculata* Nazarov, 1975, specimen GIN, no. 4046/109; scale bar, 54 μm.

Figs. 2 and 3. *Astroentactinia crassata* Nazarov, 1975: 2) specimen GIN, no. 4046/119; scale bar, 63 μm; (3) specimen GIN, no. 4046/120; scale bar, 59 μm.

Figs. 4–6. *Astroentactinia stellata* Nazarov, 1975: (4) specimen GIN, no. 4046/113; scale bar, 63 μm; (5) specimen GIN, no. 4046/126; scale bar, 63 μm; (6) specimen GIN, no. 4046/127; scale bar, 54 μm.

Fig. 7. *Moskovistella deorsiacus* (Nazarov et Ormiston, 1993), specimen GIN, no. 4046/107; scale bar, 63 μm.

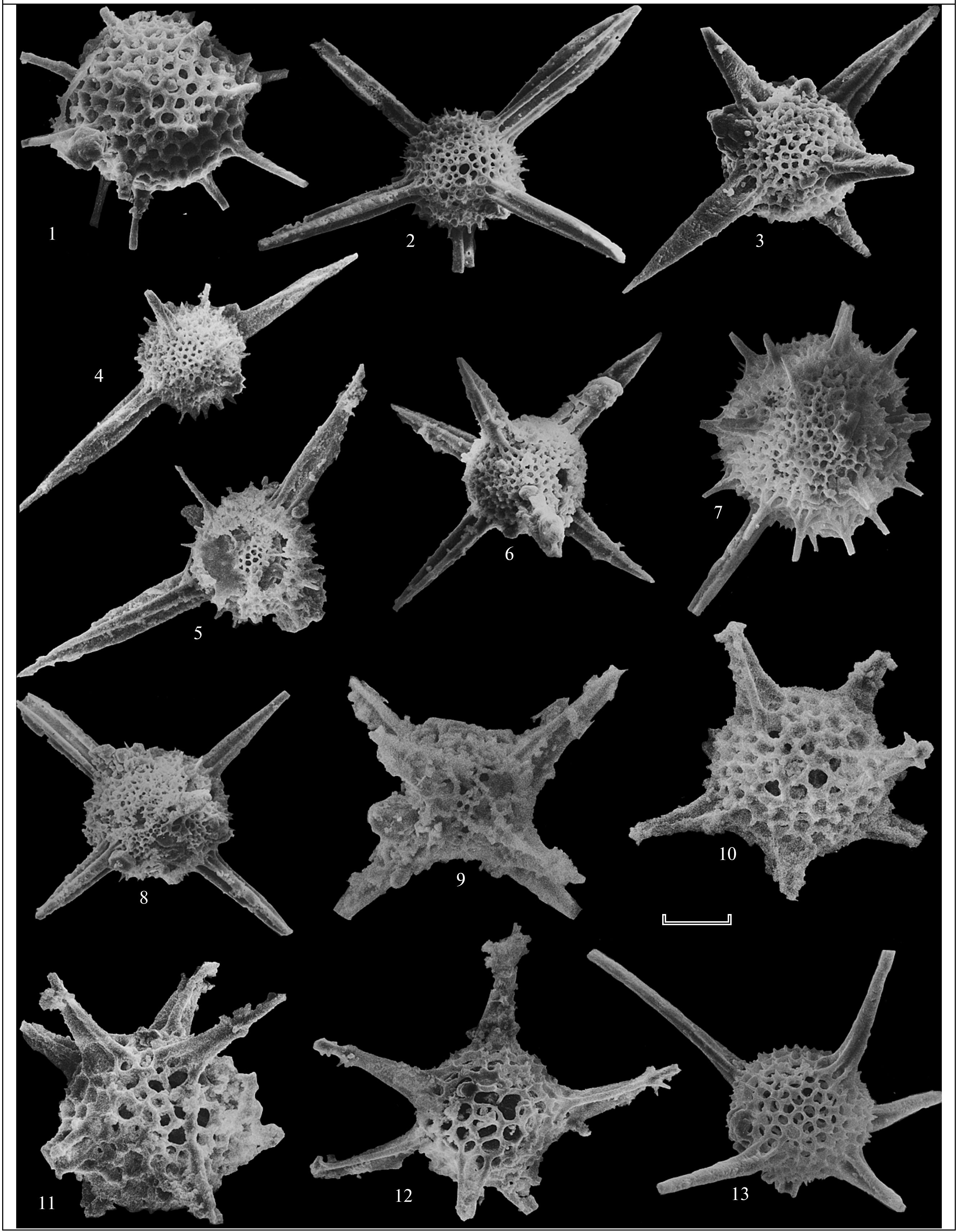
Fig. 8. *Astroentactinia paronae* (Hinde, 1899), specimen GIN, no. 4046/111; scale bar, 63 μm.

Figs. 9 and 10. *Spongentactinia diplostraca* (Foreman, 1963): (9) specimen GIN, no. 4046/123; scale bar, 89 μm; (10) specimen GIN, no. 4046/124; scale bar, 89 μm.

Figs. 11–13. *Bientactinosphaera grandis* (Nazarov, 1975): (11) specimen GIN, no. 4046/117; scale bar, 89 μm; (12) specimen GIN, no. 4046/115; scale bar, 89 μm; (13) specimen GIN, no. 4046/116; scale bar, 89 μm.

Upper Devonian, Frasnian Stage, Egindy Formation; Northern Mugodzhary, Kazakhstan, Aktyubinsk Region, Aitpaika River (Nazarov, 1984, pl. 37, figs. 1, 3, 4, 6; pl. XXXVIII, figs. 1, 3, 4, 6, 7; pl. XXXIX, figs. 1, 3, 5–7).

Plate 17



Spherical porous radiolarians of the class Sphaerellaria comprise 17 species of six genera (Pl. 20, figs. 1–9), which are dominated by the genera *Bientactinosphaera* (six species), *Entactinia* (four species), and *Astroentactinia* (four species) (Table 7). The most typical species of the assemblage are *Bientactinosphaera spinofoliacea* Nazarov et Afanasieva, *B. pulcherima* (Nazarov et Ormiston), *Entactinia comets* Foreman, and *Helioentactinia valavica* Nazarov et Ormiston (Pl. 20, figs. 3–9).

Spherical spongy and latticed radiolarians of the class Spumellaria are represented by 15 species of ten genera (Table 7; Pl. 20, figs. 10–14; Pl. 21, figs. 1–14), among which a notable position is only occupied by members of the genus *Tetrentactinia* (three species).

A distinctive feature of the assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* is the prevalence of spongy Spumellaria (ten species of six genera), of which the following are most notable *Pluristratoentactinia conspissata* Nazarov, *P. multisphaerata* Afanasieva et Amon, sp. nov., *Spongentactinella exilispina* (Foreman), *S. faceta* Nazarov et Ormiston, and *Tetrentactinia barysphaera* Foreman (Pl. 20, figs. 10–12; Pl. 21, figs. 9–14).

Latticed and reticulate Spumellaria are less diverse (five species of four genera), but abundant and very typical of this assemblage: *Retientactinosphaera unimana* (Nazarov), *Haplentactinia flagellifera* Nazarov, *Polyentactinia suavie* Nazarov, *P. rudihispida* Nazarov et Ormiston, and *Secuicollacta amoenitas* Nazarov (Pl. 20, figs. 13, 14; Pl. 21, figs. 1–8).

Spiny radiolarians of the class Aculearia are represented by 11 species of six genera (Table 7; Pl. 22, figs. 1–14). Spiny forms are dominated by members of the genus *Ceratoikiscum* with a well-developed patagium (Pl. 22, figs. 1, 2).

The lower boundary of the radiolarian assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* in the Pripyat Depression is not quite distinct, because radiolarians has not been recorded in the underlying Livny beds. In opinion of Nazarov (Kruchek and Nazarov, 1977; Nazarov, 1988), it probably corresponds to the point of mass occurrences of *Bientactinosphaera pulcherima* (Nazarov et Ormiston), *Retientactinosphaera unimana* (Nazarov), *Polyentactinia suave* Nazarov, and *Tetrentactinia barysphaera* Foreman (Pl. 20, figs. 4, 13, 14; Pl. 21, figs. 1–3, 11–14).

Early Famennian assemblage with *Tetrentactinia barysphaera–Retientactinosphaera magnifica*. Early Famennian radiolarians were investigated by Afanasieva (2000a, 2011) from siliceous–carbonate beds of the Zadonsk Formation of the Lower Famennian of borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth) of the Saremboi–Lekkeyaga Swell of the northeastern part of the Timan–Pechora Basin (Fig. 3; Fig. 6b, XI). This radiolarian assemblage corresponds to the *triangularis–crepida* Conodont Zone.

The Early Famennian radiolarian assemblage of the northeastern Timan–Pechora Basin includes 27 species of 16 genera (Fig. 15; Table 7).

Spherical porous radiolarians of the class Sphaerellaria include 14 species of seven genera, with the prevalence of the genera *Bientactinosphaera* (four species) and *Entactinia* (four species) (Pl. 23, figs. 1–12).

Spherical latticed and spongy radiolarians of the class Spumellaria are represented by nine species of six genera, of which the following are most notable: *Retientactinosphaera* (two species), *Polyentactinia* (two species), and *Spongentactinia* (two species) (Pl. 24, figs. 1–12).

Spiny radiolarians of the class Aculearia are represented by two species of the genus *Ceratoikiscum* (Table 7).

Discoidal radiolarians of the class Stauraxonaria include only two species of two genera: *Palaeodiscaleksus punctus* (Hinde) and *Primaritripus patella* (Hinde) (Pl. 23, figs. 13, 14).

Latticed *Polyentactinia rudihispida* Nazarov et Ormiston and *P. suave* (Nazarov), spongy *Spongentactinia diplostraca* (Foreman) and *Adamasirad cathedrarius* Afanasieva (Pl. 24, figs. 6, 7, 9, 11), and porous *Bientactinosphaera pinica* Afanasieva (Pl. 23, fig. 7) are

Explanation of Plate 17

Late Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Bientactinosphaera pittmani–Russirad kazintsovae*: spherical porous Sphaerellaria.

Fig. 1. *Astroentactinia biaciculata* Nazarov, 1975, specimen PIN, no. 5311/13902; scale bar, 40 μm.
Fig. 2. *Bientactinosphaera variacanthina* (Foreman, 1963), specimen PIN, no. 5311/13920; scale bar, 89 μm.
Fig. 3. *Bientactinosphaera egindyensis* (Nazarov, 1975), specimen PIN, no. 5311/13738; scale bar, 40 μm.
Fig. 4. *Bientactinosphaera obtusa* (Hinde, 1899), specimen PIN, no. 5311/13436; scale bar, 68 μm.
Fig. 5. *Bientactinosphaera pittmani* (Hinde, 1899), specimen PIN, no. 5311/13603; scale bar, 59 μm.
Fig. 6. *Bientactinosphaera pinica* Afanasieva, 2000, specimen PIN, no. 5311/13917; scale bar, 56 μm.
Fig. 7. *Helioentactinia stellaepolus* Aitchison, 1993, specimen PIN, no. 5311/13729; scale bar, 43 μm.
Fig. 8. *Ornatoentactinia beljaevorum* Afanasieva, 2000, specimen PIN, no. 5311/13907; scale bar, 79 μm.
Fig. 9. *Moskovistella sincera* Afanasieva, 2000, specimen PIN, no. 5311/13720; scale bar, 33 μm.
Fig. 10. *Moskovistella additiva* (Foreman, 1963), specimen PIN, no. 5311/13619; scale bar, 33 μm.
Fig. 11. *Moskovistella khaini* Afanasieva, 2000, specimen PIN, no. 5311/13623; scale bar, 33 μm.
Fig. 12. *Moskovistella victorialis* Afanasieva, 2000, specimen PIN, no. 5311/13916; scale bar, 33 μm.
Fig. 13. *Moskovistella deorsiacus* (Nazarov et Ormiston, 1993), specimen PIN, no. 5311/13728; scale bar, 43 μm.

Upper Devonian, Upper Frasnian Substage; Timan–Pechora Basin: (1–4, 6–9, 12, 13) Ukhta River, station 1, sample 7001; (5, 10, 11) borehole Vapovskaya-2056 (72 m of depth), sample 11.

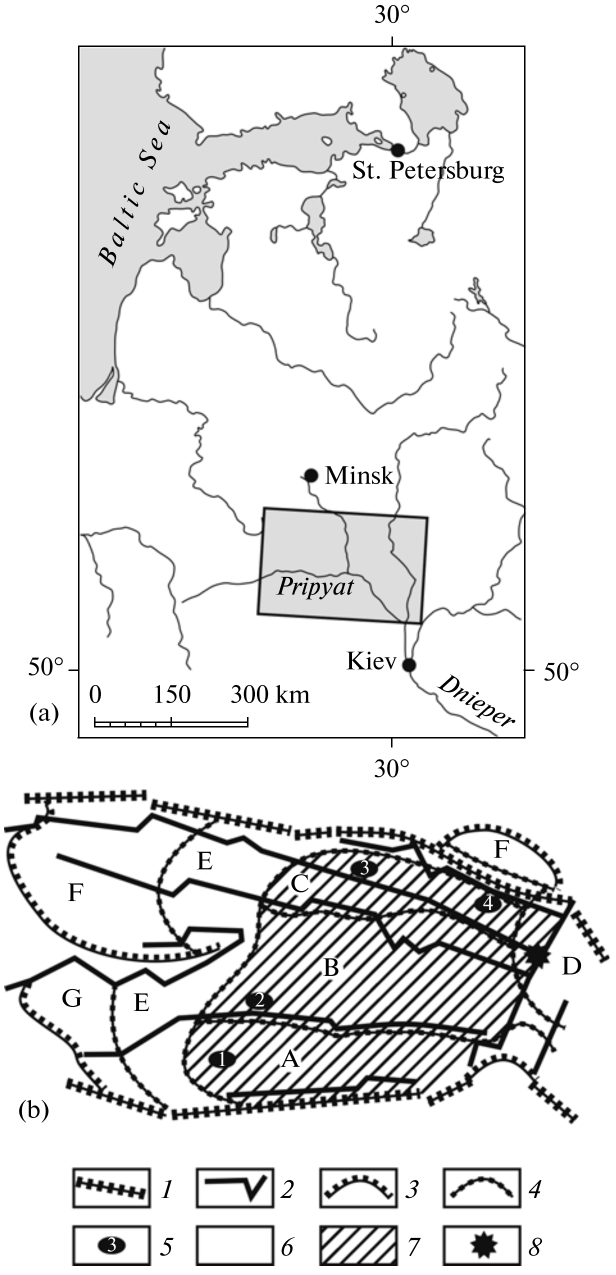


Fig. 20. Early Famennian radiolarians of the Pripyat Depression: (a) position of the working area and (b) lithologic-and-facies scheme of Elets deposits of the Pripyat Depression (Kruchek and Nazarov, 1977). Designations: (*1*) faults bordering trough; (*2*) stage-forming faults; (*3*) boundaries of Elets deposits; (*4*) boundaries of lithologic-and-facies zones; (*5*) local structures, containing radiolarians: (1) Zapadno-Valaevskaya, (2) Buinovichskaya, (3) Davydovskaya, and (4) Vostochno-Pervomaiskaya; (*6*) areas of depression facies with radiolarians: (A) carbonate–terrigenous, (B) carbonate, (C) clayey–carbonate, and (D) volcanogenic; (*7*) areas of shelf facies: (E) reef-building deposits, (F) shallow-water carbonate deposits, and (G) coastal deposits; (*8*) center of volcanic flows.

typical and abundant species of the Early Famennian radiolarian assemblage of the Timan–Pechora Basin.

A distinctive feature of the assemblage is the greatest abundance of *Tetrentactinia barysphaera* Foreman and *Retientactinosphaera magnifica* Afanasieva (Pl. 24, figs. 1–4, 12).

The Lower Famennian radiolarian association is considered according to *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006) as a new characteristic biostratigraphic assemblage with *Tetrentactinia barysphaera–Retientactinosphaera magnifica*, which corresponds to the Lower Famennian *triangularis–crepida* conodont zones (Table 6).

The new Late Devonian Lower Famennian biostraton of radiolarians (Table 6) occurs and is valid within the Timan–Pechora Basin.

Early Famennian assemblage with *Tetrentactinia barysphaera–Caspiaza spinifera*. The new rich association of Early Famennian radiolarians was investigated by us in samples on the Palnik-Yu River of the Lemvin Zone of the Polar Urals (Figs. 3; 6b, IX). The radiolarian assemblage considered corresponds to the lower part of the Famennian Stage, *triangularis–crepida* conodont zones.

The Early Famennian radiolarian assemblage from the Lemvin Zone of the Polar Urals consists of 53 species of 26 genera (Fig. 15; Table 7).

Spherical porous radiolarians of the class Sphaerellaria are represented by 21 species of six genera, which are dominated by the genera *Entactinia* (seven species), *Radiobisphaera* (five species), and *Bientactinosphaera* (four species) (Table 7; Pl. 25, figs. 1–12, 14–18); typical species are *Bientactinosphaera zuraevi* Afanasieva et Amon, sp. nov., *B. obtusa* (Hinde), *Entactinia bella* Afanasieva et Amon, sp. nov., *E. patorovaria* Afanasieva, *E. parva* Won, *Radiobisphaera assidera* (Nazarov), and *R. domanicensis* (Bykova) (Pl. 25, figs. 1, 2, 7, 8, 11, 12, 14, 16).

Spherical spongy and latticed radiolarians of the class Spumellaria are represented by 15 species of ten genera (Table 7; Pl. 26), which are dominated by the genera *Spongentactinia* (three species), *Pluristratoentactinia* (two species), *Tetragregnon* (two species), and *Haplentactinia* (two species); the most typical species, which determine the general appearance of the association are *Adamasirad cathedrarius* Afanasieva, *Pluristratoentactinia trisphaerata* Afanasieva et Amon, sp. nov., *Polyentactinia rudihispida* Nazarov et Ormiston, *Somphoentactinia multisphaerata* Afanasieva et Amon, sp. nov., *Spongentactinia marina* Afanasieva et Amon, sp. nov., *S. diplostraca* (Foreman), *S. polaris* Afanasieva et Amon, sp. nov., and *Tetrentactinia barysphaera* Foreman (Pl. 26, figs. 4, 6, 9–16).

Spiny radiolarians of the class Aculearia are represented by eight species of four genera (Table 7; Pl. 27, figs. 15–24), among which only the genera *Holoeciscus* (three species) and *Ceratoikiscum* (three species) are of special importance. The most abundant species are *Ceratoikiscum bujugum* Foreman, *C. perittacanthinum* Foreman, *Holoeciscus foremanae* Cheng, *H. auceps* Foreman, and *H. quasiauceps* Wang (Pl. 27, figs. 15, 16, 18–22).

Radiolarians with pylome from the order Pylomariata are represented by nine species of six genera (Table 7; Pl. 27, figs. 1–14), most notable of which are the genera *Archocyrtium* (three species) and *Caspiaza* (two species): *Archocyrtium amoenus* Afanasieva et Amon, sp. nov., *A. cibdelosphaera* (Foreman), *A. riedeli* Deflandre, *Caspiaza collaricostulata* Afanasieva, and *C. spinifera* Afanasieva.

A prominent distinctive feature of the assemblage is abundant spiny radiolarians of the genus *Holoeciscus* and radiolarians with pylome of the order Pylomariata (Pl. 27, figs. 1–14, 19–21).

It is noteworthy that spiny radiolarians of the genus *Holoeciscus* and forms with pylome of the order Pylomariata are widespread in North America and the Polar Urals. In Famennian radiolarian assemblages of Poland, the Pripyat Depression, and Timan–Pechora Basin, they have not been recorded.

Radiolarians with pylome of the genus *Caspiaza* (Pl. 27, figs. 8–13) are of particular interest. They appeared for the first time in the Famennian Age of the Polar Urals and, in the Famennian Age, were only distributed in this paleobasin. However, descendants of Ural *Caspiaza* expanded widely and were recorded in the Lower Carboniferous of the Caspian Region and Tien Shan.

We regard the Lower Famennian radiolarian association according to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006) as a new characteristic biostratigraphic assemblage with *Tetrentactinia barysphaera–Caspiaza spinifera*, which corresponds to the Lower Famennian, *triangularis–crepida* conodont zones (Table 6).

The new Late Devonian Lower Famennian radiolarian biostraton (Table 6) occurs and is valid in the Polar Urals.

Early Famennian assemblage with *Haplentactinia alekseevi–Haplentactinia vilvaensis*. A taxonomically poor, but very interesting association of Early Famennian radiolarians is investigated by us for the first time from the Kizelovo Depression on the western slope of the Middle Urals (Fig. 3), 2.5 km southeast of the town of Gremyachinsk, in samples of the Barminsk Beds on the Vilva River (Fig. 1, I). Judging from conodonts, the radiolarian assemblage considered corresponds to the lower part of the Famennian Stage of *triangularis–crepida* Zone (Bikbaev and Snigireva, 2005; Bikbaev et al., 2007).

The Early Famennian radiolarian assemblage of the western slope of the Middle Urals includes five species of two genera of latticed radiolarians of the class Spumellaria and one species of the class Aculearia (Table 7; Pl. 28).

Typical and dominant species of the new Early Famennian radiolarian assemblage are *Haplentactinia alekseevi* Afanasieva, *H. vilvaensis* Afanasieva et Amon, sp. nov., and *H. kuzminae* Afanasieva et Amon, sp. nov. (Pl. 28, figs. 2–4, 8–13). The species *Haplentactinia rhinophyusa* Foreman and *Polyentactinia circumretia* Nazarov et Ormiston are represented by individual specimens (Pl. 28, figs. 1, 5–7).

Spiny radiolarians are only represented by one species, *Palaeothalomnus arrhinia* (Foreman) (Fig. 15; Table 7) (Pl. 28, fig. 14).

We regard the Lower Famennian radiolarian association according to the *Stratigraficheskii kodeks Rossii* (Stratigraphic Code of Russia, 2006) as a new characteristic biostraton, beds with *Haplentactinia alekseevi–Haplentactinia vilvaensis*, which corresponds to the Lower Famennian, *triangularis–crepida* conodont zones (Table 6).

The new Late Devonian Lower Famennian radiolarian biostraton (Table 6) occurs and is valid in the Middle Urals.

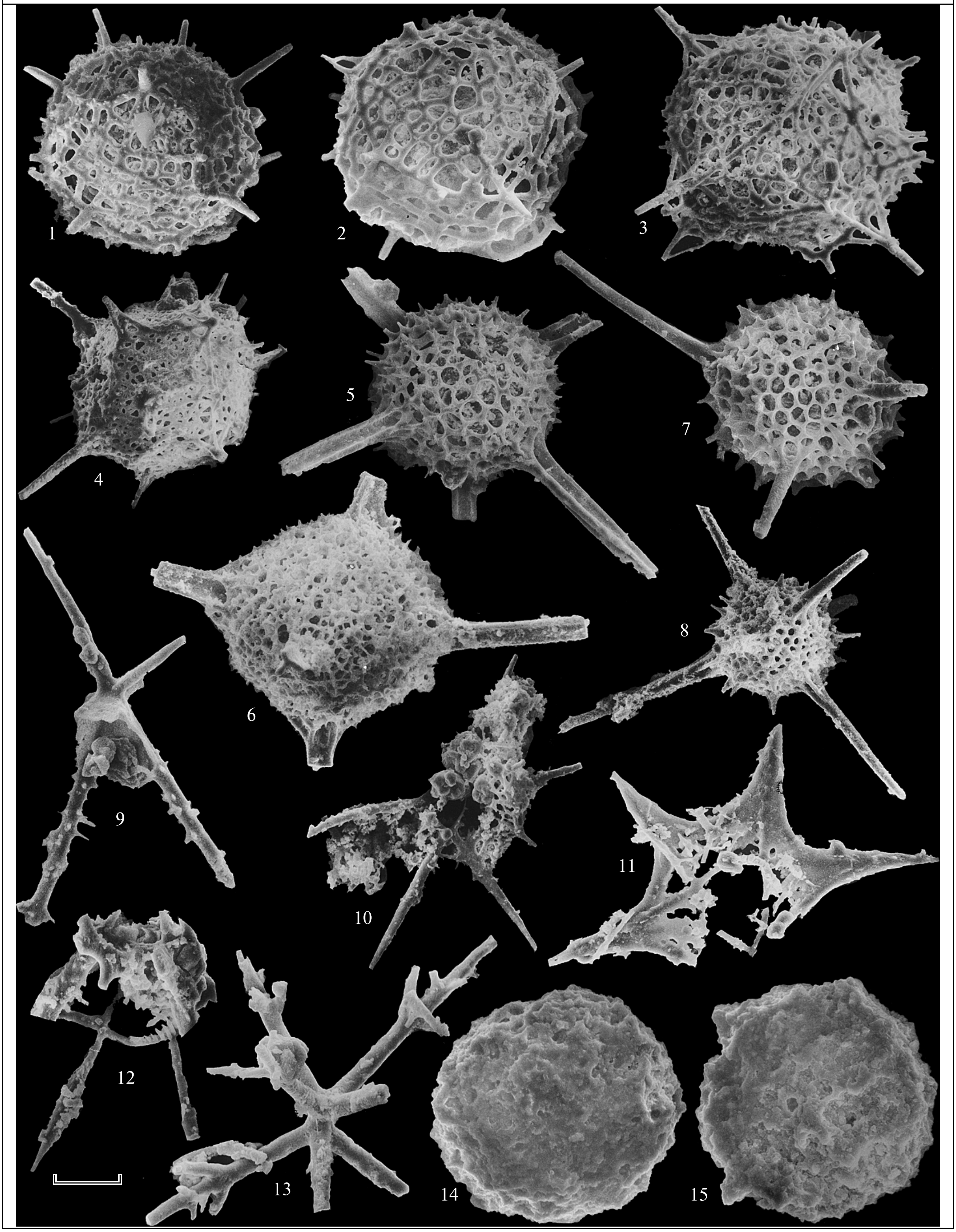
Early Famennian radiolarians of the Eastern slope of the Middle Urals. Early Famennian radiolarians have been recorded on the eastern slope of the Middle Urals in the Rezh Structural–Formational Zone (Amon and Korovko, 1992; Amon, 1995a; Korovko et al., 1999). Here, in the volcanogenic–siliceous strata of the Late Devonian of the Boroukhino Tectonic Plate, open by boreholes P-21 and P-31 (Fig. 1, III, IV), a relatively representative radiolarian association was established using thin sections. It corresponds in stratigraphic position to the *triangularis* Conodont Zone (Bikbaev and Snigireva, 2002).

The Early Famennian radiolarian assemblage from the Boroukhino Plate includes 21 species of 11 genera (Table 11): *Astroentactinia* cf. *biaciculata* Nazarov, *Astroentactinia* sp., *Bientactinosphaera* cf. *pulcherima* (Nazarov et Ormiston), *Bientactinosphaera* sp., *Ceratoikiscum* sp., *Entactinia* cf. *bella* Afanasieva et Amon, sp. nov., *E.* cf. *paula* Foreman, *Entactinia* sp., *Haplentactinia* cf. *flagellifera* Nazarov et Ormiston, *Haplentactinia* cf. *rhinophyusa* Foreman, *Haplentactinia* sp., *Helioentactinia* sp., *Polyentactinia* cf. *rudihipsida* (Nazarov et Ormiston), *P.* cf. *suave* (Nazarov), *Polyentactinia* sp., *Radiobisphaera* cf. *palimbola* (Foreman), *Somphoentactinia* cf. *somphozona* (Foreman), *Spongentactinia* cf. *nupera* Nazarov, *Spongentactinia* sp., *Tetrentactinia* cf. *barysphaera* Foreman, and *Tetrentactinia* sp.

Spherical porous radiolarians of the class Sphaerellaria include nine species of five genera, among which the genus *Entactinia* (three species) is most important.

Spherical spongy and latticed radiolarians of the class Spumellaria are represented by 11 species of five genera, most notable of which are the genera *Haplentactinia* (three species) and *Polyentactinia* (three species).

Plate 18



Spiny radiolarians of the class Aculearia are only represented by one species of the genus *Ceratoikiscum*.

The radiolarian assemblage is clearly dominated by the genera *Entactinia, Haplentactinia*, and *Polyentactinia* (Amon and Korovko, 1992).

Judging from the taxonomic composition, this association is most similar to the *Tetrentactinia barysphaera–Ceratoikiscum famennium* assemblage, despite the reduced species list and the absence of the index species *Ceratoikiscum famennium*.

At the same time, this radiolarian assemblage includes many spherical latticed radiolarians of the genera *Haplentactinia* and *Polyentactinia*. This is probably evidence of the transitional composition of the association from the *Tetrentactinia barysphaera–Ceratoikiscum famennium* epicontinental assemblage from the Pripyat Depression, dominated by spherical porous Sphaerellaria, to the *Haplentactinia alekseevi–Haplentactinia vilvaensis* assemblage from the western slope of the Middle Urals, composed exclusively of latticed Spumellaria and dwelling in local conditions of a deepwater gulf of the northern marginal area of the Ural Paleocean.

"Ural" radiolarian assemblage of the Famennian. In the Famennian Age, the distribution of radiolarians of the "Ural" Assemblage became somewhat narrower (Bykova, 1955) (Fig. 19).

In the Northern Urals, in the Vishera, Petrunikha, Storozhevaya, and Yaz'va river basins, many radiolarians of the "Ural" Assemblage have been recorded: *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella radiata* (Antropov), *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E. paulis* (Bykova), *E. subvasta* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, and *T. elegans* (Vissarionova), (Figs. 9d–9h, 11, 19; Table 5).

In Famennian limestones on the Sikaza River of the Southern Urals, only *Astroentactinia crassa* (Lipina), *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), and *Trochodiscus concavutas* Vissarionova occur (Figs. 11, 19; Table 5).

In western Bashkortostan, in Famennian limestone sections near the town of Tuimazy and villages of Kargaly and Elatminki, radiolarians of the "Ural" Assemblage occur, including *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E.* cf. *faveolata* Nazarov, *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus elegans* (Vissarionova), and *T. parva* (Bykova) (Figs. 11, 19; Table 5).

In the Famennian Stage of Tatarstan, near the villages of Verkhnii Uslon, Kamskoe Ust'e, and Shugurovo, there were the radiolarians *Astroentactinia* cf. *biaciculata* Nazarov, *A.* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E.* cf. *faveolata* Nazarov, *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), and *T. parva* (Bykova) (Figs. 11, 19; Table 5).

In the Samara Region, Famennian limestones near the town of Syzran and villages of Berezovka and Krasnovka have yielded *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Borisella* cf. *bykovae* Afanasieva, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E.* cf. *faveolata* Nazarov, *E. paulis* (Bykova), *E. tuberculata* (Lipina), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), *T. elegans* var. *subsphaera* (Vissarionova), and *T. parva* (Bykova) (Figs. 9a, 9b, 11, 19; Table 5).

Famennian limestones near the town of Pugachev and the village of Teplovka of the Saratov Region contain radiolarians *Astroentactinia* cf. *crassata* Nazarov, *A.* cf. *stellata* Nazarov, *Entactinia dagmarae* (Suleimanov) var. *crassitheca* (Antropov), *E.* cf. *faveolata* Nazarov, *E. paulis* (Bykova), *Trochodiscus concavutas* Vissarionova, *T. elegans* (Vissarionova), *T. elegans* var.

←

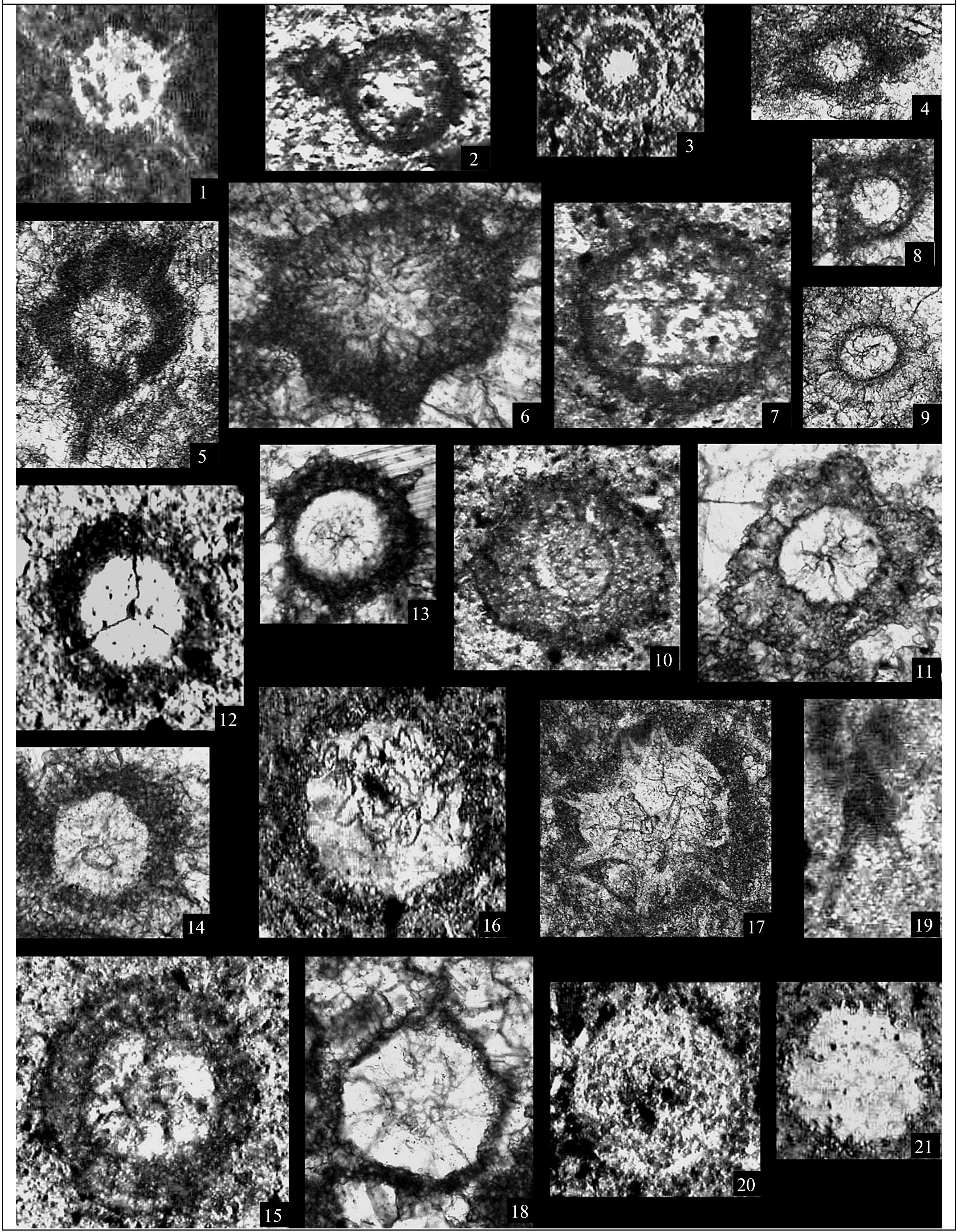
Explanation of Plate 18

Late Frasnian radiolarians of the Timan–Pechora Basin; assemblage with *Bientactinosphaera pittmani–Russirad kazintsovae*: spherical latticed (1–5) and spongy (6) Spumellaria, porous Sphaerellaria (7, 8), spiny Aculearia (9–13), and discoidal Stauraxonaria (14, 15).

Fig. 1. *Polyentactinia rudihispida* Nazarov et Ormiston, 1993, specimen PIN, no. 5311/13725; scale bar, 59 μm.
Fig. 2. *Polyentactinia circumretia* Nazarov et Ormiston, 1993, specimen PIN, no. 5311/13722; scale bar, 56 μm.
Fig. 3. *Polyentactinia zhamoidai* Afanasieva, 2000, specimen PIN, no. 5311/13919; scale bar, 56 μm.
Fig. 4. *Polyentactinia kossistekensis* Nazarov, 1975, specimen PIN, no. 5311/13501; scale bar, 63 μm.
Fig. 5. *Russirad kazintsovae* Afanasieva, 2000, specimen PIN, no. 5311/13931; scale bar, 59 μm.
Fig. 6. *Spongentactinella olafi* Afanasieva, 2000, specimen PIN, no. 5311/13435; scale bar, 59 μm.
Fig. 7. *Borisella bykovae* Afanasieva, 2000, specimen PIN, no. 5311/13930; scale bar, 43 μm.
Fig. 8. *Borisella maksimovae* Afanasieva, 2000, specimen PIN, no. 5311/13615; scale bar, 68 μm.
Fig. 9. *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 5311/13733; scale bar, 40 μm.
Fig. 10. *Ceratoikiscum bujugum* Foreman, 1963, specimen PIN, no. 5311/13734; scale bar, 68 μm.
Fig. 11. *Ceratoikiscum planistellare* Foreman, 1963, specimen PIN, no. 5311/13741; scale bar, 37 μm.
Fig. 12. *Ceratoikiscum ukhtensis* Afanasieva, 2000, specimen PIN, no. 5311/13912; scale bar, 63 μm.
Fig. 13. *Palaeothalomnus quadriramosum* (Foreman, 1963), specimen PIN, no. 5311/13740; scale bar, 33 μm.
Fig. 14. *Palaeodiscaleksus punctus* (Hinde, 1899), specimen PIN, no. 5311/12436; scale bar, 37 μm.
Fig. 15. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5311/12437; scale bar, 33 μm.

Upper Devonian, Upper Frasnian Substage; Timan–Pechora Basin: (1–3, 5, 7, 9–13) Ukhta River, station 1, sample 7001; (4, 6, 8) borehole Vapovskaya-2056 (72 m of depth), sample 11; (14, 15) Lyaiol River, outcrop 1360, sample 1'.

Plate 19



subsphaera (Vissarionova), and *T. parva* (Bykova) (Figs. 11, 19; Table 5).

Early Famennian assemblage with *Tetrentactinia barysphaera–Holoeciscus auceps*. The Caspian Depression is the deepest sedimentary basin of the world, the structural features of which in the Upper Paleozoic suggest that it belongs to structures of the "suboceanic" type. In the northern peripheral area of the Caspian Depression, the section of the Upper Paleozoic is composed of several relatively shallow-water carbonate strata of the Upper Devonian–Lower Permian.

The Karachaganak Mountain Range is an organogenic structure in the internal marginal zone south of the northern ledge of the Caspian Depression (Figs. 3, 18b).

Famennian deposits are observed in both extreme peripheral sections (boreholes 8, 14, 21, 28) and the sections in the central area of the Karachaganak bioherm (boreholes 17, 23) (Fig. 18b). They are composed everywhere of biomorphic detrital, algal–spherical, pelitomorphic, and spherical–patterned limestones.

Famennian organogenic–detrital spherical micrograin limestones contain many green tubular calciferous algae *Kamaena*, abundant small spherical foraminifers: *Archaesphaera minima* Suleimanov, *Vicinesphaera angulata* Antropov, *V. squailda* Antropov, *Parathurammina cushmani* Suleimanov, *P. suleimanovi* Lipina, *P.* ex gr. *stellata* Lipina, *P.* ex gr. *tuberculata* Lipina, *Radiosphaera panderosa* Reitlinger, *R. basilica* Reitlinger, *Sphaerella* sp., and individual foraminifers *Septatournayella* (Il'in et al., 1987).

Spherical skeletal remains in thin sections are traditionally regarded as small single-chamber foraminifers. At the same time, many of them undoubtedly belong to radiolarians because of the skeleton pattern, which is distinguished from foraminiferal tests. This association shares two forms with the "Ural" Radiolarian Assemblage, i.e., *Astroentactinia* cf. *stellata* Nazarov and *Entactinia* ex gr. *tuberculata* (Lipina) (Table 5).

Radiolarians have been extracted for the first time from Famennian rocks of the Karachaganak bioherm (Afanasieva, 1987, 2000a) and investigated in thin sections, except for individual electron microscope photographs of some samples treated with acetic acid and containing radiolarian remains (Pl. 24, figs. 13–15). The assemblage includes 12 species of 11 genera of typical Famennian radiolarians.

Spherical porous radiolarians of the class Sphaerellaria are represented by six species of five genera: *Astroentactinia* sp., *Bientactinosphaera* sp., *Borisella praenuntia* (Nazarov et Ormiston), *Entactinia micula* Foreman, *Entactinia* sp., and *Radiobisphaera domanicensis* (Bykova).

Spherical spongy radiolarians of the class Spumellaria are represented by three species of three genera: *Pluristratoentactinia* cf. *conspissata* Nazarov, *Somphoentactinia* cf. *somphozona* (Foreman), and *Tetrentactinia barysphaera* Foreman.

Radiolarians with pylome of the order Pylomariata are represented by one species, *Caspiaza collaricostulata* Afanasieva.

Spiny radiolarians of the class Aculearia are represented by two species of two genera, *Holoeciscus auceps* Foreman and *Palacantholithus* sp.

The distribution of radiolarians in the Devonian section of the Karachaganak bioherm and taxonomic com-

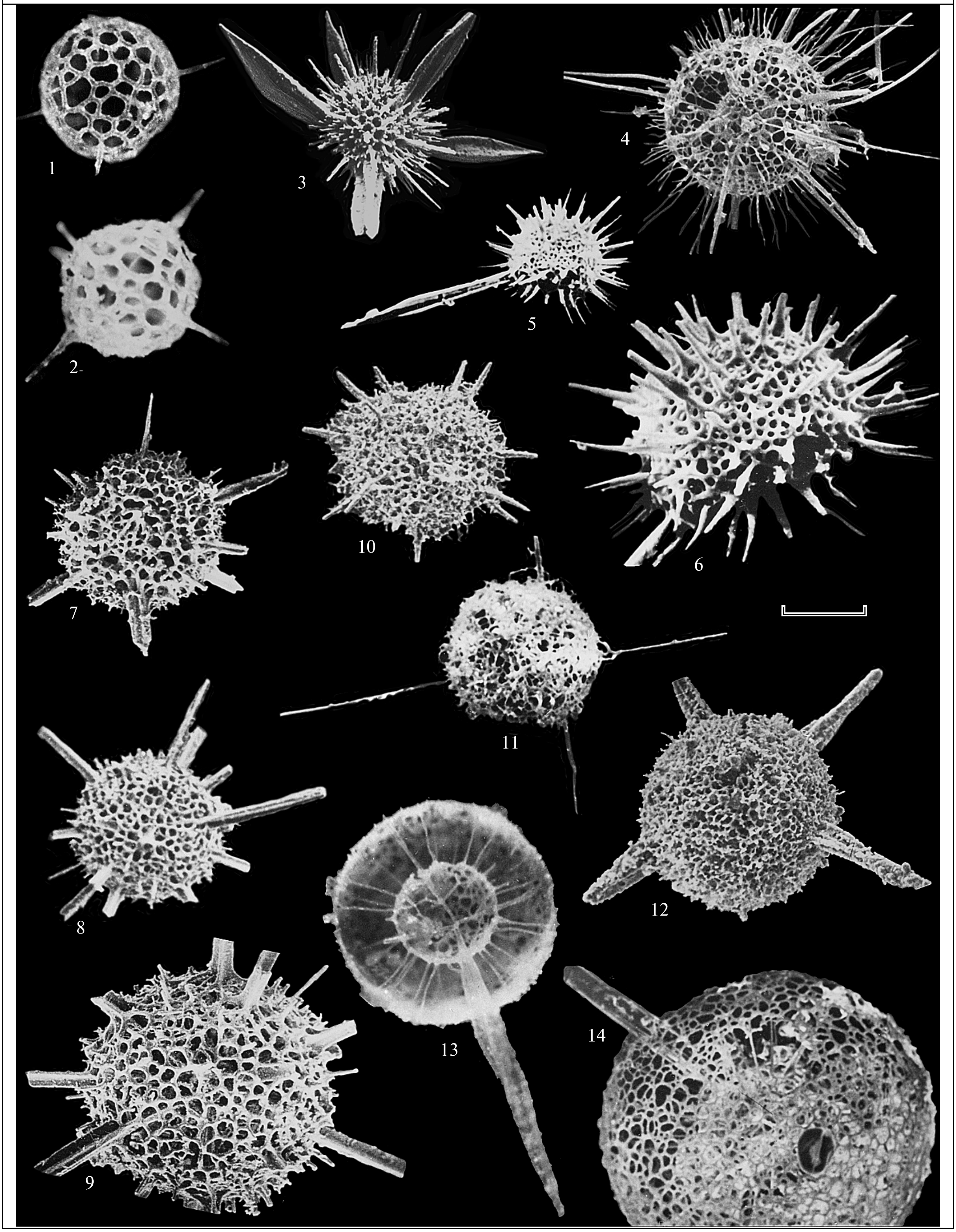
Explanation of Plate 19

Late Frasnian radiolarians of the Middle Urals; assemblage with *Bientactinosphaera pittmani–Russirad kazintsovae*: spherical porous Sphaerellaria (1–8), spongy (9–15) and latticed (16–18) Spumellaria, radiolarians with pylome from the order Pylomariata, Nassellaria (19), and discoidal Stauraxonaria (20, 21).

Fig. 1. *Bientactinosphaera* cf. *pittmani* (Hinde, 1899), specimen IGG, no. 5510/045-1-06.
Fig. 2. *Radiobisphaera* cf. *rozanovi* Afanasieva et Amon, 2009, specimen IGG, no. 5510/053-15.
Fig. 3. *Bientactinosphaera* cf. *pinica* Afanasieva, 2000, specimen IGG, no. 5510/053-14.
Fig. 4. *Bientactinosphaera* cf. *egindyensis* (Nazarov, 1975), specimen IGG, no. 5510/623.
Fig. 5. *Astroentactinia* cf. *paronae* (Hinde, 1899), specimen IGG, no. 5510/619.
Fig. 6. *Astroentactinia* cf. *biaciculata* Nazarov, 1975, specimen IGG, no. 5510/430.
Fig. 7. *Entactinia* cf. *bella* Afanasieva et Amon, sp. nov., specimen IGG, no. 5510/053-75.
Fig. 8. *Moskovistella* cf. *khaini* Afanasieva, 2000, specimen IGG, no. 5510/331.
Figs. 9–11. *Spongentactinia* cf. *fungosa* Nazarov, 1975: (9) specimen IGG, no. 5510/565; (10) specimen IGG, no. 5510/052–95; (11) specimen IGG, no. 5510/423.
Figs. 12–14. *Spongentactinella* cf. *veles* (Foreman, 1963): (12) specimen IGG, no. 5510/045-1-13, (13) specimen IGG, no. 5510/355, (14) specimen IGG, no. 5510/465.
Fig. 15. *Adamasirad* cf. *cathhedrarius* (Afanasieva, 2000), specimen IGG, no. 5510/053-91.
Fig. 16. *Polyentactinia* cf. *circumretia* Nazarov et Ormiston, 1993, specimen IGG, no. 5510/045-1-30.
Fig. 17. *Polyentactinia* cf. *kossistekensis* Nazarov, 1975, specimen IGG, no. 5510/510.
Fig. 18. *Russirad* cf. *kazintsovae* Afanasieva, 2000, specimen IGG, no. 5510/354.
Fig. 19. *Archocyrtium* cf. *riedeli* Deflandre, 1960, specimen IGG, no. 5510/049-4.
Fig. 20. *Palaeodiscaleksus* cf. *punctus* (Hinde, 1899), specimen IGG, no. 5510/053-78.
Fig. 21. *Palaeodiscaleksus* cf. *tumefactus* Afanasieva et Amon, 2008, specimen IGG, no. 5510/045-18-03.

Upper Devonian, Upper Frasnian Substage; Middle Urals, eastern slope, Sverdlovsk Region, Rezh River, type section "Sokharevo," outcrop 5510: (8, 19) Bed 5; (1, 12, 13, 15, 18, 21) Bed 6; (6, 10, 11) Bed 12; (9, 14, 16) Bed 14; (2, 3, 7, 4, 5, 17, 20), Bed 15; magnification: (1–4, 7–10, 12–15, 19–21) × 150; (5, 6, 11, 16–18) × 160; photographs (1–3, 7, 10, 12, 15, 17, 19–21) taken by E.O. Amon and (4–6, 8, 9, 11, 13, 14, 16, 18) by A.L. Anfimov.

Plate 20



position of the assemblage allowed us to recognize a new biostraton, beds with *Tetrentactinia barysphaera–Holoeciscus auceps*, the age of which is confirmed by the data on foraminifers and conodonts (Shumova et al., 1981; Klenina and Ovnatanova, 1986; Il'in et al., 1987).

Geographical Distribution of Famennian Radiolarians

Foreman (1963) described a rich Early Famennian radiolarian association near Lake Erie, Ohio, North America (Fig. 3). These radiolarians come from three carbonate nodules (Milan 4, Milan 33, Norfolk) of a siliceous shaly formation of the Ohio Shale of the Huron Member, the bottom of which corresponds to the beginning of the Lower Famennian *triangularis* Conodont Zone (Over, 2007).

Foreman (1963) made a new step in the study of Devonian radiolarians. The radiolarian assemblage consists of 58 species (Table 7) and is represented by many spherical and spiny forms, many of which (*Bientactinosphaera variacanthina, Ceratoikiscum bujugum, Entactinia cometes, E. crustescens, E. herculea, Haplentactinia rhinophyusa, Spongentactinia diplostraca, Spongentactinella exilispina, Tetrentactinia barysphaera*, etc.) occur in limestones of the Lower Famennian of the Pripyat Depression, Urals, and Timan–Pechora Basin. On the other hand, North America deposits have yielded *Holoeciscus auceps*, which is not recorded in Belarus, but occurs in the Famennian of the Timan–Pechora Basin, and the North American species *Corythoecia dichoptera* has not been recorded in Belarus or the Timan–Pechora Basin. On the contrary, various Palaeoscenidiidae (particularly *Palhindeolithus* and *Palaeothalomnus*) and some Astroentactiniinae are more diverse in the Lower Famennian of the Pripyat Depression and Timan–Pechora Basin than in shales of Ohio.

Holdsworth et al. (1978) described Famennian radiolarians from eastern Alaska, which are represented by many spongy and porous spherical species; radiolarians from Alaska are distinguished by the presence of Pylentonemiidae with pylome. The assemblage has been recorded in the lower part of black layered siliceous shales of the Ford Lake Shale Formation, which outcrops on the northern bank of the Yukon River (Fig. 3). The Formation is dated based on brachiopods, gastropods, bryozoans, foraminifers, and wood remains of the Late Devonian–Late Mississippian age. Holdsworth and coauthors assign the radiolarian association from the Ford Lake Formation to the Late Famennian, because it lacks Albaillellidae, which are characteristic of the Lower Carboniferous.

Subsequently, Won et al. (1999) found a Late Famennian radiolarian assemblage in the Chulitna Terrane in the south of central Alaska (Fig. 3).

Beyond the Urals and eastern Russian Platform, Famennian radiolarians have been recorded in the lower part of the siliceous–terrigenous strata of the Late Devonian–Early Carboniferous, which are recognized in a wide area of the Kolyma Uplift in Eastern Siberia (Fig. 3) under the name Duksunda Formation. In the stratotypic area of the formation in the Duksunda River Basin, in limestone interbeds, among dark siltstones, tuff-siltstone, clayey and siliceous shales radiolarians were accompanied by foraminifers of the *Quasiendothyra communis* and *Quasiendothyra kobeitusana* zones (Famennian–Early Tournasian). The Famennian radiolarian assemblage from the Kolyma region is distinguished by the presence of only spherical forms (Nazarov et al., 1981; Nazarov, 1988).

An analogous radiolarian assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* has been recorded in the condensed section of the Alai Mountains of Central Asia and in ophiolitic formations of the Chara Zone of eastern Kazakhstan (Fig. 3) (Nazarov, 1988, 1989). Later, Iwata et al. (1994, 1997) confirmed and expanded these results. The Famennian radiolarian assemblage established by these authors in light brown cherts of the Urumbaevo Formation in the southern Chara Zone contains more than ten species, including the index species *Tetrentactinia barysphaera.* Note that, in opinion of these authors, Devonian silicides of the Chara Ophiolitic Zone were formed in various geodynamic and paleo-

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Explanation of Plate 20

Early Famennian radiolarians of Belarus; assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium*: spherical porous Sphaerellaria (1–9), spongy (10–12) and reticulate (13, 14) Spumellaria.

Figs. 1 and 2. *Borisella praenuntia* (Nazarov et Ormiston, 1993): (1) specimen GIN, no. 4467/8; scale bar, 98 μm; (2) specimen GIN, no. 4467/10; scale bar, 98 μm.

Fig. 3. *Bientactinosphaera spinofoliacea* Nazarov et Afanasieva, 2000, specimen GIN, no. 4467/111; scale bar, 98 μm.

Fig. 4. *Bientactinosphaera pulcherima* (Nazarov et Ormiston, 1993), specimen GIN, no. 4467/95; scale bar, 63 μm.

Figs. 5 and 6. *Entactinia comets* Foreman, 1963, specimen GIN, no. 4467/108: (5) scale bar, 80 μm and (6) fragment, scale bar, 40 μm.

Figs. 7–9. *Helioentactinia valavica* Nazarov et Ormiston, 1993: (7) specimen GIN, no. 4467/8104; scale bar, 98 μm; (8, 9) specimen GIN, no. 4467/126: (8) scale bar, 85 μm) and (9) fragment, scale bar, 50 μm.

Fig. 10. *Somphoentactinia* sp., specimen GIN, no. 4467/129; scale bar, 117 μm.

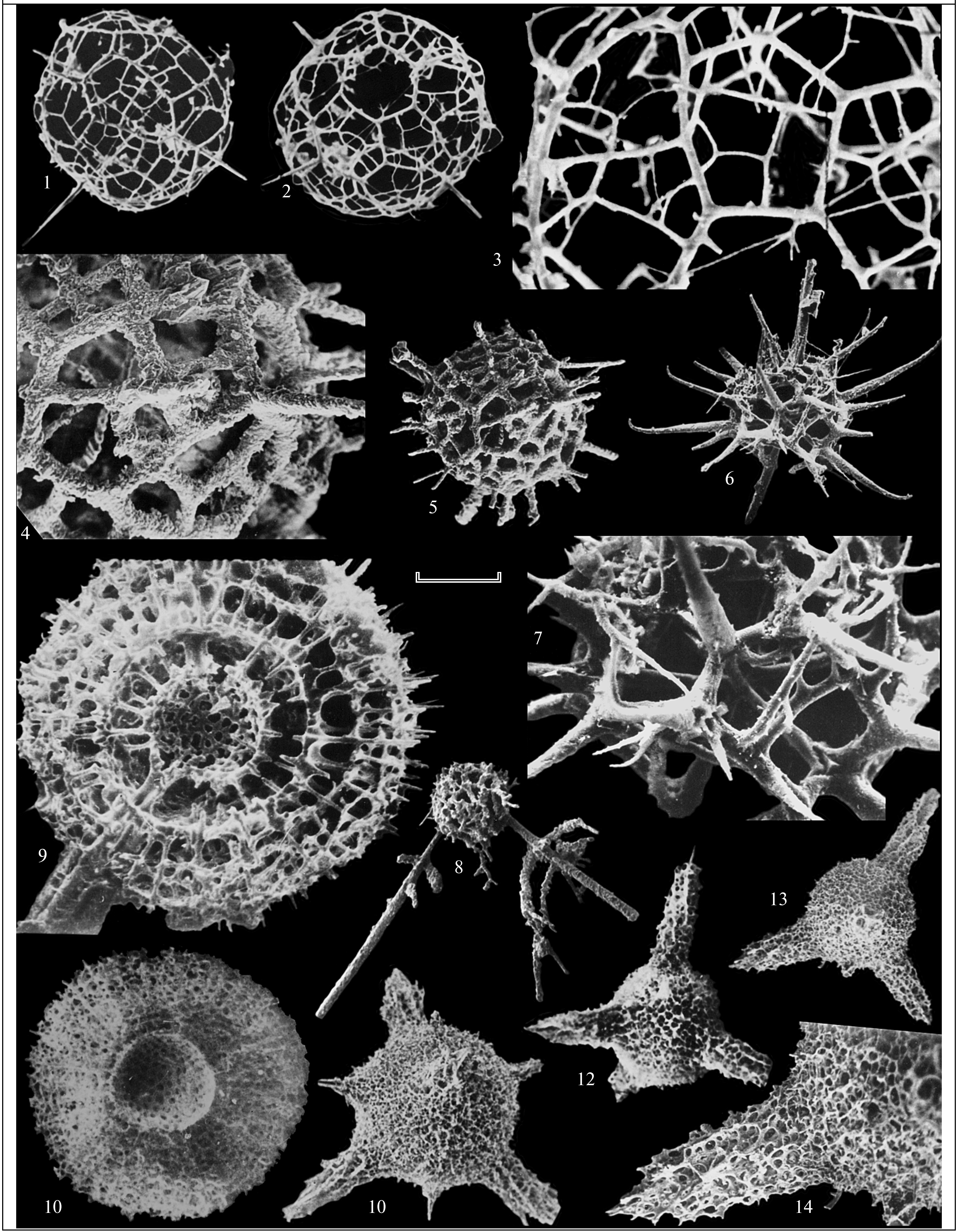
Fig. 11. *Spongentactinella faceta* Nazarov et Ormiston, 1993, specimen GIN, no. 4467/116; scale bar, 98 μm.

Fig. 12. *Spongentactinella exilispina* (Foreman, 1963), specimen GIN, no. 4467/113; scale bar, 30 μm.

Figs. 13 and 14. *Retientactinosphaera unimana* (Nazarov, 1977): (13) specimen GIN, no. 4467/13; scale bar, 150 μm; (14) specimen GIN, no. 4467/117; scale bar, 86 μm.

Upper Devonian, Lower Famennian Substage, Elets Formation; Belarus, Pripyat Depression, borehole Zapadno-Valavskaya 1R (after Nazarov, 1984, pl. 40, figs. 1–4, 6, 7; pl. XLI, figs. 2, 4–6; pl. XLIV, figs. 3, 4, 7; pl. XLV, fig. 7).

Plate 21



geographic conditions of the Paleoasian Ocean, i.e., on the ocean bottom, slopes of underwater mountains and mountain ridges, and in the basin before the island arch.

Aitchison (1988a, 1988b) revealed and described an unusual radiolarian assemblage of the Late Devonian–Early Mississippian age from clayey–siliceous shales of the Cara Formation and the Gundahl Assemblage from the Gwydir Terrane, New England Range, eastern Australia (Fig. 3). Judging from the generic composition, including *Archocyrtium, Helenifore, Palaeoscenidium, Holoeciscus*, and others, this assemblage is correlated with the Upper Devonian radiolarian assemblage of Germany, considered above. This assemblage has little in common with the Devonian radiolarian association of the Ural Mountains; this is probably accounted for by the presence in the eastern Australian assemblage of Early Carboniferous taxa.

The data on radiolarians from the Gwydir Terrane of eastern Australia changed the concept of the age and developmental model of the terrane and provided a more precise estimate of the age of metamorphism. In particular, it turned out that it is much younger than was previously supposed. In addition to Late Devonian–Early Mississippian radiolarians, the Gwydir Terrane has yielded Early Carboniferous radiolarians from limestones and clayey–siliceous rocks of the Veismens Arm Formation and Hastings Block, New England Fold Belt (Ishiga, 1988; Ishiga and Letch, 1988).

In Western Europe, Schmidt-Effing (1988) recorded an analogue of the Famennian assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium* in flinty slates of Frankenwald (Bavaria, Germany) (Fig. 3). Radiolarians are represented by spherical, bilateral symmetrical, and spiny taxa (more than 30 species). The Frankenwald assemblage is dated Late Famennian based on co-occurrence with conodonts (Schmidt-Effing, 1988; Kiessling and Tragelehn, 1994). The section wherefrom radiolarians come (Probe 5233) was described in detail (Gandl and Sdzuy, 1981) and this was the first record of Famennian radiolarians in Europe in an indigenous position.

Braun (1990a) found a Famennian radiolarian assemblage in siliceous pebbles in the Pleistocene talus of the Main River valley in its lower reaches, near Frankfurt-on-Main (Fig. 3). The source of pebbles is the flinty slates of Frankenwald mentioned above. Somewhat later, Braun et al. (1992) described a similar radiolarian assemblage from northern Vogesen in Alsace.

Schwartzapfel and Holdsworth (1996) studied the Upper Famennian–Mississippian sections of Arbuckle and Ouachita mountains and Criner Hills of Oklahoma (Fig. 3) and found rich and diverse radiolarian assemblages of good preservation in claystones, carbonate and phosphate nodules, and flinty slates rich in organic matter. The analysis of stratigraphic distribution and monographic description of 185 radiolarian species, with the establishment of two new subfamilies, three new genera, and 50 new species resulted in the development of a new biostratigraphic scale of radiolarians from the Upper Devonian–Lower Carboniferous of North America, including ten radiolarian zones. In the Famennian part of the section, the following four zones were established: *Pylentonema* spp.–*Staurentactinia* spp. (Middle Famennian?), *Staurentactinia* spp.–*Lapidopiscum* spp. (Upper Famennian), *Lapidopiscum* spp.–*Protoalbaillella deflandrei* (terminal Upper Famennian), and *Protoalbaillella deflandrei–Holoeciscus* spp. (terminal Famennian–basal Kinderhookian).

Wang (1997) described a diverse assemblage of Famennian radiolarians of northwestern China (northern Xinjiang Province) (Fig. 3), including 21 species of 12 genera. This fauna consists of two morphological groups; the first is dominated by spherical radiolarians of the family Entactiniidae and the second comprises members of the families Ceratoikiscidae and Holoeciscidae. These radiolarians were regarded as a Famennian biostratigraphic assemblage with *Holoeciscus foremanae.*

←

Explanation of Plate 21

Early Famennian radiolarians of Belarus; assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium*: spherical latticed (1–8) and spongy (9–14) Spumellaria.

Figs. 1–3. *Polyentactinia suavie* (Nazarov, 1977): (1) specimen GIN, no. 4467/119; scale bar, 89 μm; (2, 3) specimen GIN, no. 4467/118: (2) scale bar, 89 μm and (3) fragment, scale bar, 48 μm.

Figs. 4 and 5. *Polyentactinia rudihispida* Nazarov et Ormiston, 1993, specimen GIN, no. 4467/90: (4) fragment, scale bar, 43 μm; (5) scale bar, 120 μm.

Figs. 6 and 7. *Secuicollacta amoenitas* Nazarov et Ormiston, 1993, specimen GIN, no. 4467/100: (6) scale bar, 73 μm; (7) fragment, scale bar, 21 μm.

Fig. 8. *Haplentactinia flagellifera* Nazarov et Ormiston, 1993, specimen GIN, no. 4467/115; scale bar, 120 μm.

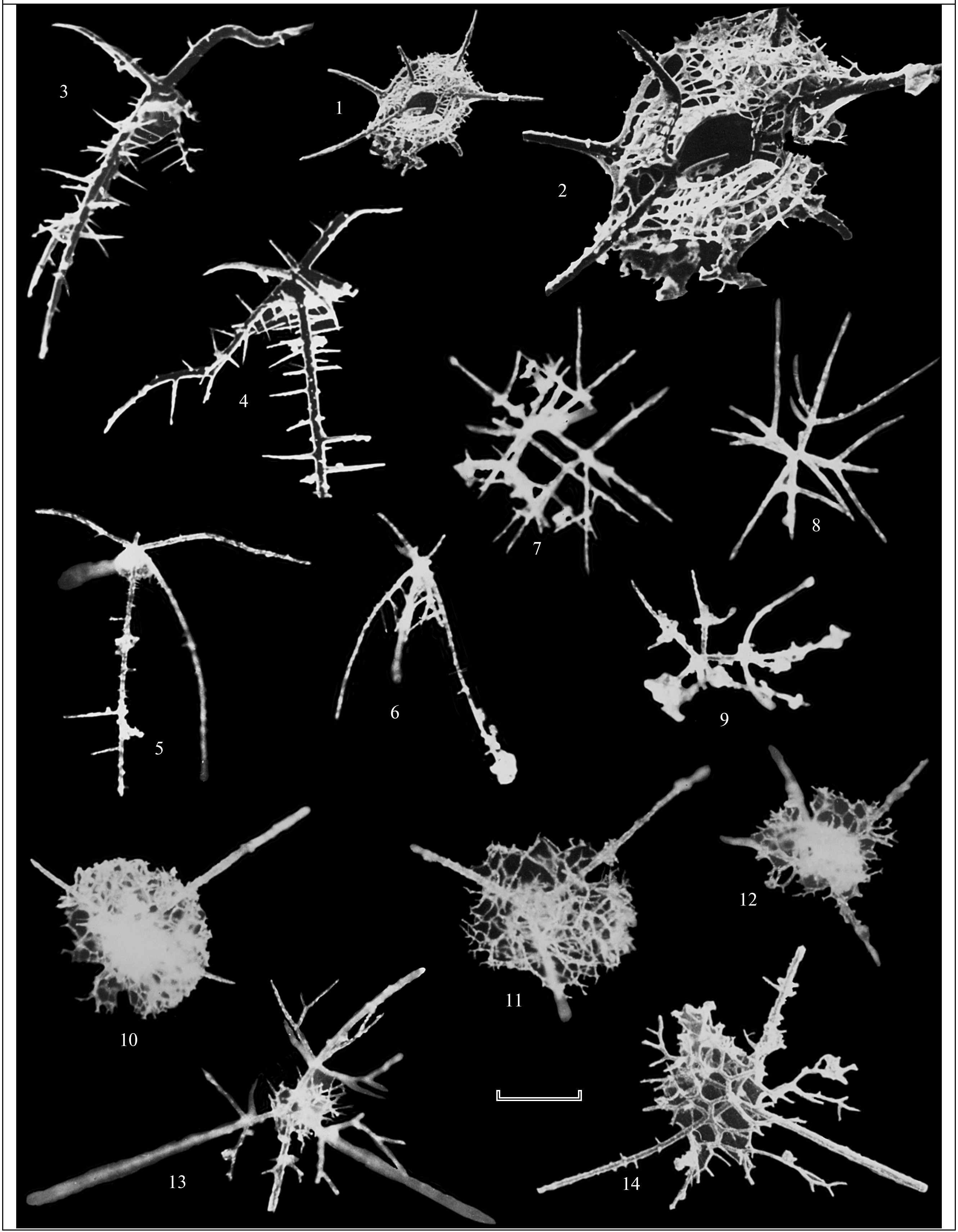
Fig. 9. *Pluristratoentactinia conspissata* Nazarov, 1981, specimen GIN, no. 4467/124; scale bar, 33 μm.

Fig. 10. *Pluristratoentactinia multisphaerata* Afanasieva et Amon, sp. nov., specimen GIN, no. 4467/90; scale bar, 85 μm.

Figs. 11–14. *Tetrentactinia barysphaera* Foreman, 1963: (11) specimen GIN, no. 4467/122; scale bar, 162 μm; (12) specimen GIN, no. 4467/123; scale bar, 130 μm; (13, 14) specimen GIN, no. 4467/121: (13) scale bar, 140 μm; (14) fragment, scale bar, 50 μm.

Upper Devonian, Lower Famennian Substage, Elets Formation; Belarus, Pripyat Depression, borehole Zapadno-Valavskaya 1R (Nazarov, 1984, pl. XLI, fig. 1; pl. XLII, figs. 1–5; pl. XLIII, figs. 1, 2, 4–6; pl. XLIV, figs. 1, 2, 6; Nazarov, 1988, pl. VI, fig. 1).

Plate 22



Racki (Racki and Balinski, 1998; Racki, 1999, Racki et al., 2002) recorded abundant radiolarians of poor, satisfactory, and good preservation in the reference section of the Kowala Basin (Holy Cross Mountains, central Poland) (Fig. 3) at the Frasnian–Famennian boundary (*linguiformis–crepida* conodont zones) in the rhythmically built carbonate strata with chert interbeds, which corresponds to a postreef phase in the evolution of the shelf. A preliminary study of the radiolarian assemblage from the Famennian part of the section, which is accompanied by conodonts of the *crepida* Zone has shown that this is a rather unusual assemblage, which is characterized by abundant spherical taxa and the absence of bilateral symmetrical species of Ceratoikiscidae and Palaeoscenidiidae. Typical species of this assemblage are *Astroentactinia coryacantha* Nazarov et Ormiston, *A. paronae* (Hinde), *A. stellata* Nazarov, *Bientactinosphaera assidera* (Nazarov), *B. grandis* (Nazarov), *B. echinata* (Hinde), *Entactinia additiva* Foreman, *Spongentactinia somphormis* Foreman, *Haplentactinia rhinophyusa* Foreman, and *H. inaudita* Nazarov (Vishnevskaya et al., 1997, 2002); however, it includes an intricate mixture of Frasnian and Famennian elements.

At the beginning of the 21st century, Wang et al. (2000, 2003), describing Devonian radiolarians from four new localities in Yunnan, Guizhou, Guangxi, and Hunan provinces, southern China (Fig. 3), established an abundant and diverse Late Devonian (Famennian) assemblage of *Holoeciscus foremanae*, with morphotypic variations of members of *Holoeciscus laticlavium*.

Spiller (2002) emphasized a great significance of radiolarians (12 localities from siliceous beds limited by breaks of blocks) of the Late Devonian (Famennian), Early Carboniferous (Tournasian–Visean), and Early Permian age for gaining an insight into the paleogeodynamic conditions of the Bentong–Raub Sutural Zone of the Malacca Peninsula, Malaysia (Fig. 3).

CHAPTER 3. WESTERN SIBERIA AND RUDNY ALTAI

The first records of Devonian radiolarians in Western Siberia were in the Barabinskaya reference borehole (2234–2470 m of depth) in the southern West Siberian Plain, wherefrom Lipman has established a radiolarian assemblage referred to the Silurian?–Devonian (Balakhmatova and Lipman, 1955; Osyko, 1958) (Fig. 21). In the northwestern West Siberian Plain, Devonian radiolarians were recorded in a section of borehole 35-PR of the Verkhnerechenskaya area (485–482 m of depth). In the radiolarian assemblage, Lipman determined *Cenospaera* sp., *Thecosphaera* sp., *Cenellipsis* sp., *Druppula* sp., *Carposphaera* sp., *Cromyosphaera* sp., *Dorysphaera* sp., *Xiphospaera* sp., *Trilonche* sp., *Sphaerostylits* sp., *Amphyspaera* sp., *Staurostylus* sp., *Stylostaurus* sp., *Staurolonche* sp., and *Staurocoruium* sp. Unfortunately, Lipman used the generic names of the system of Haeckel (1887), which has not been used in the description of Paleozoic radiolarians since the 1970s, because new classifications have been developed (Foreman 1963; Nazarov, 1973, 1975, 1988; Afanasieva, 2000a, 2002; Afanasieva and Amon, 2003, 2006a; Afanasieva et al., 2005d).

Lipman also recorded a radiolarian assemblage of similar composition in Tuiskaya borehole 1-R (2432–2439 m of depth), which is also located in southern Western Siberia (Bogush et al., 1975). Sadrislamov (*Stratigrafiya* ..., 1990, p. 16) recorded the radiolarian *Entactinia* sp. in the Pragian beds of the forest strata (borehole Zarechnaya-1, 3090–2871 m of depth).

The data on Upper Devonian radiolarians in thin sections are provided by many reports on materials from boreholes bored in the southeastern areas of the West Siberian Geosyneclise (Fig. 21): Barabinskaya reference borehole (2470 m of depth), Bochkarevskaya-1 (2848 m of depth), and Vostochnaya-1 (2862 m of depth) in the Novosibirsk Region (Osyko, 1958; Aleskerova et al., 1960); and Lontyn'yakhskaya-64 (2899 m of depth) and Murashovskaya-1 (3000 m of depth) boreholes in the Tomsk Region.

Explanation of Plate 22

Early Famennian radiolarians of Belarus; assemblage with *Tetrentactinia barysphaera–Ceratoikiscum famennium:* spiny Aculearia.

Figs. 1 and 2. *Ceratoikiscum famennium* Nazarov et Ormiston, 1993, specimen GIN, no. 4467/134: (1) scale bar, 115 μm; (2) fragment, scale bar, 40 μm.

Figs. 3 and 4. *Palaeoscenidium cladophorum* Deflandre, 1953: (3) specimen GIN, no. 4467/132; scale bar, 98 μm; (4) specimen GIN, no. 4467/133; scale bar, 98 μm.

Figs. 5 and 6. *Palaeoscenidium bicorne* Deflandre, 1960: (5) specimen GIN, no. 4467/27; scale bar, 89 μm; (6) specimen GIN, no. 4467/23; scale bar, 83 μm.

Figs. 7–9. *Palhindeolithus* aff. *diductus* (Deflandre, 1973): (7) specimen GIN, no. 4467/29; scale bar, 73 μm; (8) specimen GIN, no. 4467/52; scale bar, 92 μm; (9) specimen GIN, no. 4467/46; scale bar, 98 μm.

Figs. 10–12. *Palaeothalomnus piletocladus* Nazarov et Ormiston, 1993: (10) specimen GIN, no. 4467/35; scale bar, 98 μm; (11) specimen GIN, no. 4467/17; scale bar, 98 μm; (12) specimen GIN, no. 4467/24; scale bar, 98 μm.

Figs. 13 and 14. *Archinella antiquus* (Deflandre, 1973): (13) specimen GIN, no. 4467/26; scale bar, 98 μm; (14) specimen GIN, no. 4467/128; scale bar, 72 μm.

Upper Devonian, Lower Famennian Substage, Elets Formation; Belarus, Pripyat Depression, borehole Zapadno-Valavskaya 1R (Nazarov, 1984, pl. XLIV, fig. 5; pl. XLV, figs. 1–6; pl. XLVI, figs. 1–7).

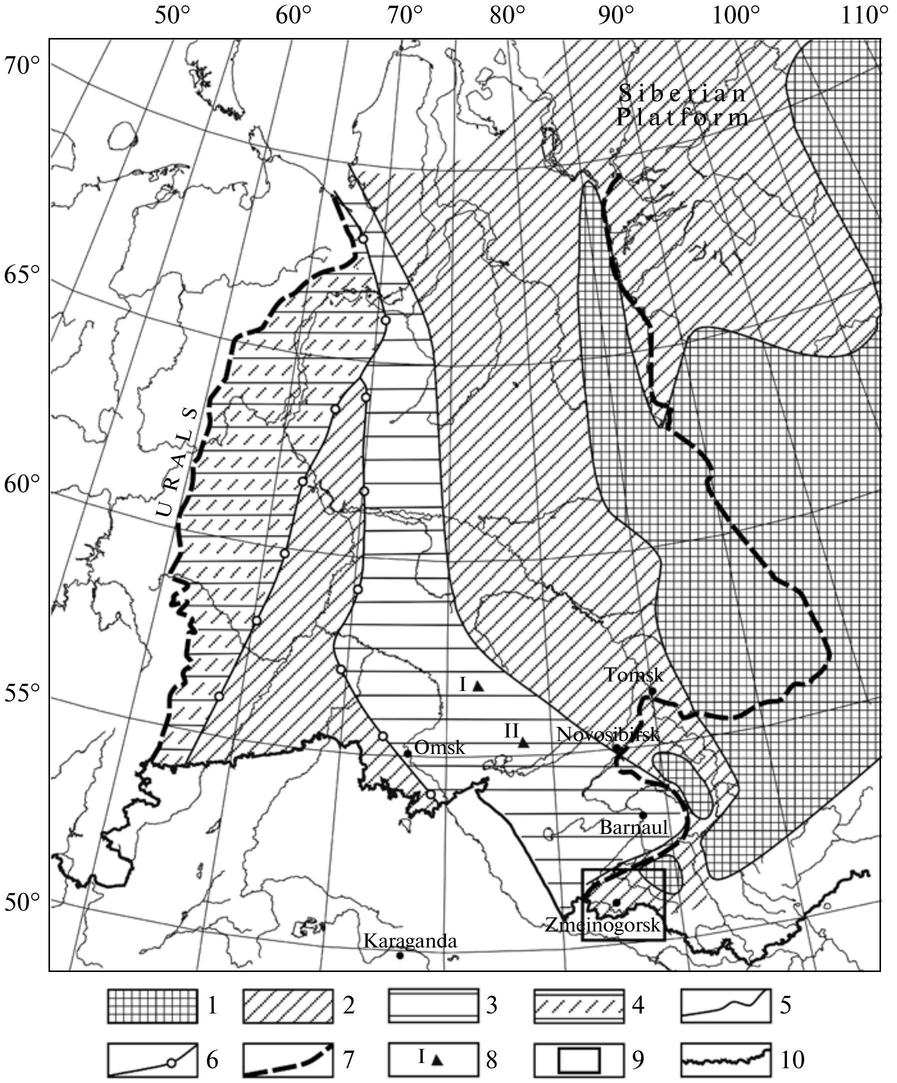


Fig. 21. Paleogeographic map of Siberia in the Late Devonian (after Yolkin et al., 2003a): (1) land; (2) shallow-water deposits of the shelf and epicontinental sea; (3) deepwater deposits; (4) complexes of island arches; (5) boundaries of facies megazones; (6) carbonate sutures; (7) boundary of fold framework; and (8) boreholes: (I) Bochkarevskaya-1R, (II) Barabinskaya-1; (9) working area; and (10) national boundary of Russia.

Explanation of Plate 23

Early Famennian radiolarians of the Timan–Pechora Basin; assemblage with *Tetrentactinia barysphaera–Retientactinosphaera magnifica*: spherical porous Sphaerellaria (1–12) and discoidal Stauraxonaria (13, 14).

Fig. 1. *Entactinia bella* Afanasieva et Amon, sp. nov., specimen PIN, no. 5311/12801; scale bar, 63 μm.
Fig. 2. *Entactinia bogdanovi* Afanasieva, 2000, specimen PIN, no. 5311/13021; scale bar, 33 μm.
Fig. 3. *Entactinia crustescens* Foreman, 1963, specimen PIN, no. 5311/12629; scale bar, 56 μm.
Fig. 4. *Entactinia parva* Won, 1983, specimen PIN, no. 5311/13019; scale bar, 33 μm.
Fig. 5. *Bientactinosphaera symphypora* (Foreman, 1963), specimen PIN, no. 5311/12634; scale bar, 33 μm.
Fig. 6. *Bientactinosphaera maslakovae* Afanasieva, 2000, specimen PIN, no. 5311/12628; scale bar, 40 μm.
Fig. 7. *Bientactinosphaera pinica* Afanasieva, 2000, specimen PIN, no. 5311/13007; scale bar, 63 μm.
Fig. 8. *Bientactinosphaera spinifoliacea* Nazarov et Afanasieva, 2000, specimen PIN, no. 5311/12822; scale bar, 59 μm.
Fig. 9. *Ornatoentactinia solita* Afanasieva, 2000, specimen PIN, no. 5311/12624; scale bar, 33 μm.
Fig. 10. *Astroentactinia biaciculata* Nazarov, 1975, specimen PIN, no. 5311/12633; scale bar, 37 μm.
Fig. 11. *Helioentactinia valavica* Nazarov et Ormiston, 1993, specimen PIN, no. 5311/12806; scale bar, 43 μm.
Fig. 12. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009, specimen PIN, no. 5311/12636; scale bar, 45 μm.
Fig. 13. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5311/12702; scale bar, 63 μm.
Fig. 14. *Palaeodiscaleksus punctus* (Hinde, 1899), specimen PIN, no. 5311/12619; scale bar, 43 μm.

Upper Devonian, Lower Famennian Substage; Timan–Pechora Basin, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth), sample 86g.

Plate 23

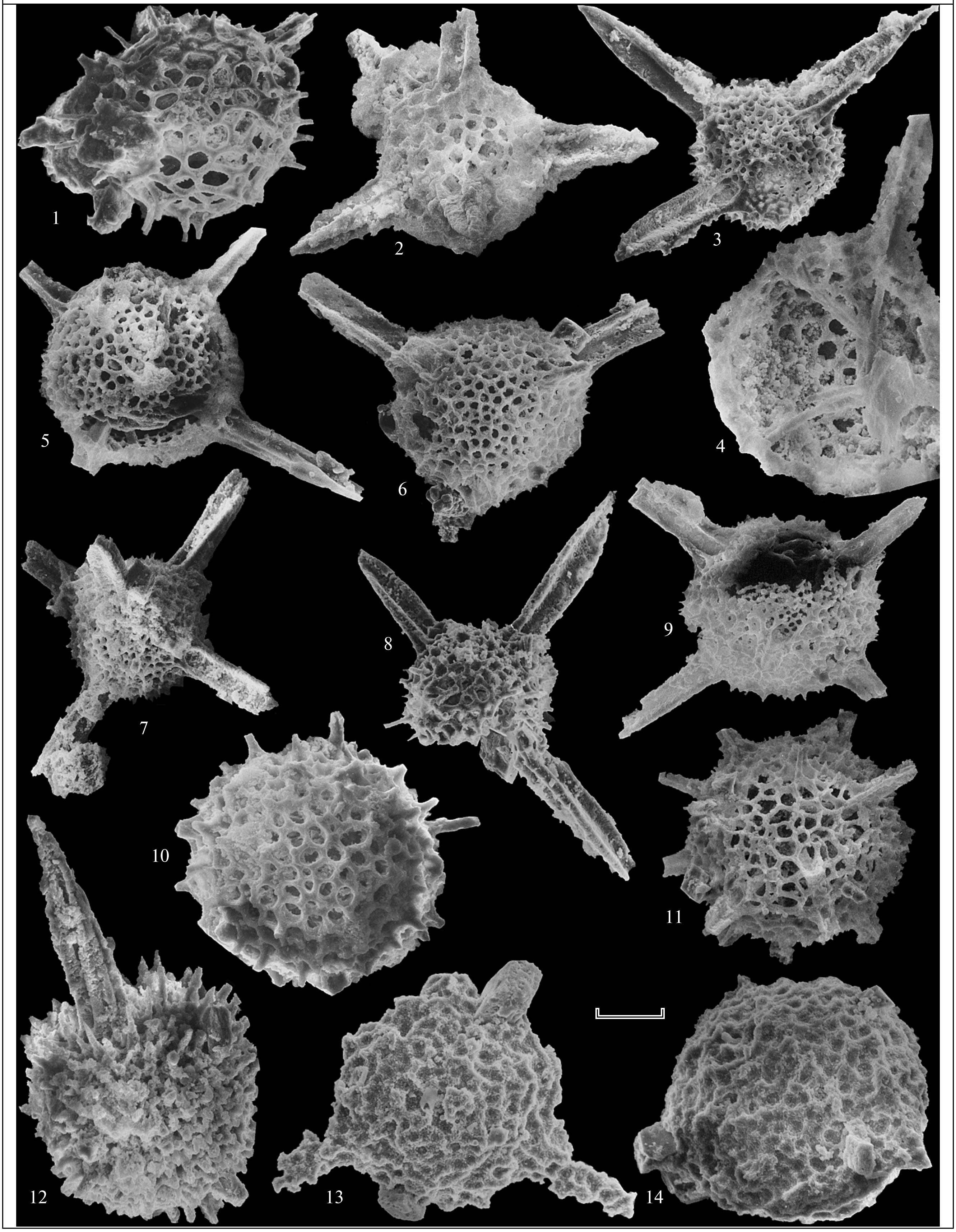
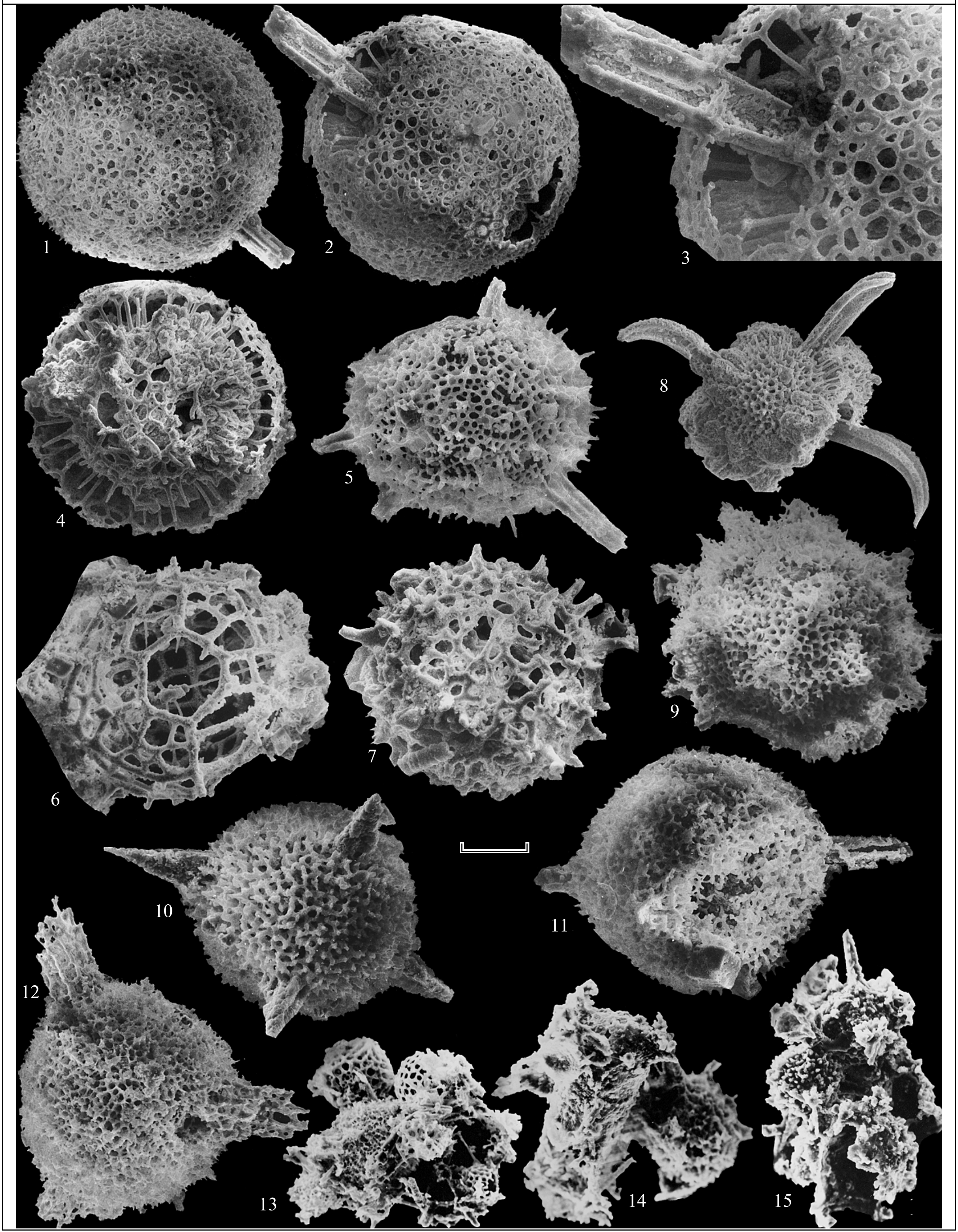


Plate 24



Bochkarev et al. (2003) briefly mentioned the presence of radiolarian remains in the Silurian?–Lower–Middle Devonian of Kasmanskaya-2 (2996 m of depth) and Zarechnaya-1 (3963 m of depth) boreholes, located in the Novosibirsk Region; however, datings of beds in these boreholes are based on poor paleontological materials and, hence, rather contradictory or show a wide stratigraphical range, which covers several systems.

Unfortunately, at present, it is very difficult to use the first publications on Devonian radiolarians of Western Siberia (Balakhmatova and Lipman, 1955; Lipman, 1973, 1979; Bogush et al., 1975; Sadrislamov, 1990), since they were studied in thin sections and identified following the obsolete classification of Haeckel (1887).

WESTERN SIBERIA

The Siberian Platform displays small Devonian outcrops. The Lower Devonian is traced in the extreme northwest; the Middle and Upper Devonian are recorded more widely. The Devonian System on the Siberian Platform is represented by variegated clayey–carbonate, frequently gypsiferous, less often, saliferous deposits with scarce organic fossils. Gray clayey and carbonate strata with marine fossils occur much more rarely (Podobina and Rodygin, 2000).

Some reports provide data on Early–Middle Devonian radiolarians from sections of reference boreholes. The Lower–Middle Devonian beds are mostly represented by shallow-water carbonate and terrigenous–carbonate rocks (Yolkin et al., 2003c). This area is probably a continuation of the external shelf of Siberian continent, which extended along the northern Altai and on Salair (Yolkin et al., 2001) (Fig. 21).

Lipnitskaja (1995) described the first reliable Early Devonian (Late Emsian) radiolarians of Russia (Fig. 3) from light brown slime limestones of borehole 16-Gerasimovskaya (2952.2–2941.2 m of depth) in the Nyurol'skaya Structural–Facies Region of southern Western Siberia. The radiolarian assemblage is dominated by *Bientactinosphaera echinata* (Hinde), *B. limpida* (Lipnitskaja), *B. (?) tortilispina* (Lipnitskaja), and *Bientactinosphaera* sp. *A* (Lipnitskaja, 2002). The genera *Entactinia* and *Spongentactinia* are represented by isolated specimens. The Late Emsian age of these deposits is supported by conodonts, ostracodes, and tentaculites, which are combined at this stratigraphical level into a complex faunal zone, *Clathroceilona abeona, Berounella spinosa, Nowakia richteri* (Isaev et al., 1992).

In the Late Devonian, the shelf zone was in contact with a deepwater zone situated westerly (Fig. 21). It is characterized by thin terrigenous siliceous–clayey formations with radiolarians (Yolkin et al., 2003a, 2003b, 2003c).

RUDNY ALTAI

The Rudny Altai Tectonic Block is located in the western Altai–Sayan sector of the Ural–Mongolian Fold Belt. The working area (Fig. 22) includes the Zmeinogorsk Volcanic Zone and, partially, Shipunikha Zone with a weakened volcanism. The time interval considered (Middle–Late Devonian) belongs to the stage of the formation of active continental marginal area (Gutak et al., 2000; Murzin et al., 2001a, 2001b).

In the Paleozoic, the Altai–Sayan Fold Region of southern Western Siberia was a shelf marginal area of Siberian continent, which existed from the Ordovician to the beginning of the Carboniferous. Devonian marine deposits are widespread in the western Altai–Sayan Fold Region, in Salair, Kuznetsk Basin, Rudny Altai, and Gornyi Altai. In eastern areas (Minus, Western Sayan, Tuva), the marine Devonian formations compose only some levels of the Upper Emsian

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Explanation of Plate 24

Early Famennian radiolarians from the Timan–Pechora Basin (1–12); assemblage with *Tetrentactinia barysphaera–Retientactinosphaera magnifica*: spherical latticed (1–7) and spongy (8–12) Spumellaria; and from the Caspian Depression (13–15).

Figs. 1–4. *Retientactinosphaera magnifica* Afanasieva, 2011: (1) specimen PIN, no. 5311/12932; scale bar, 98 μm; (2, 3) specimen PIN, no. 5311/12920: (2) scale bar, 89 μm; (3) fragment, scale bar, 43 μm; (4) specimen PIN, no. 5311/129294; scale bar, 89 μm.

Fig. 5. *Retientactinosphaera clavata* Afanasieva, 2011, specimen PIN, no. 5311/12623; scale bar, 33 μm.

Fig. 6. *Polyentactinia suave* (Nazarov, 1977), specimen PIN, no. 5311/12802; scale bar, 68 μm.

Fig. 7. *Polyentactinia rudihispida* Nazarov et Ormiston, 1993, specimen PIN, no. 5311/13002; scale bar, 63 μm.

Fig. 8. *Duplexia spinocurva* Afanasieva, 2000, specimen PIN, no. 5311/12719; scale bar, 98 μm.

Fig. 9. *Adamasirad cathedrarius* (Afanasieva, 2000), specimen PIN, no. 5311/12713; scale bar, 59 μm.

Fig. 10. *Spongentactinia polaris* Afanasieva et Amon, sp. nov., specimen PIN, no. 5311/12836; scale bar, 33 μm.

Fig. 11. *Spongentactinia diplostraca* (Foreman, 1963), specimen PIN, no. 5311/12918; scale bar, 63 μm.

Fig. 12. *Tetrentactinia barysphaera* Foreman, 1963, specimen PIN, no. 5311/12818; scale bar, 59 μm.

Figs. 13–15. Rock samples with fossil radiolarians, treated with acetic acid: (13) PIN, no. 5311/02605; scale bar, 63 μm: *Astroentactinia* sp., *Borisella praenuntia* (Nazarov et Ormiston, 1993), *Entactinia micula* Foreman, 1963, *Palacantholithus* sp., *Tetrentactinia barysphaera* Foreman, 1963; (14) PIN, no. 5311/02603; scale bar, 56 μm: *Bientactinosphaera* sp., *Holoeciscus auceps* Foreman, 1963, *Palacantholithus* sp.; (15) PIN, no. 5311/02604; scale bar, 56 μm: *Caspiaza collaricostulata* Afanasieva, 1993, *Entactinia* sp., *Radiobisphaera domanicensis* (Bykova, 1955).

Upper Devonian, Lower Famennian Substage: (1–12) Timan–Pechora Basin, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth), sample 86g; (13–15) Kazakhstan, Caspian Depression, northern slope, Karachaganak Mountain Range, borehole 27 (5305–5311 m of depth), sample 861280).

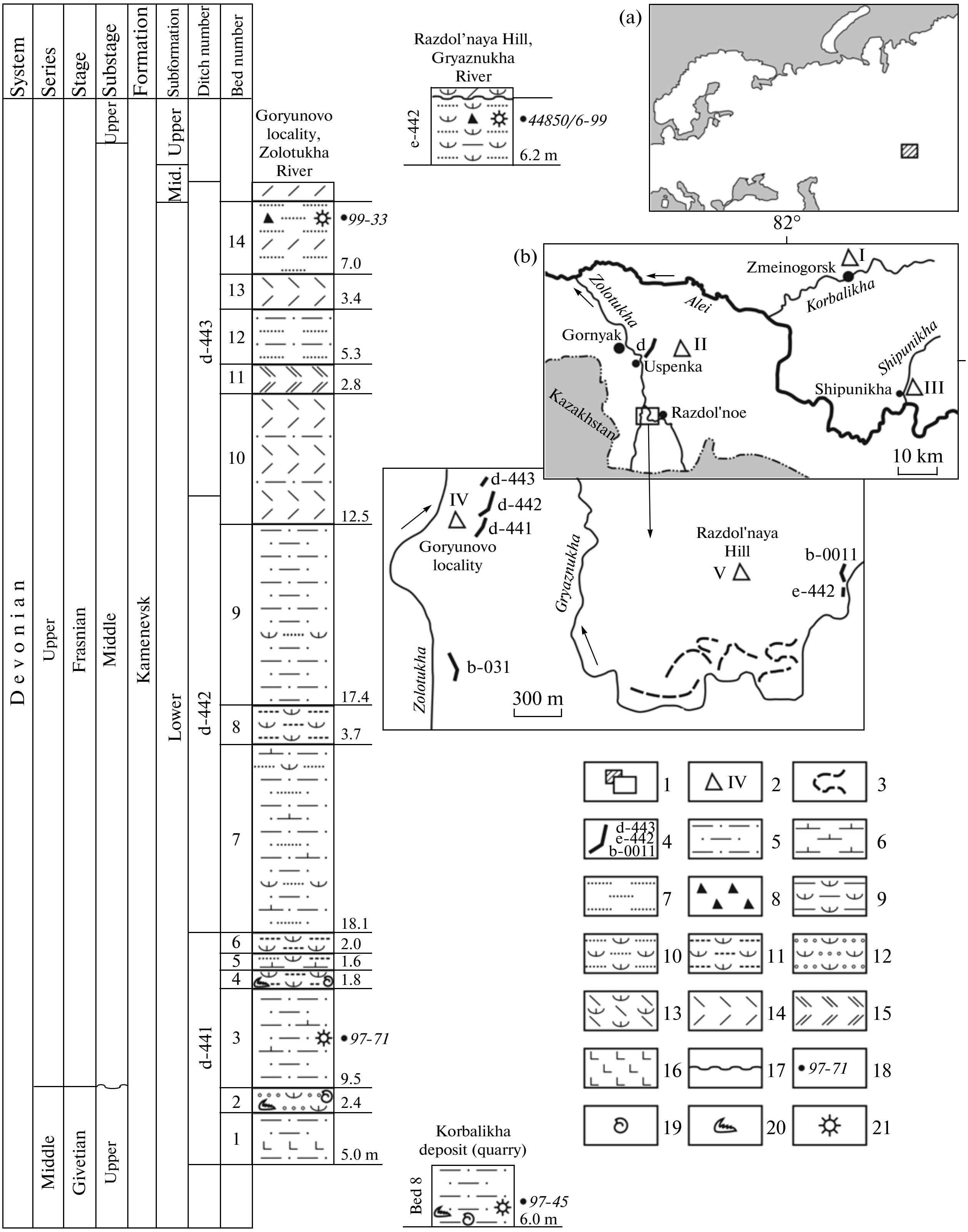

Fig. 22. Positions of sections of the Middle and Upper Devonian in the Rudny Altai: (a) position of the working area; (b) Rudny Altai. Designations: (1) working area; (2) observation points: (I) Korbalikha quarry, (II) village of Uspenka, (III) Shipunikha River, (IV) Goryunovo locality, Zolotukha River, (V) Razdol'naya Hill, Gryaznukha River; (3) paleoreefs; (4) ditches (d), excav tions (e), beds (b), and their nos.; (5) siliceous, clayey–siliceous siltstones; (6) calcareous siltstones; (7) sabulous siltstones; (8) cherts; (9) tuff siltstones; (10) tuff sandstone; (11) tuff gravelites; (12) tuff conglomerates; (13) tuffites of acid composition; (14) tuffs of acid composition; (15) xenotuffs of acid composition; (16) dolerites; (17) breaks, unconformity; (18) samples and their nos.; (19) fauna; (20) conodonts; and (21) radiolarians.

and Upper Givetian substages in the Devonian section of the continental type (Fig. 21).

In the Early and Middle Devonian, the western Altai–Sayan Fold Region was dominated by formations in shallow-water facies, whereas the Upper Devonian beds are characterized by more deepwater sedimentation conditions, which are well pronounced in sections of the Rudny Altai.

In the Rudny Altai, near the Zolotukha and Gryaznukha rivers, in the vicinity of the village of Razdol'noe (Fig. 22), outcrops show deepwater deposits of siliceous claystones and siltstones, cherts associated with acid volcanites (rhyolites, dacites) as well as neighboring shallow-water reef limestones, with corals and a benthic fauna, which likely occupied the slopes of underwater volcanoes (Gutak et al., 2000; Bakharev et al., 2004; Yolkin et al., 2005).

The first data on Upper Devonian radiolarians of the Rudny Altai, in the Goryunovo gully on the right bank of the Zolotukha River (Fig. 22b, IV, d-441) were reported by Lyakhnitsky and Gutak (1998, 2000) and Gutak et al. (2000). The researchers extracted and established the radiolarian assemblage of *Palaeoscenidium cladophorum* Defl., *Bientactinosphaera* sp., *Haplentactinia* sp., and *Ceratoikiscum* sp.

Recent studies on the right bank of the Zolotukha and Gryaznukha rivers (Fig. 22b, b-031, b-0011) allowed Obut and coauthors to establish Middle–Upper Frasnian radiolarian assemblages (Sennikov et al., 2002, 2007; Umeda et al., 2004; Obut and Iwata, 2005; Obut et al., 2005, 2007; Obut, 2006).

Our study of radiolarians confirmed and expanded the data obtained by the first researchers of radiolarians in the Rudny Altai (Afanasieva et al., 2008, 2009).

We were the first to record Middle–Late Devonian radiolarians in six sections of the Shipunikha and Zmeinogorsk zones of the Rudny Altai (Fig. 22); they are represented by 42 species of 15 genera (Table 12), including spherical porous Sphaerellaria (18 species of six genera) (Pl. 29, figs. 1–18), latticed and spongy Spumellaria (seven species of three genera) (Pl. 29, figs. 19, 20; Pl. 30, figs. 1–5), spiny Aculearia (ten species of four genera) (Pl. 30, figs. 6–15), and discoidal Stauraxonaria (seven species of two genera) (Pl. 30, figs. 16–21; Pl. 40, figs. 1–6).

The study of radiolarians from the Shipunikha and Zmeinogorsk zones of the Rudny Altai allowed us to reveal for the first time:

- Late Givetian radiolarians, which include a new species, *Palaeodiscaleksus saturniformis* Afanasieva et Amon, sp. nov.;
- the Middle Frasnian age of the Lower Kamenevsk Subformation in the section on the right bank of the Zolotukha River in the Goryunovo gully;
- to confirm the Late Frasnian age of the Upper Kamenevsk Subformation in the upper part of the section of a deepwater facies on the right bank of the Gryaznukha River in the vicinity of Razdol'naya Hill;
- to determine Late Frasnian radiolarians in the boundary beds of the Upper Kamenevsk Subformation of the Upper Frasnian and the Pikhtovsk Formation of the Famennian near the village of Uspenka;
- to reconstruct paleobiogeographic conditions of the existence of radiolarians.

Middle Devonian

Upper Givetian

The most ancient, Late Givetian radiolarians have been found in the stratotype of the Shipunikha Formation on the Shipunikha River and in the first parastratotype section of the Lower Kamenevsk Subformation of the Kamenevsk Formation in the Korbalikha quarry of polymetal deposits (located north of the town of Zmeinogorsk) (Fig. 22b, I; Table 12).

Late Givetian radiolarian associations are regarded as the biostraton *Spongentactinella windjanensis–Bientactinsphaera nigra* (Table 6), which corresponds to *disparilis–early falsiovalis* conodont zones.

Shipunikha Formation. The stratotype of the section of the Shipunikha Formation is situated on the interfluve range between the Shipunikha and Cherepanikha rivers, near the eastern marginal area of the village of Shipunikha (Fig. 22b, III) and divided into two members (Murzin, 2001a).

The lower member is represented by alternating lavas, lavobreccia basalts, andesitic basalts, and andesites (massive and almond-shaped), with dark gray aleurolites, argillites, less often, tuff-sandstones and volcanites of acid composition. The deposits contain the brachiopod *Dalejina hanusi* (Havl.), ammonoids *Trianoceras* sp. and *Pharciceras* sp., flora *Pseudosporochnus* cf. *nodosus* Lecl. et Banks., and spore assemblages of *Acanthotriletes corneolus* Naum., *Lophotriletes tacatinicus* Tschibr., and *Retusotriletes dubius* Tschibr.

The upper member of the Shipunikha Formation is composed of rhythmical interbedding gray and greenish gray, fine-grain sandstones, siltstones, and claystones containing the brachiopod *Delthyris* sp., flora *Candophyton (?) aquatilis* S. Step., and spore assemblages of *Camarotriletes minutus* Naum., *Acanthotriletes parvispinosus* Naum., and *Retusotriletes immeroratus* Tschibr. Based on paleontological data, the Shipunikha Formation is dated Late Givetian–Frasnian (Murzin, 2001a).

Radiolarians were found at the level of the Givetian–Frasnian boundary. The assemblage includes many discoidal taxa, including *Palaeodiscaleksus punctus* (Hinde) and *P. saturniformis* Afanasieva et Amon, sp. nov. (Table 12; Pl. 30, fig. 17; Pl. 40, figs. 1–6).

The first Parastratotype of the Kamenevsk Formation. The first parastratotype of the Kamenevsk Formation is located near the Korbalikha deposits of polymetal ores (Fig. 22b, I).

Table 12. Stratigraphic distribution of Middle and Late Devonian radiolarians of the Rudny Altai Mountains

System	Devonian					
Series	Middle		Upper			
Stage	Givetian		Frasnian			
Substage	Upper		Middle		Upper	
Formation	Shipunikha	Kamenev				
Subformation		Lower			Upper	
Sampling site	Shipunikha Zone	Zmeinogorsk Zone				
	Alei subzone Shipunikha River	Korbalikha deposit (quarry)	Goryunovo Locality, Zolotukha River		Razdol’naya Hill, Gryaznukha River	village of Uspenka, Zolotukha River
Radiolarians	97-59	97-45	97-71	99-33	44850/6-99	44-8
Palaeodiscaleksus punctus (Hinde, 1899)	—					
Palaeodiscaleksus saturniformis Afanasieva et Amon, sp. nov.	—					
Primaritripus patella (Hinde, 1899)		—	—		—	—
Astroentactinia tikhomirovi Afanasieva, 2000			—			
Bientactinosphaera egindyensis (Nazarov, 1975)			—			
Bientactinosphaera hystricosa (Foreman, 1963)			—			
Ceratoikiscum incomptum Nazarov, 1975			—			
Entactinia bifida Afanasieva, 2000			—			
Entactinia sp. *A*			—			
Haplentactinia barskovi Afanasieva, 2000			—			
Haplentactinia labyrinthica (Aitchison, 1993)			—			
Moskovistella allbororum Afanasieva, 2000			—			
Moskovistella mira Afanasieva, 2000			—			
Moskovistella victorialis Afanasieva, 2000			—			
Nazarovites mikhailovae Afanasieva, 2000			—			
Palacantholithus stellatus Deflandre, 1973			—			
Palaeoscenidium delicatum Aitchison, 1993			—			
Palaeoscenidium tabernaculum Aitchison, 1993			—			
Radiobisphaera assidera (Nazarov, 1975)			—			
Spongentactinella corynacantha Nazarov et Orm., 1983			—			
Spongentactinella veles (Foreman, 1963)			—			
Spongentactinella windjanensis Nazarov, 1982			—			
Ceratoikiscum spinosum Cheng, 1986			—	—		
Ceratoikiscum ukhtensis Afanasieva, 2000			—	—		
Entactinia herculea Foreman, 1963			—	—	—	
Bientactinosphaera pittmani (Hinde, 1899)			—		—	
Spongentactinia fungosa Nazarov, 1975			—		—	
Bientactinosphaera pinica Afanasieva, 2000			—	—		—
Spongentactinia diplostraca (Foreman, 1963)			—	—		—
Borisella bykovae Afanasieva, 2000			—			—
Radiobisphaera domanicensis (Bykova, 1955)			—			—
Bientactinosphaera obtusa (Hinde, 1899)			—	—	—	—
Radiobisphaera rozanovi Afanasieva et Amon, 2009			—	—	—	—
Ceratoikiscum planistellare Foreman, 1963				—		
Ceratoikiscum simplum Cheng, 1986				—		
Palaeodiscaleksus cribrarius (Hinde, 1899)				—		
Palaeoscenidium robustum Aitchison, 1993				—		
Primaritripus buribayensis Afanasieva et Amon, 2008				—		
Primaritripus chuvashovi Afanasieva et Amon, 2008				—		
Primaritripus kariukmasensis Afanasieva et Amon, 2009				—		
Astroentactinia biaciculata Nazarov, 1975						—
Astroentactinia vishnevskayae Afanasieva, 2000						—

Lower Kamenevsk Subformation. In the upper part of the section of the Korbalikha quarry (Bed 8), the Lower Kamenevsk Subformation outcrops; it is composed of siliceous–clayey and clayey indistinctly layered siltstones (Fig. 22b, I). The lower part of Bed 8 has yielded abundant goniatites *Pharciceras* cf. *lunulicosta* (Sand, et Sand.), *Tamarites subitus* Bog., and *Trianoceras* cf. *gerassimovi* Bog., ostracodes, tentaculites, rare brachiopods and bivalves, individual nautiloideans, tubutales, crinoids, and the conodont *Polygnathus* ex gr. *varcus* Stauf. (Gutak et al., 2000; Murzin, 2001b).

Radiolarians are only represented by many discoidal *Primaritripus patella* (Hinde) (Table 12; Pl. 30, fig. 20).

Southerly, on the right bank of the Zolotukha River (Fig. 22b, b-031), Obut and Iwata (2005) recorded a more diverse radiolarian assemblage from the upper part of the Upper Givetian, which includes seven species of three genera: *Astroentactinia stellata* Nazarov, *A. paronae* (Hinde), *Trilonche*[14] *davidi* Hinde, *T.* cf. *inusitata* (Foreman), *T. minax* (Hinde), *T. palimbola* (Foreman), and *Palaeoscenidium cladophorum* Deflandre.

Upper Devonian

The second parastratotype of the Kamenevsk Formation. The second parastratotype of the Kamenevsk Formation is situated in the interfluve of the Zolotukha and Gryaznukha rivers (Fig. 22b) and composed of three subformations: Lower Kamenevsk, Middle Kamenevsk, and Upper Kamenevsk (Gutak et al., 2000; Murzin, 2001b).

Middle Frasnian

Lower Kamenevsk Subformation. A section of the Lower Kamenevsk Subformation outcrops on the Zolotukha River in the Goryunovo gully (Fig. 22b, IV, d-441, d-442, d-443).

The taxonomic composition of radiolarians from the Lower Kamenevsk Subformation suggests to regard the radiolarian assemblages recognized within the framework of the Middle Frasnian biostraton *Moskovistella allbororum–Ceratoikiscum ukhtensis* (Table 6), which corresponds to the *punctata–early rhenana* conodont zones.

The lower part of the section of the Lower Kamenevsk Subformation is composed of siliceous and clayey–siliceous siltstones, with rare horizons of nodular limestones, and contains two interbeds of gravelstones with limestone fragments (Beds 2 and 4) (Fig. 22), which are extremely rich in tubutales, tetracorals, brachiopods, ostracodes, and the conodonts *Klapperina disparilis* (Ziegler et Klapper), *Polygnathus ovatinodosus* Ziegler et Klapper, *Belodella devonica* (Stauffer), and *Icriodus difficilis* (Ziegler et Klapper), which support the assignment of this member to the *disparilis* Conodont Zone (Late Givetian) (Gutak et al., 2000).

Between the gravelstone interbeds, there is Bed 3, which is formed of siliceous, clayey–siliceous, and, rarely, calcareous siltstones (Fig. 22). From a syngenetic chert interbed in Bed 3, perfect radiolarians have been determined (Table 12). The rich radiolarian assemblage established for the first time (31 species of 14 genera) is strong evidence of the Middle Frasnian age of enclosing matter.

Spherical porous radiolarians of the class Sphaerellaria are represented by 16 species of six genera (Pl. 29, figs. 1–18): *Astroentactinia, Bientactinosphaera, Borisella, Entactinia, Moskovistella,* and *Radiobisphaera.*

Spherical latticed and spongy radiolarians of the class Spumellaria are represented by seven species of three genera (Pl. 29, figs. 19, 20; Pl. 30, figs. 1–5): *Haplentactinia, Spongentactinella*, and *Spongentactinia.*

Spiny radiolarians of the class Aculearia are represented by seven species of four genera (Pl. 30, figs. 6–15): *Ceratoikiscum, Nazarovites, Palacantholithus*, and *Palaeoscenidium.*

Discoidal radiolarians of the class Stauraxonaria are only represented by one species, *Primaritripus patella* (Hinde) (Pl. 30, fig. 20).

In the other Middle Frasnian section from the vicinity of the village of Gornyak (Fig. 22b), Obut et al. (2007) described the conodonts *Palmatolepis hassi* Muller et Muller and *Polygnathus* sp. accompanied by a less diverse radiolarian assemblage, which includes seven species of three genera: *Astroentactinia stellata* Nazarov, *Trilonche*[15] *davidi* (Hinde), *T. echinata*[16] (Hinde), *T. hindea* (Hinde), *T. minax* (Hinde), *T. vetusta* Hinde, and *Palaeoscenidium cladophorum* Deflandre.

The upper part of the section of the Lower Kamenevsk Subformation is volcanogenic–sedimentary, composed mostly of tuffs and xenotuffs with interbeds of siliceous, clayey–siliceous, and sabulous siltstones (Fig. 22).

This part of the section lacks reliable macrofaunal remains. At the same time, chert interbeds of Bed 14 (Fig. 22) have yielded abundant radiolarians of 14 species of eight genera (Table 12). The radiolarian assemblage suggests Middle Frasnian age of enclosing matter.

Spherical porous radiolarians of the class Sphaerellaria are represented by four species of three genera (Pl. 29, figs. 1, 3, 7, 10): *Bientactinosphaera obtusa* (Hinde), *B. pinica* Afanasieva, *Entactinia herculea* Foreman, and *Radiobisphaera rozanovi* Afanasieva et Amon.

Spherical spongy radiolarians of the class Spumellaria are only represented by one species, *Spongentactinia diplostraca* (Foreman) (Pl. 30, fig. 5).

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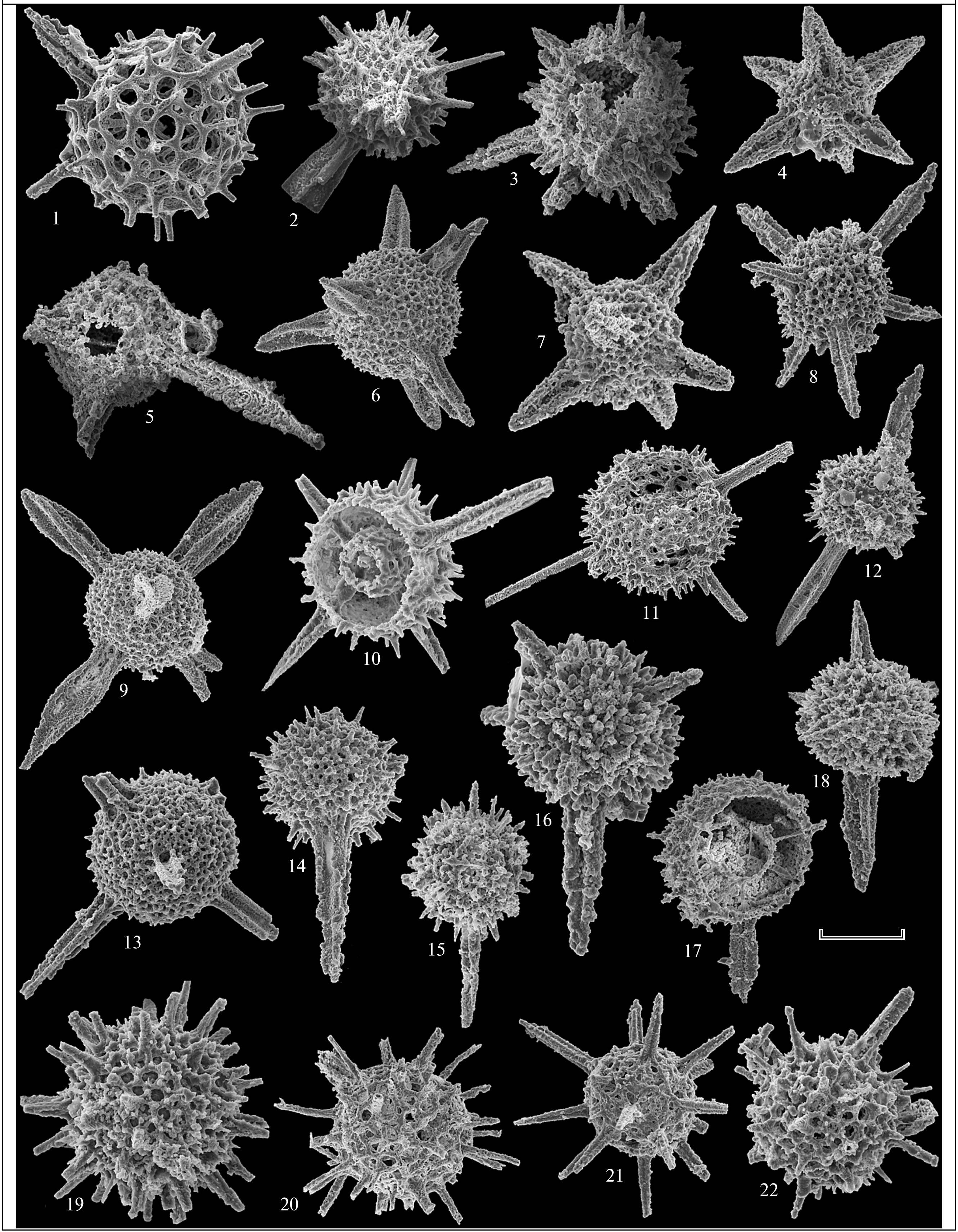
[14] See Footnote 5.

[15] See Footnote 5.

[16] See Footnote 9.

Plate 25



Spiny radiolarians of the class Aculearia are represented by five species of two genera: *Ceratoikiscum planistellare* Foreman, *C. simplum* Cheng, *C. spinosum* Cheng, *C. ukhtensis* Afanasieva, and *Palaeoscenidium robustum* Aitchison (Pl. 30, figs. 7–11).

Abundant discoidal radiolarians of the class Stauraxonaria are represented by four species of two genera (Pl. 30, figs. 16, 18, 19, 21): *Palaeodiscaleksus cribrarius* (Hinde), *Primaritripus buribayensis* Afanasieva et Amon, *P. chuvashovi* Afanasieva et Amon, and *P. kariukmasensis* Afanasieva et Amon.

Middle Kamenevsk Subformation. Volcanogenic–sedimentary rocks of the Middle Kamenevsk Subformation with lenses of bioherm limestones and reefoid buildups lack radiolarians (Fig. 22).

Upper Frasnian

Upper Kamenevsk Subformation. Variegated siliceous–siltstone deposits of the Upper Kamenevsk Subformation were investigated in two facies (Fig. 22b), deepwater (section of Razdol'naya Hill) and reef-building (sections of the Razdolninsk Organogenic Massif) (Gutak et al., 2000; Murzin, 2001b).

The deepwater section of the Upper Kamenevsk Subformation on the Gryaznukha River near Razdol'naya Hill, which is formed of variegated (gray and green tones) sandstones, siltstones, and cherts (Fig. 22b, V, e-442), is dominated by the ammonoids *Ponticeras* sp., *Manticoceras bullatum* Wedekind, *M. neverovi* Bog., *M. sinuosum* (Hall), *M. altaicum* Bog., *M. eliseevi* Bog., *M. drevermanni* Wedekind, *M. carinatum* (Beyrich), and *Beloceras sagittarium* (Sandberger); bivalves, crinoids, and the conodonts *Palmatolepis jamieae* Ziegler et Sandberg, *P. rhenana* Bischoff, *P.* cf. *subrecta* Mill. et Joungq., *P. hassi* Mul. et Mul., *P.* aff. *proversa* Ziegler, *P. gigas* Mill. et Joungq., *Synprioniodina gracilis* Stauffer, *Hindeodella subtilis* Ulrich et Bassler, *Ancyrodella nodosa* Ulrich et Bassler., *A. curvata* (Br. et Mehl), *A. lobata* Br. et Mehl, and *Icriodus symmetricus* Br. et Mehl.; based on this, the bed is dated Late Frasnian (*jamieae–rhenana* zones) (Gutak et al., 2000).

The radiolarian assemblage from the deepwater facies of the upper part of the section of the Upper Kamenevsk Subformation is less diverse than that from the Lower Kamenevsk Subformation and is only represented by six species of five genera of spherical and discoidal radiolarians (Table 12).

Spherical porous radiolarians of the class Sphaerellaria are represented by four species of three genera (Pl. 29, figs. 1, 7, 10, 11): *Entactinia herculea* Foreman, *Bientactinosphaera obtusa* (Hinde), *B. pittmani* (Hinde), and *Radiobisphaera rozanovi* Afanasieva et Amon.

Spherical spongy radiolarians of the class Spumellaria are represented by the species *Spongentactinia fungosa* Nazarov (Pl. 30, fig. 4).

Discoidal radiolarians of the class Stauraxonaria are represented by the species *Primaritripus patella* (Hinde) (Pl. 30, fig. 20).

This radiolarian assemblage is evidence of the Late Frasnian time of the formation of beds.

Upward in the section of the Upper Frasnian, near the boundary with the Famennian beds (Fig. 22b, V, b-0011), Obut et al. (2007) revealed conodonts of the *rhenana–linguiformis* Zone and a more diverse radiolarian assemblage represented by 24 species of 11 genera of spherical and spiny taxa.

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Explanation of Plate 25

Early Famennian radiolarians of the Polar Urals; assemblage with *Tetrentactinia barysphaera–Caspiaza spinifera*: spherical porous Sphaerellaria.

Figs. 1 and 2. *Entactinia bella* Afanasieva et Amon, sp. nov.; scale bar, 62 μm: (1) specimen PIN, no. 5312/15731, (2) specimen PIN, no. 5312/15788.

Fig. 3. *Entactinia herculea* Foreman, 1963, specimen PIN, no. 5312/15806; scale bar, 55 μm.

Fig. 4. *Entactinia bogdanovi* Afanasieva, 2000, specimen PIN, no. 5312/15784; scale bar, 56 μm.

Fig. 5. *Entactinia crustescens* Foreman, 1963, specimen PIN, no. 5312/15922; scale bar, 57 μm.

Fig. 6. *Entactinia oumonhaoensis* Wang, 1997, specimen PIN, no. 5312/15750; scale bar, 68 μm.

Fig. 7. *Entactinia patorovaria* Afanasieva, 2000, specimen PIN, no. 5312/15758; scale bar, 47 μm.

Fig. 8. *Entactinia parva* Won, 1983, specimen PIN, no. 5312/15814; scale bar, 72 μm.

Fig. 9. *Bientactinosphaera guangxiensis* (Li et Wang, 1991), specimen PIN, no. 5312/15740; scale bar, 74 μm.

Fig. 10. *Bientactinosphaera variacanthina* (Foreman, 1963), specimen PIN, no. 5312/15734; scale bar, 38 μm.

Fig. 11. *Bientactinosphaera zuraevi* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15718; scale bar, 108 μm.

Fig. 12. *Bientactinosphaera obtusa* (Hinde, 1899), specimen PIN, no. 5312/15751; scale bar, 86 μm.

Fig. 13. *Ornatoentactinia solita* Afanasieva, 2000, specimen PIN, no. 5312/15778; scale bar, 55 μm.

Fig. 14. *Radiobisphaera domanicensis* (Bykova, 1955), specimen PIN, no. 5312/15768; scale bar, 61 μm.

Fig. 15. *Radiobisphaera menneri* Afanasieva, 2000, specimen PIN, no. 5312/15947; scale bar, 54 μm.

Fig. 16. *Radiobisphaera assidera* (Nazarov, 1975), specimen PIN, no. 5312/15776; scale bar, 40 μm.

Fig. 17. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009, specimen PIN, no. 5312/15752; scale bar, 64 μm.

Fig. 18. *Radiobisphaera palimbola* (Foreman, 1963), specimen PIN, no. 5312/15759; scale bar, 59 μm.

Fig. 19. *Astroentactinia biaciculata* Nazarov, 1975, specimen PIN, no. 5312/15813; scale bar, 38 μm.

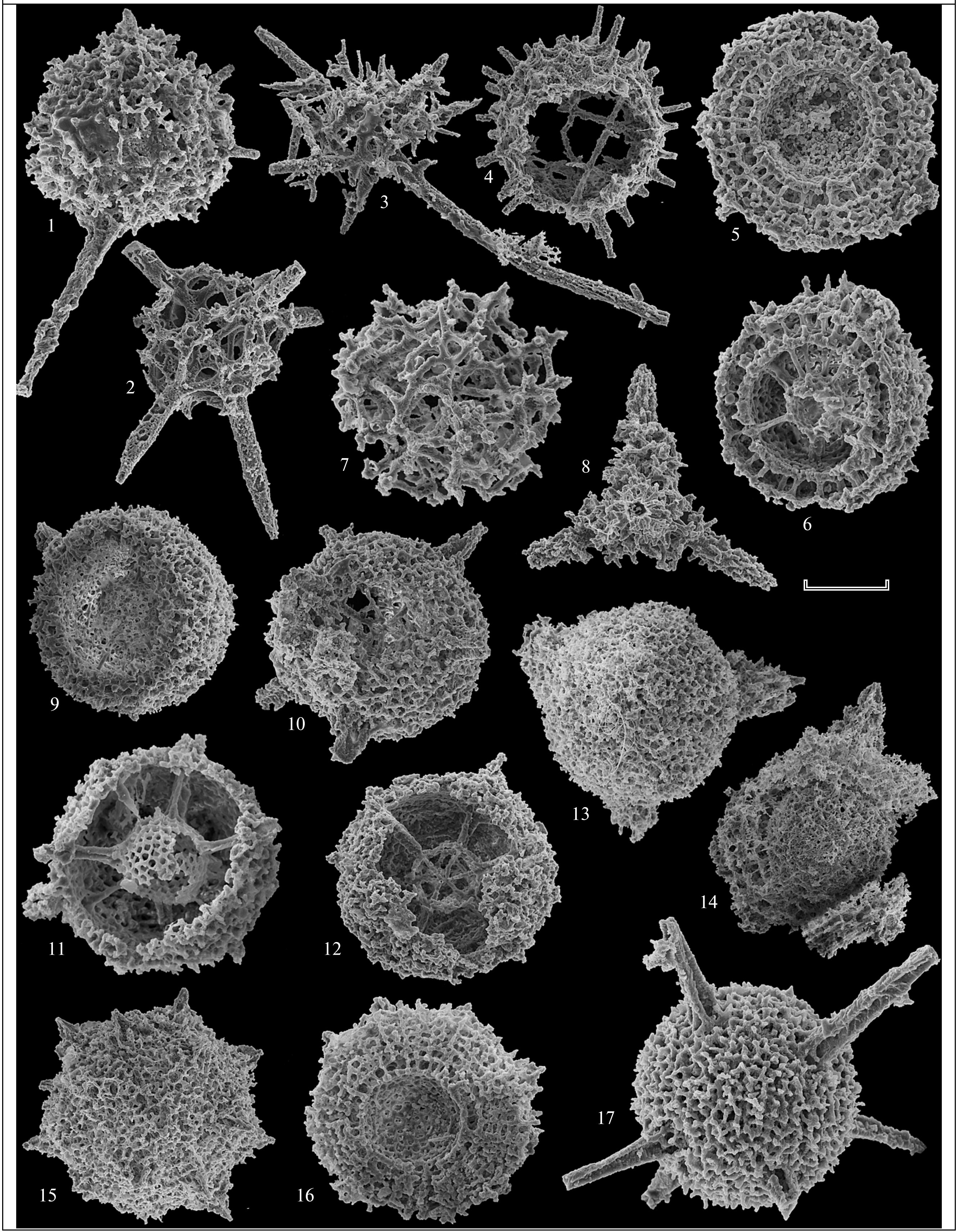
Fig. 20. *Astroentactinia crassata* Nazarov, 1975, specimen PIN, no. 5312/15914; scale bar, 86 μm.

Fig. 21. *Astroentactinia stellata* Nazarov, 1975, specimen PIN, no. 5312/15811; scale bar, 62 μm.

Fig. 22. *Helioentactinia valavica* Nazarov et Ormiston, 1993, specimen PIN, no. 5312/15764; scale bar, 47 μm.

Upper Devonian, Lower Famennian Substage; Polar Urals, Lemvin Zone, Palnik-Yu River: (1–4, 6–14, 16–19, 21, 22) sample 101/594; (5, 15, 20) sample 101/593.

Plate 26



Explanation of Plate 26

Early Famennian radiolarians of the Polar Urals; assemblage with *Tetrentactinia barysphaera–Caspiaza spinifera*: spherical latticed (1–4) and spongy (5–17) Spumellaria.

Fig. 1. *Retientactinosphaera clavata* Afanasieva, 2011, specimen PIN, no. 5312/15746; scale bar, 42 μm.
Fig. 2. *Haplentactinia kuzminae* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15957; scale bar, 61 μm.
Fig. 3. *Haplentactinia rhinophyusa* Foreman, 1963, specimen PIN, no. 5312/15952; scale bar, 56 μm.
Fig. 4. *Polyentactinia rudihispida* Nazarov et Ormiston, 1993, specimen PIN, no. 5312/15723; scale bar, 68 μm.
Fig. 5. *Pluristratoentactinia conspissata* Nazarov, 1981, specimen PIN, no. 5312/15766; scale bar, 42 μm.
Fig. 6. *Pluristratoentactinia trisphaerata* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15744; scale bar, 43 μm.
Fig. 7. *Tetragregnon quadrispinosa* (Foreman, 1963), specimen PIN, no. 5312/15951; scale bar, 36 μm.
Fig. 8. *Tetragregnon sycamorensis* Ormiston et Lane, 1976, specimen PIN, no. 5312/15938; scale bar, 66 μm.
Fig. 9. *Spongentactinia marina* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15722; scale bar, 68 μm.
Fig. 10. *Spongentactinia polaris* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15773; scale bar, 56 μm.
Figs. 11 and 12. *Spongentactinia diplostraca* (Foreman, 1963): (11) specimen PIN, no. 5312/15729; scale bar, 34 μm; (12) specimen PIN, no. 5312/15720; scale bar, 61 μm.
Figs. 13 and 14. *Tetrentactinia barysphaera* Foreman, 1963: (13) specimen PIN, no. 5312/15939; scale bar, 62 μm; (14) specimen PIN, no. 5312/15912; scale bar, 72 μm.
Fig. 15. *Adamasirad cathedrarius* (Afanasieva, 2000), specimen PIN, no. 5312/15754; scale bar, 69 μm.
Fig. 16. *Somphoentactinia multisphaerata* Afanasieva et Amon, sp. nov., specimen PIN, no. 5312/15728; scale bar, 46 μm.
Fig. 17. *Spongentactinella exilispina* (Foreman, 1963), specimen PIN, no. 5312/15779; scale bar, 69 μm.

Upper Devonian, Lower Famennian Substage; Polar Urals, Lemvin Zone, Palnik-Yu River: (1–6, 9–12, 15–17) sample 101/594; (7) sample 101/599; (8, 13, 14) sample 101/593.

Spherical porous radiolarians of the class Sphaerellaria are represented by 11 species of five genera: *Astroentactinia stellata* Nazarov, *A. vishnevskayae* Afanasieva, *Borisella* cf. *maksimovae* Afanasieva, *Entactinia* sp. *A*, *Moscovistella allbororum* Afanasieva, *Trilonche davidi* (Hinde), *T. echinata*[17] (Hinde), *T. guangxiensis* (Li et Wang), *T. minax* (Hinde), *T. tanheensis* Luo, Aitchison et Wang, and *T. vetusta* Hinde.

Spherical spongy radiolarians of the class Spumellaria are represented by three species of two genera: *Haplentactinia rhinophyusa* Foreman, *Polyentactinina circumretia* Nazarov et Ormiston, and *P.* cf. *kossistekensis* Nazarov.

Spiny radiolarians of the class Aculearia are represented by ten species of four genera: *Ceratoikiscum avimexpectans* Deflandre, *C. delicatum* Cheng, *C. labyrintheum* Cheng, *C. mirum* Cheng, *Circuliforma robusta* Cheng, *Nazarovites bioculus* Afanasieva, *N. pinnula* Afanasieva, *Palaeoscenidium cladophorum* Deflandre, *P. delicatum* Aitchison, and *P. tabernaculum* Aitchison.

The taxonomic composition of radiolarians from the Upper Kamenevsk Subformation enables the consideration of the radiolarian assemblages established within the framework of the Middle Frasnian biostraton *Polyentactinia circumretia–Bientactinosphaera egindyensis* (Table 6), which corresponds to the *late rhenana–linguiformis* conodont zones.

Upper Frasnian–Lower Famennian. On the right bank of the Zolotukha River near the village of Uspenka (Fig. 22b, II), there are two quarries, in which the Pikhtovsk Formation of the Famennian Stage outcrops. On the interfluve between two hills, the main ditch was investigated; its dumps of light gray siltstones and silicides have yielded a great number of very small tentaculites, several imprints of Upper Devonian plants, many small bivalves of the genus *Buchiola*, several imprints of valves of the brachiopods *Cyrtospirifer* sp., small *Spinulicosta spinulicosta* (Hall), *Rynchospirina tschernyshewi* (Peetz), and *Athytis concentrica* (Buch).

The radiolarian assemblage from dumps of the ditch shows good preservation and consists of nine species of six genera of spherical and discoidal taxa (Table 12).

Spherical porous radiolarians of the class Sphaerellaria are represented by seven species of four genera (Pl. 29, figs. 3, 7, 8, 10, 12, 16, 18): *Astroentactinia vishnevskayae* Afanasieva, *A. biaciculata* Nazarov, *Bientactinosphaera obtusa* (Hinde), *B. pinica* Afanasieva, *Borisella bykovae* Afanasieva, *Radiobisphaera domanicensis* (Bykova), and *R. rozanovi* Afanasieva et Amon.

Spherical spongy radiolarians of the class Spumellaria are represented by the species *Spongentactinia diplostraca* (Foreman) (Pl. 30, fig. 5).

Discoidal radiolarians of the class Stauraxonaria are represented by the species *Primaritripus patella* (Hinde) (Pl. 30, fig. 20).

The radiolarian assemblage suggests the Late Frasnian age of deposits near the boundary with the Pikhtovsk Formation of the Famennian Stage.

Paleobiogeographic Conditions of Environments of Radiolarians in the Devonian of the Rudny Altai

Devonian radiolarians of the Rudny Altai inhabited various biotopes, ranging from relatively shallow coastal water areas of the internal shelf to deepwater pelagic spaces of the external shelf, they existed near reefs and occupied areas with active tectonic mode.

Late Givetian radiolarian assemblages are formed of abundant, but taxonomically poor discoidal taxa

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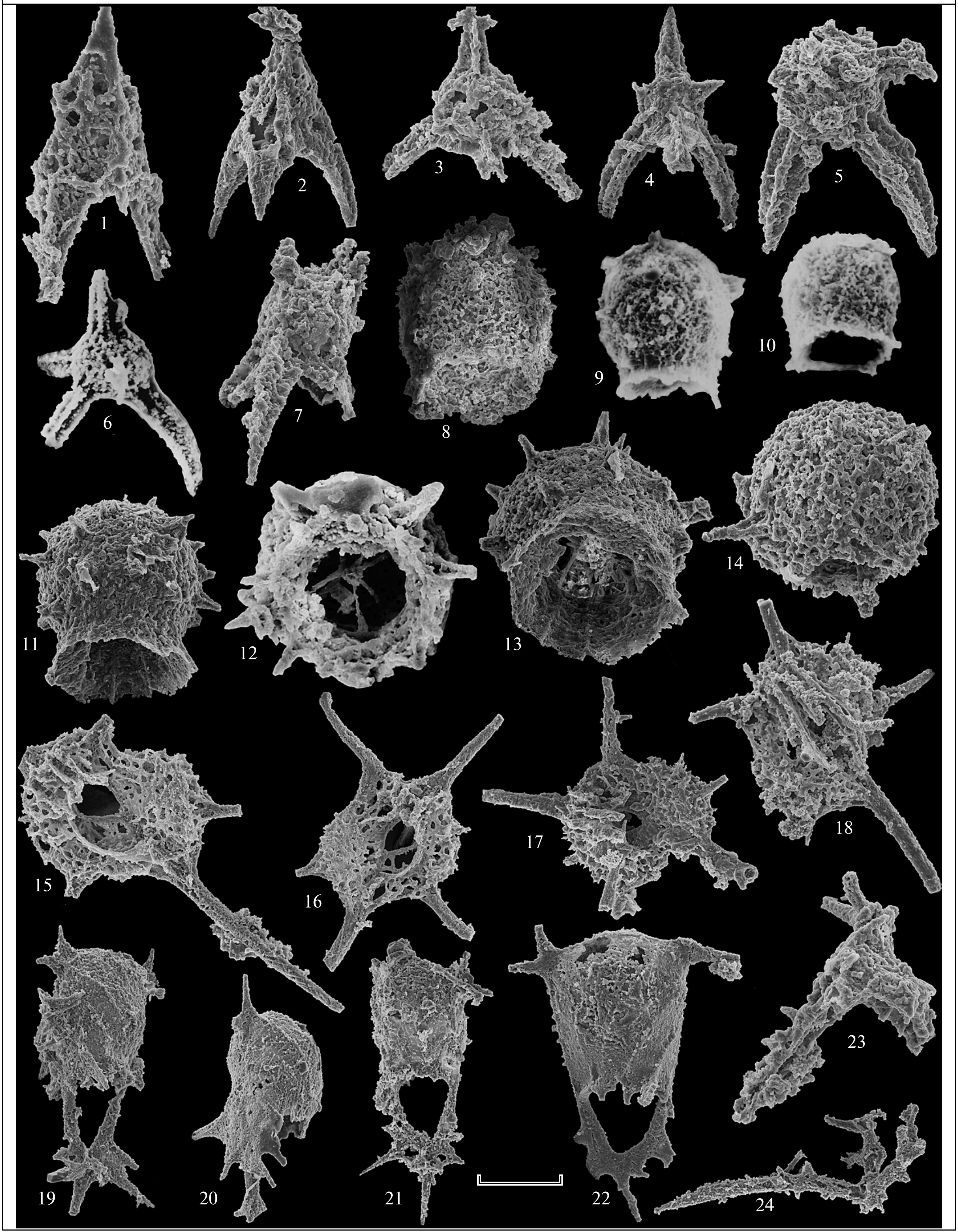
[17] See Footnotes 5 and 9.

Plate 27



(three species of two genera), which are evidence of shallow marine sedimentation conditions of the internal shelf.

A rich Middle Frasnian radiolarian assemblage from the lower part of the section of the Lower Kamenevsk Subformation shows a wide taxonomic diversity, including 31 species of 14 genera. The Middle Frasnian radiolarian assemblage is a biomarker of the formation of deposits in relatively deepwater conditions of the external shelf.

The prevalence in the radiolarian oryctocoenosis (14 species of eight genera) from the upper volcanogenic–sedimentary part of the section of the Lower Kamenevsk Subformation of abundant discoidal taxa (up to 30% of the total number of individuals) is probably evidence of the relatively shallow marine character of this sedimentation basin at the end of the Middle Frasnian.

The radiolarian assemblage from the deepwater facies of the marginal area of the external shelf is revealed in the upper part of the section of the Upper Kamenevsk Subformation of the Upper Frasnian and only represented by six species of five genera of spherical and discoidal radiolarians.

CHAPTER 4. FEATURES AND GENERAL PATTERS OF EXISTENCE OF RADIOLARIANS IN THE DEVONIAN OF THE RUSSIAN PLATFORM

At the boundary between the Early and Middle Frasnian (Ust'-Yarenga and Domanik Time), in the southern Ukhta part of the Timan–Pechora Basin, paleobiogeographic conditions of sedimentation sharply changed and gave rise to unusual rocks, which caused the formation of the so-called "Domanik." The Domanik Formation is composed of relatively deepwater (100–400 m) depressive facies (Menner, 1989; Menner et al., 1991, 1992; Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2000, 2001; Belyaeva et al., 1998; Becker et al., 2000). The Domanik beds are oil-bearing rocks which are markers of special paleogeographic conditions of the sedimentation basin. The term *Domanik* designates the strata of interbedding bituminous siliceous–carbonate rocks, with interbeds of shale oil, with a specific fossil assemblage. At present, the terms "domanik" and "domanikit" designate not only Middle Frasnian beds of the Domanik Formation, but also rocks of various age of the "Domanik" appearance with the organic content (C_{org}) from 2.5 to 10–40% (Vassoevich, 1972).

Distinctive features of the Domanik beds are (1) a high content of organic matter; (2) characteristic lithologic facies (silicides, chert limestones, limestones, clayey–siliceous–carbonate claystones), which show strict cyclicity of sedimentation; (3) a general increase in chert content of rocks; (4) specific assemblages of planktonic organisms; and (5) absence of normal marine benthos.

HISTORY OF THE STUDY OF THE DOMANIK BEDS

Domanik has been attracting attention of geologists for more than 300 years. Even at the end of the 17th century, the Ukhta oil and Domanik combustible shales were well known to Peter the Great and, in 1697, he ordered to send samples of Domanik rocks to Holland for investigation. At that time, the first report

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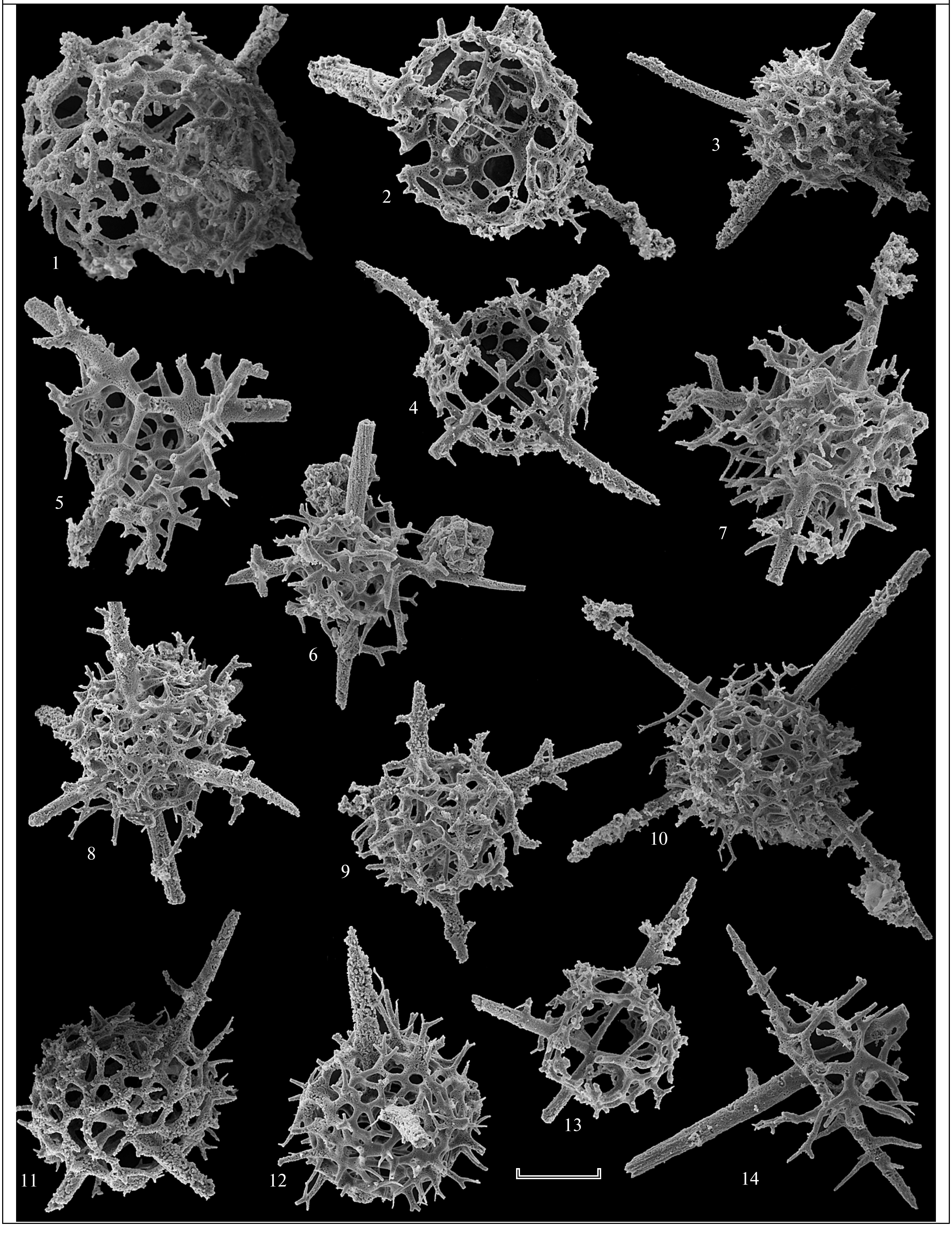
Explanation of Plate 27

Early Famennian radiolarians of the Polar Urals; assemblage with *Tetrentactinia barysphaera–Caspiaza spinifera:* radiolarians with pylome from the order Pylomariata, Nassellaria (1–14), and spiny Aculearia (15–24).

Figs. 1 and 2. *Archocyrtium amoenus* Afanasieva et Amon, sp. nov.: (1) specimen PIN, no. 5312/15839; scale bar, 25 μm; (2) specimen PIN, no. 5323/15828; scale bar, 40 μm.
Fig. 3. *Archocyrtium cibdelosphaera* (Foreman, 1963), specimen PIN, no. 5312/15894; scale bar, 37 μm.
Fig. 4. *Archocyrtium riedeli* Deflandre, 1960, specimen PIN, no. 5312/15918; scale bar, 39 μm.
Fig. 5. *Cyrtisphaeractenium mendax* Deflandre, 1972, specimen PIN, no. 5312/15825; scale bar, 44 μm.
Fig. 6. *Cyrtisphaeronemium spinosum* (Cheng, 1986), specimen PIN, no. 5312/07808; scale bar, 35 μm.
Fig. 7. *Robotium validum* Cheng, 1986, specimen PIN, no. 5312/15883; scale bar, 32 μm.
Figs. 8–10. *Caspiaza collaricostulata* Afanasieva, 1993: (8) specimen PIN, no. 5312/15833; scale bar, 43 μm; (9) specimen PIN, no. 5312/03407 ((stroke = 33 μm; (10) specimen PIN, no. 5312/03409 ((stroke = 33 μm.
Figs. 11–13. *Caspiaza spinifera* Afanasieva, 1993: (11) specimen PIN, no. 5312/15830; scale bar, 56 μm; (12) specimen PIN, no. 5312/03405; scale bar, 33 μm; (13) specimen PIN, no. 5312/16091; scale bar, 41 μm.
Fig. 14. *Pylentonema antiqua* Deflandre, 1963, specimen PIN, no. 5312/15727; scale bar, 46 μm.
Figs. 15 and 16. *Ceratoikiscum bujugum* Foreman, 1963: (15) specimen PIN, no. 5312/15762; scale bar, 47 μm; (16) specimen PIN, no. 5312/15823; scale bar, 61 μm.
Fig. 17. *Ceratoikiscum famennium* Nazarov et Ormiston, 1993, specimen PIN, no. 5312/15748; scale bar, 62 μm.
Fig. 18. *Ceratoikiscum perittacanthinum* Foreman, 1963, specimen PIN, no. 5312/15873; scale bar, 48 μm.
Figs. 19 and 20. *Holoeciscus foremanae* Cheng, 1986: (19) specimen PIN, no. 5312/15892; scale bar, 68 μm; (20) specimen PIN, no. 5312/15837; scale bar, 66 μm.
Fig. 21. *Holoeciscus quasiauceps* Wang, 1997, specimen PIN, no. 5312/15902; scale bar, 72 μm.
Fig. 22. *Holoecicus auceps* Foreman, 1963, specimen PIN, no. 5312/15864; scale bar, 52 μm.
Fig. 23. *Palaeoscenidium cladophorum* Deflandre, 1953, specimen PIN, no. 5312/15842; scale bar, 40 μm.
Fig. 24. *Palaeothalomnus arrhinia* (Foreman, 1963), specimen PIN, no. 5312/15726; scale bar, 79 μm.

Upper Devonian, Lower Famennian Substage; Polar Urals, Lemvin Zone, Palnik-Yu River: (1, 2, 5, 6, 8–17, 19, 21–23) sample 101/594; (3, 4, 18, 20) sample 101/593.

Plate 28



on Domanik was published by the employee of the Dutch embassy in Russia Nicolaes Witsen (1692). He indicated that, on the Ukhta River, at a distance of 1.5 miles from the portage, water contained oil and, in the same region, the "domanik" occurred, which burnt like a candle. In 1745, Fedor Pryadunov began oil production on the Ukhta River and built the world first oil refinery. In 1855, the first borehole 50 m deep was bored there (Fishman, 1991; Kuznetsov, 1995).

The Domanik deposits in the Ukhtinskii District were described for the first time by A.A. Keyserling in the mid-19th century after his travel to the Pechora Region (Tikhomirov, 1960). Already in the first reports from the expedition, Keyserling provided extensive new data; in particular, on the bank of the Syasya River, he discovered transitional beds from the Silurian to Devonian, which were not recorded in westerly sections (Keyserling, 1843). He revealed that the so-called "Domanik" (marly–clayey bituminous shale impregnated with oil and containing goniatites and other faunal remains) is oil-bearing rock. Keyserling assigned domanik deposits to the Lower Devonian–Silurian and proposed that they were the most ancient rocks of the Ukhta River Basin. As field studies and examination of the material were accomplished, Keyserling and Kruzenshteyn (1846) published a fundamental study, which was devoted to huge and previously poorly investigated field and provided extensive material of geology and geography of the Pechora Region. This work has shown that the Timan Mountain Ridge extends northwesterly and is mostly composed of Devonian and Carboniferous deposits and, between the Timan and Ural Mountains, there is a large area covered by Quaternary deposits of the Bolshezemelskaya Tundra.

At the same time, to get a complete report on all available materials, the tsarist government invited the English geologist R.J. Murchison and French paleontologist E. Verneuil. They were provided with very favorable conditions for work and used not only published data, but also hand-written reports of Russian researchers. To the arrival of Murchison everything necessary had already been prepared, including new geological maps, descriptions of sections and outcrops, museum collections, etc. (Tikhomirov, 1960). Murchison had an opportunity to familiarize himself with thorough paleontological and stratigraphical works of Russian geologists. However, when considering the material of Silurian and Devonian formations of northwestern Russia, he did not mention the contribution of researchers who worked there earlier.

This naturally caused discontent of Russian geologists; in this connection Eichwald (1846, p. 412) indicated that "... Mr. Murchison unjustly tries to assure that, before his arrival, we had complete geological confusion... On the contrary, it is better to say that Mr. Murchison has determined and described only rock formations of Russia that we knew before his arrival."

At the same time, the geological part of this work was completely included in the monograph of Murchison, Verneuil, and Keyserling (1845) on the geology of European Russia as a separate section. The map prepared by Keyserling and Kruzenshteyn has become a unique source for geological reconstructions used for almost 100 years.

From the end of the 19th century, the main attention was paid to the general geological (paleontological, stratigraphical, and tectonic) aspects of the study of Domanik deposits. The major studies of the Domanik beds were connected with searching for oil.

The lithology, stratigraphy, geochemistry, oil-and-gas-bearing, paleontology, and paleogeography of Domanik were considered by Tikhonovich (1930, 1941, 1951), Tikhomirov (1967, 1995), Kushnareva (1959, 1963), Zav'yalov (1966), Maksimova (1970, 1975), Sorokin (1978, 1994), Menner (1989), Menner et al. (1991, 1992), Becker et al. (2000), Telnova (1995, 2009), Belyaeva et al. (1998), and many other researchers.

In the study of Domanik, detailed examination of radiolarians, which are literally conserved in carbonate nodules among siliceous differences of rocks, is of particular interest (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2001).

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Explanation of Plate 28

Early Famennian radiolarians of the Middle Urals; assemblage with *Haplentactinia alekseevi–Haplentactinia vilvaensis:* spherical latticed Spumellaria (1–13) and spiny Aculearia (14).

Fig. 1. *Polyentactinia circumretia* Nazarov et Ormiston, 1993, specimen PIN, no. 5369/15657; scale bar, 45 μm.

Figs. 2–4. *Haplentactinia alekseevi* Afanasieva, 2000: (2) specimen PIN, no. 5369/15619; scale bar, 59 μm; (3) specimen PIN, no. 5369/15636; scale bar, 95 μm; (4) specimen PIN, no. 5369/15652; scale bar, 86 μm.

Figs. 5–7. *Haplentactinia rhinophyusa* Foreman, 1963: (5) specimen PIN, no. 5369/15622; scale bar, 57 μm; (6) specimen PIN, no. 5369/15644; scale bar, 86 μm; (7) specimen PIN, no. 5369/15635; scale bar, 68 μm.

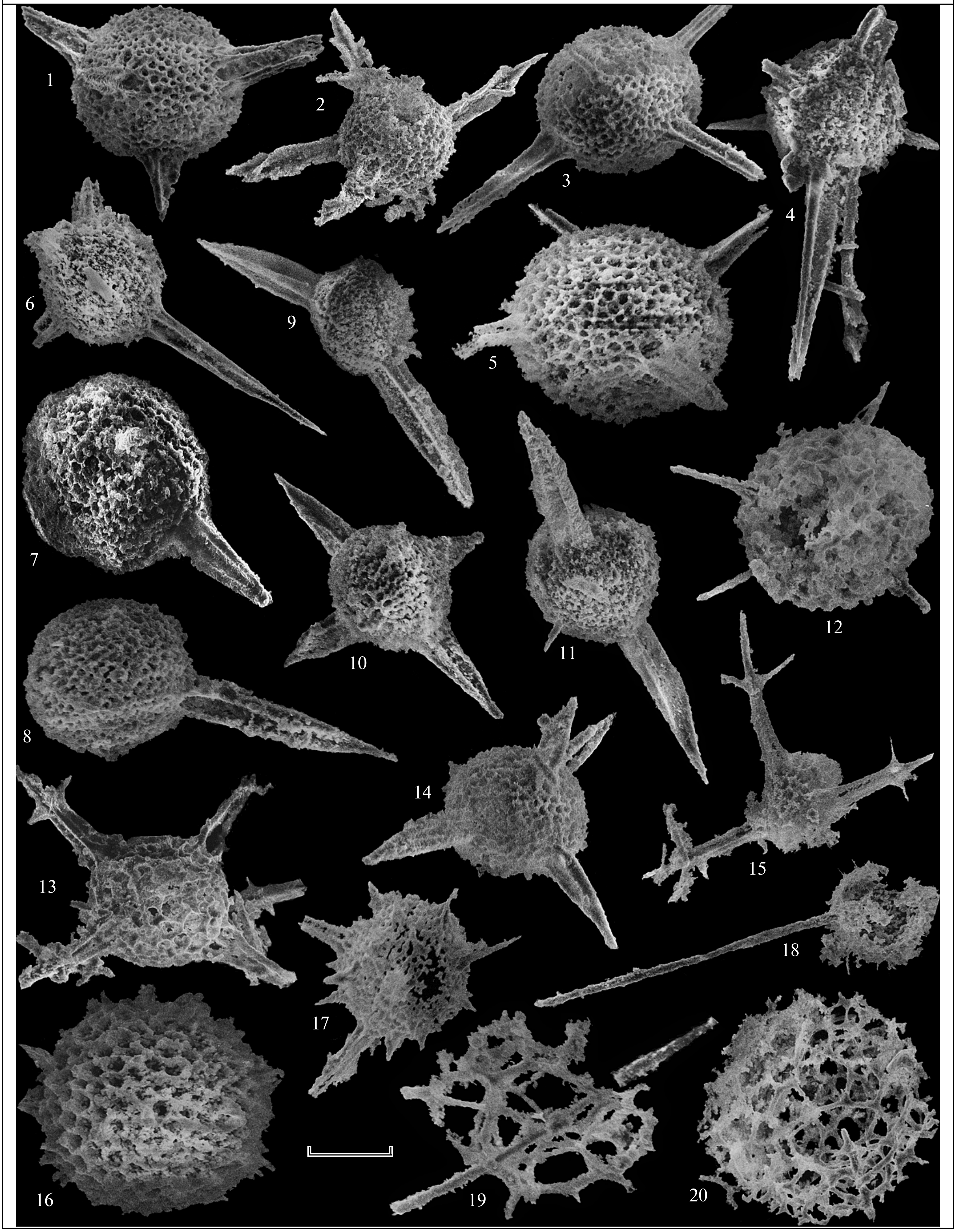
Figs. 8–10. *Haplentactinia vilvaensis* Afanasieva et Amon, sp. nov.: (8) specimen PIN, no. 5369/15616; scale bar, 89 μm; (9) specimen PIN, no. 5369/15617; scale bar, 85 μm; (10) specimen PIN, no. 5369/15641; scale bar, 64 μm.

Figs. 11–13. *Haplentactinia kuzminae* Afanasieva et Amon, sp. nov.: (11) specimen PIN, no. 5369/15625; scale bar, 72 μm; (12) specimen PIN, no. 5369/15639; scale bar, 74 μm; (13) specimen PIN, no. 5369/15648; scale bar, 86 μm.

Fig. 14. *Palaeothalomnus arrhinia* (Foreman, 1963), specimen PIN, no. 5369/15631; scale bar, 86 μm.

Upper Devonian, Lower Famennian Substage; Middle Urals, Perm Region, Vilva River, southeast of the town of Gremyachinsk: (1–3, 5–12, 14) sample k-25; (4) sample k-07/2; and (13) sample k-07/1.

Plate 29



DOMANIK BEDS

Tikhonovich (1930) established the Domanik Formation, extending from the village of Shuda-Yag and closely approaching the Yarega River, based on outcrops on the Ukhta River and its tributaries, the Domanik and Chut rivers (Fig. 6c). The lower part of the section outcrops most completely at the lower reaches of the Chut River (Figs. 14, 23), and the middle and upper parts are on the banks of the Ukhta and Domanik rivers (near the village of Shuda-Yag) (Fig. 14). For more complete characteristics of the continuous sequence and specificity of Domanik deposits, a complete section of the stratotype of the Domanik Formation open by boreholes Shuda-Yag-1002, Shuda-Yag-1003, and Ukhtinskaya-3B in the vicinity of the town of Ukhta (Fig. 14) was studied (Menner et al., 1992; Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2000, 2001; Becker et al., 2000).

Cyclicity in the Formation of the Domanik Beds

One of the main distinctive features of the Domanik beds is the cyclicity of sedimentation, which reflects the pulsating evolutionary pattern of the basin. At the same time, Maksimova (1970, p. 76) marked that, although “the Domanik beds show thin and microscopic, irregularly horizontal lamination, the rocks of different types form relatively thin, frequently alternating layers, they lack a clear rhythm in this alternation.” The lamination of Domanik rocks, on the one hand, is in fact extremely irregular, changeable in the thickness of particular layers, sequence of replacement of rocks, set of rocks in particular cyclites, and in the number and composition of fossils in different interbeds. However, on the other hand, deposits of the Domanik Formation display strict cyclicity of sedimentation.

The study of a complete Domanik section has shown for the first time that the Domanik beds have units of cyclicity of several orders (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2000, 2001). The planetary Domanik cycle of development (Tikhomirov, 1967, 1995; Sorokin, 1978, 1994) corresponds to accumulation of deposits of the Domanik Formation as a whole and to the maximum transgression in the Ukhta Basin. Regional developmental stages of lower orders, which correspond to the formation of subformations and members (Fig. 14), are probably of tectonic–eustatic nature and connected with activation of underwater volcanism and inflow of silica from thermal springs of deep magmatic centers (Maksimova, 1970; Klevtsova and Afanasieva, 1998; Klevtsova, 2000). Even smaller pulsations apparently reflect climatic and ecological fluctuations fixed in deposits. These are particular strata, layers in samples, and even thin layers, which are only seen in thin sections or with the aid of SEM (Fig. 23; Pl. 31).

The section of the Domanik Formation is 59–69 m thick and distinctly divided into three subformations (Fig. 14) (Afanasieva, 2000a; Afanasieva and Mikhailova, 2001).

The lower subformation is formed of interbedding limestones and cherty limestones with silicides. These are so-called combustible shales with siliceous and siliceous–carbonate nodules. Three layers of massive limestones with abundant shells of various organisms are distinct.

The middle subformation is more siliceous. It is mostly composed of platy cherty limestones, silicides, fine schistose bituminous–clayey–carbonate–siliceous matter. The middle subformation differs from

Explanation of Plate 29

Middle–Late Frasnian radiolarians of the Rudny Altai: spherical porous Sphaerellaria (1–18) and latticed Spumellaria (19, 20).

Fig. 1. *Entactinia herculea* Foreman, 1963, specimen PIN, no. 5253/50219; scale bar, 55 μm.
Fig. 2. *Entactinia* sp. *A*, specimen PIN, no. 5253/50327; scale bar, 62 μm.
Fig. 3. *Bientactinosphaera pinica* Afanasieva, 2000, specimen PIN, no. 5253/50215; scale bar, 55 μm.
Fig. 4. *Entactinia bifida* Afanasieva, 2000, specimen PIN, no. 5253/50126; scale bar, 44 μm.
Fig. 5. *Bientactinosphaera hystricosa* (Foreman, 1963), specimen PIN, no. 5253/50224; scale bar, 40 μm.
Fig. 6. *Radiobisphaera assidera* (Nazarov, 1975), specimen PIN, no. 5253/50225; scale bar, 55 μm.
Fig. 7. *Radiobisphaera rozanovi* Afanasieva et Amon, 2009, specimen PIN, no. 5253/50310; scale bar, 30 μm.
Fig. 8. *Radiobisphaera domanicensis* (Bykova, 1955), specimen PIN, no. 5253/50301; scale bar, 37 μm.
Fig. 9. *Bientactinosphaera pittmani* (Hinde, 1899), specimen PIN, no. 5253/50121; scale bar, 55 μm.
Fig. 10. *Bientactinosphaera egindyensis* (Nazarov, 1975), specimen PIN, no. 5253/50133; scale bar, 75 μm.
Fig. 11. *Bientactinosphaera obtusa* (Hinde, 1899), specimen PIN, no. 5253/50117; scale bar, 44 μm.
Fig. 12. *Borisella bykovae* Afanasieva, 2000, specimen PIN, no. 5253/50325; scale bar, 37 μm.
Fig. 13. *Moskovistella victorialis* Afanasieva, 2000, specimen PIN, no. 5253/50411; scale bar, 37 μm.
Fig. 14. *Moskovistella mira* Afanasieva, 2000, specimen PIN, no. 5253/50330; scale bar, 37 μm.
Fig. 15. *Moskovistella allbororum* Afanasieva, 2000, specimen PIN, no. 5253/50415; scale bar, 37 μm.
Fig. 16. *Astroentactinia biaciculata* Nazarov, 1975, specimen PIN, no. 5253/50611; scale bar, 33 μm.
Fig. 17. *Astroentactinia tikhomirovi* Afanasieva, 2000, specimen PIN, no. 5253/50104; scale bar, 56 μm.
Fig. 18. *Astroentactinia vishnevskayae* Afanasieva, 2000, specimen PIN, no. 5253/50612; scale bar, 55 μm.
Fig. 19. *Haplentactinia labyrinthica* (Aitchison, 1993), specimen PIN, no. 5253/50407; scale bar, 32 μm.
Fig. 20. *Haplentactinia barskovi* Afanasieva, 2000, specimen PIN, no. 5253/50401; scale bar, 40 μm.

Upper Devonian; Rudny Altai, Zmeinogorskii District: (1–15, 17, 19, 20) Middle Frasnian Substage, Lower Kamenevsk Subformation; Goryunovo locality, Zolotukha River, sample 97-71; (16, 18) Upper Frasnian Substage, Upper Kamenevsk Subformation; village of Uspenka, Zolotukha River, sample 44-8.

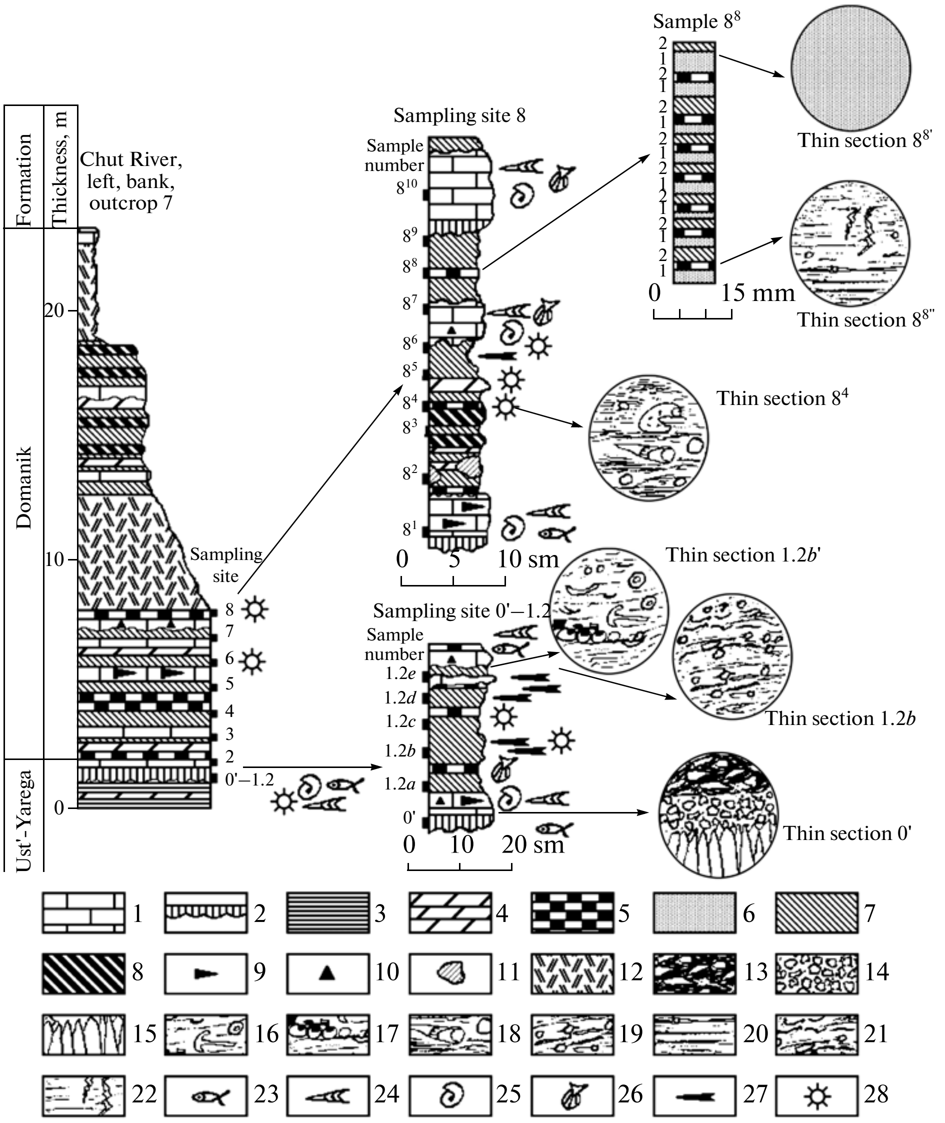


Fig. 23. Section of the lower part of the Domanik Formation on the Chut River, outcrop 7: (1) limestone, (2) "boundary" coarse-crystalline limestone, (3) clay, (4) clayey cherty limestone; (5, 6) cherty limestone: (5) inequigranular, (6) microgranular; (7) fine-platy silicides, (8) massive flint; (9) bituminous, (10) silicification, (11) carbonate nodules, (12) talus; (13–22) schematic drawings of thin sections: (13) ferrugination, (14, 15) calcite: (14) granular and tabular, (15) columnar; (16–21) organogenic limestone: (16) spicular–detrital, (17) linguloid with extraction of phosphate, (18) ammonoid–orthoceratoid, (19) radiolarian; (20–21) microlamination in limestones: (20) horizontal, (21) wavy and oblique; (22) traces of rhizoids; (23–28) fauna: (23) fish remains, (24) orthoceratoids, (25) ammonoids, (26) bivalves, (27) tentaculites, and (28) radiolarian.

other parts of the Domanik section in the impoverished fauna, which occur in individual limestone interbeds.

The upper subformation is characterized by an increase in carbonate content of rocks and differs in the increase in diversity of various fossils.

The next level of cyclicity of deposits (members) is distinct in the outcrop or at the base of boreholes. For example, the upper subformation of Domanik is divided into four members, from below upward in the section (Fig. 14): (1) clay (up to 3–4 m thick); (2) interbedding platy cherty limestones, limestones, combustible shales, and infrequent thin clay interbeds (up to 6 m thick); (3) clay with limestone interbeds (up to 4.5 m thick); (4) cherty limestones, combustible shales with carbonate nodules (up to 8 m thick). Each member includes several groups of layers.

Further, each bed consists of a series of layers (Fig. 23; Pl. 31, figs. 1–5); in particular, at the base of a cyclite, there is always carbonate–clayey or carbonate–siliceous claystone, and the roof contains a carbonate, frequently organogenic layer which is distinguished by scattered skeletal remains of ammonoids and tentaculites on the surface of the strata. The micro- and macrolamination, accentuated by the distribution of tentaculite skeletons, is typical of the Domanik beds (Pl. 31, fig. 5; Pl. 32, figs. 9, 10); organogenic limestones (Pl. 33, figs. 1, 3–8) and cherty limestones (Pl. 33, fig. 2) with faunal remains are of particular interest. Rock samples treated with acetic acid show fine alternation of thin siliceous and carbonate strongly bituminous layers with abundant radiolarian remains, sponges, and tentaculites (Pl. 31, fig. 5; Pl. 32, fig. 10; Pl. 33, figs. 3–8; Pl. 34), which are frequently pyritized (Pl. 35). This is the lowest visually discernible macrolevel of cyclicity.

In thin sections, microscopic studies allow the recognition of the next level of cyclic lamination, depending on magnification (Fig. 23). For example, in the Verkhneizhemskii District, the core of a 46-m-thick borehole showed 310000 thin layers (Tikhonovich, 1951), i.e., about six thin layers per 1 mm. The study of the Domanik beds from boreholes Ukhtinskaya-3B and Shuda-Yag-1003 and an outcrop on the Chut River has shown from three to seven thin layers per 1 mm (Fig. 23; Pl. 31, fig. 6). Siliceous carbonate rocks are formed of fine mixture of compounds of $CaCO_3$ and SiO_2. Ultralamination is distinct in this case only under an electron microscope (magnification × 1000 or more) (Pl. 31, fig. 7) (Afanasieva, 2000a; Afanasieva and Mikhailova, 2000).

The lower and upper boundaries of cyclites of all orders are distinct, sharp, sometimes rough (Pl. 31, figs. 2–7). Inside a cyclite, gradual transitions between layers are frequently observed (Pl. 31, fig. 1), which are particularly prominent, as marked by changes in abundance of faunal remains and their composition (Pl. 32, fig. 10) (Afanasieva, 2000a; Afanasieva and Mikhailova, 2000).

Chert Content in Domanik Rocks

Another specific feature of the Domanik Formation is the increased chert content. This was probably caused by increased content of dissolved silicic acid, which was produced by amplified underwater volcanic activity. The mean chert content of Domanik rocks (without pure cherts) is 37.2%. The primarily high concentration of SiO_2 in waters of the Domanik Sea agrees well not only with the distribution of the fauna, but also with very early sedimentary extraction of silica. As a rule, silica does not precipitate just from supersaturated marine water; instead it forms colloid and, then, precipitates in the shape of gel globules and concentrates abundantly at the bottom (Maksimova, 1970). However, the composition of admixture in the sediment and, especially, organic matter suppresses the crystallization of silica. The greater content of organic matter was in deposits, the weaker crystallization of siliceous deposits occurred (Khvorova and Dmitrik, 1972).

In this case, siliceous skeletons under conditions of hydrosulphuric contamination and normal salinity dissolved almost instantly, in two weeks: skeletal remains merely sunk in gel and were gradually dissolved and fused into enclosing matter (Khvorova and Dmitrik, 1972). In bituminous flinty slates, “shadows” of skeletal remains of various organisms are frequently seen; their shells were dissolved in surrounding cherts and “merged” with the host matter, with complete decomposition of the skeleton.

On the other hand, the rapid burial of organisms in Domanik deposits oversaturated with silica is evidenced by wide development of siliceous crustification of living cells of acritarchs (?), which retain the lifetime shape and sculptural details of the organic wall (Pl. 32, figs. 1–5).

In addition, in deposits of the Domanik Formation, calciferous formations of diagenetic origin in the shape of more or less extended lenses are widespread. The siliceous–carbonate and carbonate nodules, which are sometimes observed among completely silent cherts, are very rich in fossils, primarily, radiolarians, spicules of sponges, and acritarchs. Perhaps, they are only preserved due to partial calcification of the matter of nodules. The extraction of diagenetic calcite probably protected the shells of abundant organisms inhabiting the Domanik Basin from dissolution in siliceous silt (Tikhomirov, 1967, 1995).

The phenomena considered are evidence of sharp changes in saturation of waters of the Domanik Basin by silica in different times at different levels.

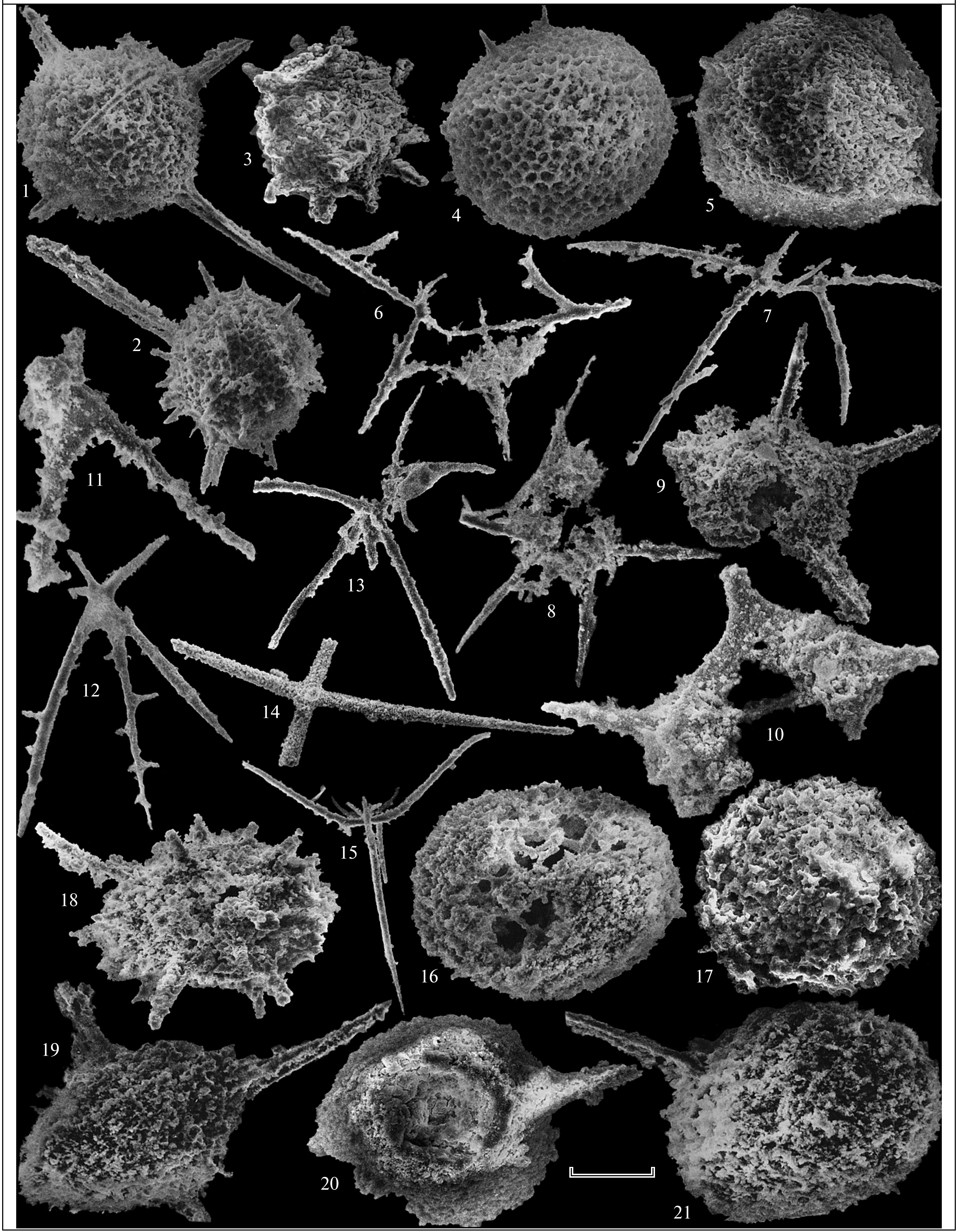
RADIOLARIANS AND ECOLOGICAL FEATURES OF BASINS OF THE DOMANIK TYPE

It is noteworthy that, during the Late Devonian, radiolarians of the Russian Platform showed selective distribution of regions of mass dwelling and stable preservation throughout the Late Devonian. These are regions of deposits of the Domanik type, which are enriched by organic matter and biogenic silica, which are traced within a wide band along the eastern marginal area of the Russian Platform. In this case, the pattern of silica sedimentation is well known; it was biogenically extracted from marine water and fell into the deposits as spicules of siliceous sponges and radiolarians.

The central basins of the Russian Platform lack domanik-like rocks. Detailed lithologic and lithologic–ecological studies of Hekker (1941, 1983), Birina (1948a, 1948b), Maksimova and Osipova (1950), Vishnyakov (1953), Bykova (1955), Shvetsov (1958), Maksimova (1970, 1975), Rodionova et al. (1995), Afanasieva and Mikhailova (2000, 2001), and many other researchers have not revealed any siliceous organisms in the central areas of the Russian Platform. Only Makhlaev (1964) mentioned the presence “in some cherts” of the Upper Famennian of questionable “traces of spicules of sponges.”

However, even presuming that, in the central part of the platform, rare siliceous sponges occurred in

Plate 30



places, “we only smoothen somewhat the contrast between central and eastern regions rather than do away with it” (Maksimova, 1975, p. 22).

Mass development of siliceous organisms (radiolarians and sponges) occurred in water areas of the eastern part of the Russian Platform, which displayed high content of silica in marine water due to the rise of deep highly siliceous waters along fractures (Bykova, 1955; Maksimova, 1975; Afanasieva, 2000a).

Note that, in general, cherts relatively frequently occur in the central part of the platform, although they are replacement silicides, which retain the structure of the initial carbonate rocks (Khvorova, 1968).

This stable confinement of mass development of essentially different siliceous organisms to a certain zone of the ancient sea is not casual. It is evident that we deal with a general, specific factor which is equally important for both sponges and radiolarians, i.e., the high content of silica in the water, which is required for the construction of siliceous skeletons.

In the Late Devonian, the marginal marine areas of the eastern part of the Russian Platform, which were inhabited by radiolarians and sponges, were a zone of high concentration of silica in marine water, in contrast to water areas of the central part of the platform, where siliceous organisms have not been recorded. The range of siliceous organisms is restricted from the east and from the west to deep fractures and exits of effusive structures. In this area, “magnificent development of sponges and radiolarians coincides with intensive inflow in the basin of volcanogenic matter, including silica” (Maksimova, 1975, p. 24).

The most active volcanic activity occurred in the Frasnian Age:

- in the Ural Geosyncline, effusive and pyroclastic rocks of the Frasnian Age occur in all regions of Late Devonian volcanism;
- in the Ukhtinskii District of the Timan–Pechora Basin, highly siliceous deposits of the Domanik Formation (Middle Frasnian), with rich radiolarian and sponge assemblages, are literally “pressed” close to the fracture zone and occur in approximately the same area as Early Frasnian covers of diabases;
- in the Russian Platform, lava flows (Kirov–Kazan Graben, Timan Region) are dated Early Frasnian and all known tuff interbeds are confined to the Frasnian.

The increased content of silica in oceanic water could have been connected with either volcanic eruptions or accompanying processes of fluid relieving in the fracture zones of the oceanic crust (Syvorotkin, 1994, 1998, 2002; Egorkin, 2000). In the areas of fluid relieving on the oceanic bottom, the concentration of silica increases, providing organisms with the building matter for the skeleton (Syvorotkin, 1994, 1998, 2002).

The content of silicium in the area of the juvenile water inflow occasionally increases by 20–40 time compared with the usual values and such siliceous water expands for hundreds of kilometers (Maksimova, 1975; Lisitsyn, 1978; Klevtsova, 2000). Moreover, the maxima of silica (65–70%) in the consolidated crust fall just on the eastern marginal areas of the platform (Egorkin, 2000). However, westerly, with the distance from the fractures, highly siliceous domanik

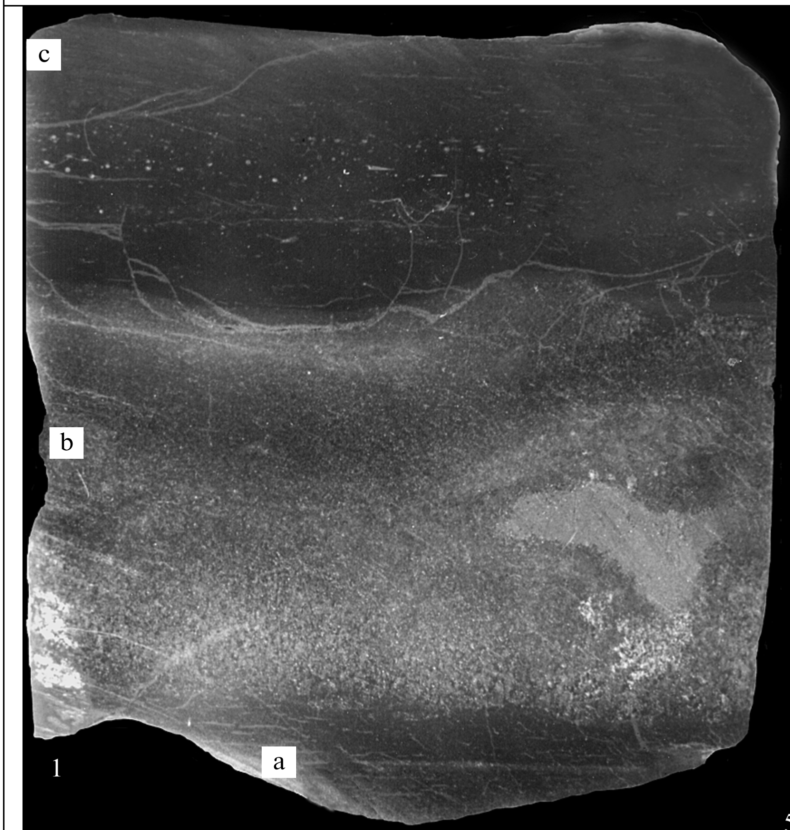
Explanation of Plate 30

Middle–Late Devonian radiolarians Rudny Altai: spherical spongy Spumellaria (1–5), spiny Aculearia (6–15), and discoidal Stauraxonaria (16–21).

Fig. 1. *Spongentactinella windjanensis* Nazarov, 1982, specimen PIN, no. 5253/50313; scale bar, 56 µm.
Fig. 2. *Spongentactinella corynacantha* Nazarov et Ormiston, 1983, specimen PIN, no. 5253/50102; scale bar, 56 µm.
Fig. 3. *Spongentactinella veles* (Foreman, 1963), specimen PIN, no. 5253/50111; scale bar, 74 µm.
Fig. 4. *Spongentactinia fungosa* Nazarov, 1975, specimen PIN, no. 5253/50109; scale bar, 44 µm.
Fig. 5. *Spongentactinia diplostraca* (Foreman, 1963), specimen PIN, no. 5253/50613; scale bar, 55 µm.
Fig. 6. *Ceratoikiscum incomptum* Nazarov, 1975, specimen PIN, no. 5253/50518; scale bar, 44 µm.
Fig. 7. *Ceratoikiscum ukhtensis* Afanasieva, 2000, specimen PIN, no. 5253/50514; scale bar, 44 µm.
Fig. 8. *Ceratoikiscum spinosum* Cheng, 1986, specimen PIN, no. 5253/50523; scale bar, 44 µm.
Fig. 9. *Ceratoikiscum simplum* Cheng, 1986, specimen PIN, no. 5253/50435; scale bar, 55 µm.
Fig. 10. *Ceratoikiscum planistellare* Foreman, 1963, specimen PIN, no. 5253/50503; scale bar, 52 µm.
Fig. 11. *Palaeoscenidium robustum* Aitchison, 1993, specimen PIN, no. 5253/50504; scale bar, 40 µm.
Fig. 12. *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 5253/50508; scale bar, 37 µm.
Fig. 13. *Palaeoscenidium delicatum* Aitchison, 1993, specimen PIN, no. 5253/50512; scale bar, 55 µm.
Fig. 14. *Palacantholithus stellatus* Deflandre, 1973, specimen PIN, no. 5253/50507; scale bar, 55 µm.
Fig. 15. *Nazarovites mikhailovae* Afanasieva, 2000, specimen PIN, no. 5253/50513; scale bar, 55 µm.
Fig. 16. *Palaeodiscaleksus cribrarius* (Hinde, 1899), specimen PIN, no. 5312/50428; scale bar, 52 µm.
Fig. 17. *Palaeodiscaleksus saturniformis* Afanasieva et Amon sp. nov., specimen PIN, no. 5312/50712; scale bar, 33 µm.
Fig. 18. *Primaritripus kariukmasensis* Afanasieva et Amon, 2009, specimen PIN, no. 5253/50421; scale bar, 52 µm.
Fig. 19. *Primaritripus chuvashovi* Afanasieva et Amon, 2008, specimen PIN, no. 5253/50423; scale bar, 40 µm.
Fig. 20. *Primaritripus patella* (Hinde, 1899), specimen PIN, no. 5253/50628; scale bar, 61 µm.
Fig. 21. *Primaritripus buribayensis* Afanasieva et Amon, 2008, specimen PIN, no. 5253/50433; scale bar, 33 µm.

Upper Devonian: (1–4, 6–8, 12–15) Middle Frasnian Substage, Lower Kamenevsk Subformation; (5) Upper Frasnian Substage, Upper Kamenevsk Subformation. Middle Devonian: (17) Upper Givetian, Shipunikha Formation. Rudny Altai, Zmeinogorskii District: Goryunovo gully, Zolotukha River: (1–4, 6–8, 12–15) sample 97-71 and (9–11, 16, 18, 19, 21) sample 99–33); (20) Korbalikha deposits, sample 97-45); (5) village of Uspenka, Zolotukha River, sample 44-8; (17) Shipunikha River, sample 97-59.

Plate 31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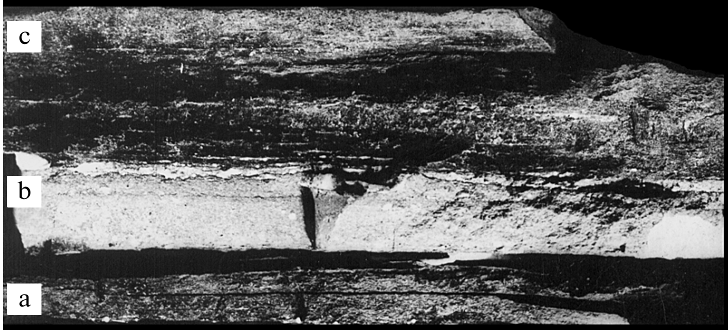
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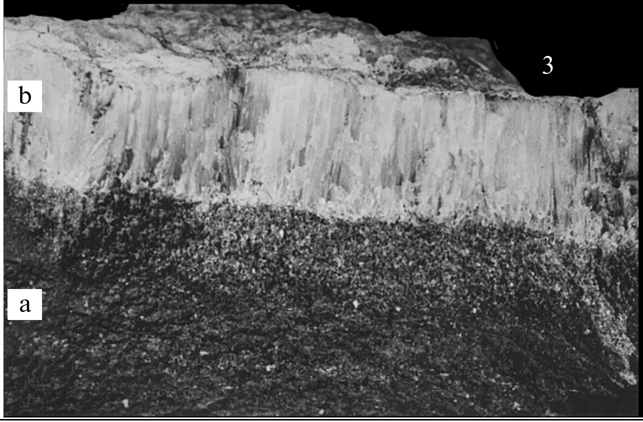
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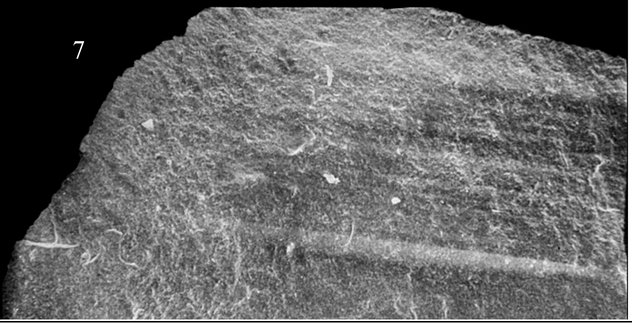
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is rapidly replaced by almost pure limestones with calciferous faunal fossils and without radiolarians.

The influence of volcanism and degassing on biological production of the ocean was considered by Bykova (1955), Maksimova (1970, 1975), Zhamoida (1972), and Lisitsyn (1978). These researchers paid attention for the first time to the correlation of volcanic activity and pulses of violent development of siliceous plankton, which is marked in the fossil record by accumulation of jaspers, cherts, and other silicides.

Thus, the development of zones of increased biodiversity is probably under control of tectonic factors; above the fracture zones, the sources of nutritive matter of endogenous nature, unique conditions for life are created. In addition, the areas of rich sponge and radiolarian oryctocoenoses coincide with the aulacogen zones.

Abrupt Explosions of Life in the Earth's History

The distribution of living substance over the Earth's surface is one of the most surprising and remarkable properties. Just the smallest organisms reproduce and expand surprisingly rapidly. At the beginning of the 19th century, Ehrenberg showed that one freely reproducing diatom and its descendants are capable of giving the biomass of our planet during eight days and can double this biomass during the subsequent hour. An ordinary infusoria (e.g., *Paramecium*) can produce during five years cytoplasm mass that is 104 times as great as the Earth's mass. These are only hypothetical examples of the rate of production of organic matter by living organisms (Vernadsky, 1926, 1983).

However, explosive expansion of fantastic scope of life is sometimes observed. In particular, in the Adriatic Sea, the phenomenon of abrupt reproduction of diatoms, which is named by the Italians "mare sporco" is sometimes observed. At the Latin American coasts, during the El Niño Time, the "red tide" is recorded, i.e., vigorous development of other unicellular algae, Dinoflagellata (Syvorotkin, 1994, 2002).

The study of living diatom algae in the Black Sea has shown that, during one hour, they throw into surrounding medium up to 30% of organic matter produced by photosynthesis (Borodkin, 1995; Volkov, 1995).

Under conditions less favorable for photosynthesis, particularly, as the balance between nitrogen and phosphorus is disturbed, cell fission stops. In this case, the volume of outflowing extracellular organic matter reaches 100% of the total biomass produced. Threadlike accumulations of organic matter enriched with sulfur are formed. Subsequently, aggregations of threadlike organic matter in the shape of flaky matter may be formed, some units of which are up to 10 cm^2 in cross section (Alldredge and Gotschalk, 1990; Borodkin, 1995; Herndl, 1995; Volkov, 1995).

In the period of red efflorescence in the surface water layer of the northwestern part of the Black Sea, the biomass of diatom algae sharply increases and their concentration reaches 10 g per 1 m^3. Diatoms reproduce at such a rate that the concentration of silicium dissolved in marine water sharply decreases and there is no time to restore it.

As a result, mass accumulations of diatoms impoverished by silica and flakes of extracellular organic matter are formed. They cover the sea surface by a several meter thick layer, under which anoxic conditions of hydrosulphuric contamination develop (Borodkin, 1995; Volkov, 1995; Agarkov, 2000).

At this time, "marine snow" appears, as accumulations of diatoms and extracellular organic matter form jellylike sediments on the bottom, which are rapidly consumed or decomposed. Thus, the disturbed balance is restored again (Agarkov, 2000; Afanasieva et al., 2005d).

However, hydrogen sulfide may be of endogenous nature, and it is frequently excreted above the fracture zones (Syvorotkin, 1998, 2002).

Explanation of Plate 31

Macro- (1–4) and microlamination (5–7) in Domanik rocks.

Fig. 1. Gradual replacement of (a) black thin-layer calcareous silicides by (b) dark gray siliceous limestones with fine detritus, radiolarian skeletons, tentaculites, and a large inclusion of pyrite, (c) passing into black cherty limestone with thin interbeds of tentaculite limestone: specimen PIN, no. 5311/K-447d-90; scale bar, 12 mm.

Fig. 2. Distinct interbedding of (a) flinty slate, (b) silicides, (c) cherty limestones with minor inclusions of tentaculite shells in interbeds: specimen PIN, no. 5311/007; scale bar, 8 mm.

Fig. 3. Sharp boundary between coarse-grained bituminous limestone (a) and coarse-crystalline, columnar limestone (b): specimen PIN, no. 5311/000', scale bar, 9 mm.

Fig. 4. Banded thick-layer bluish gray and blackish brown bituminous partially calcareous silicides, specimen PIN, no. 5311/006; scale bar, 9 mm.

Fig. 5. Thin broken layers of tentaculite shells in black and brownish gray bituminous calcareous–siliceous shales, specimen PIN, no. 5311/008^6; scale bar, 10 mm.

Fig. 6. Interbedding oblique and lenticular-layered limestones (white), calciferous cherts (gray), and siliceous claystones (black), specimen PIN, no. 5311/014, thin section; scale bar, 1.5 mm.

Fig. 7. Ultralamination in cherty limestones (sample was treated with 15% acetic acid), specimen PIN, no. 5311/12530; scale bar, 300 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation. Timan–Pechora Basin: (1) borehole Zapadnaya Vissertynskaya-1 (3601–3616 m of depth), sample K-447d-90; Chut River, outcrop 7: (2) sample 7, (3) sample 0', (4) sample 6, (5) sample 8^6, (7) sample 8^7; (6) borehole Shuda-Yag-1002 (65.2–65.8 m of depth), sample 19.

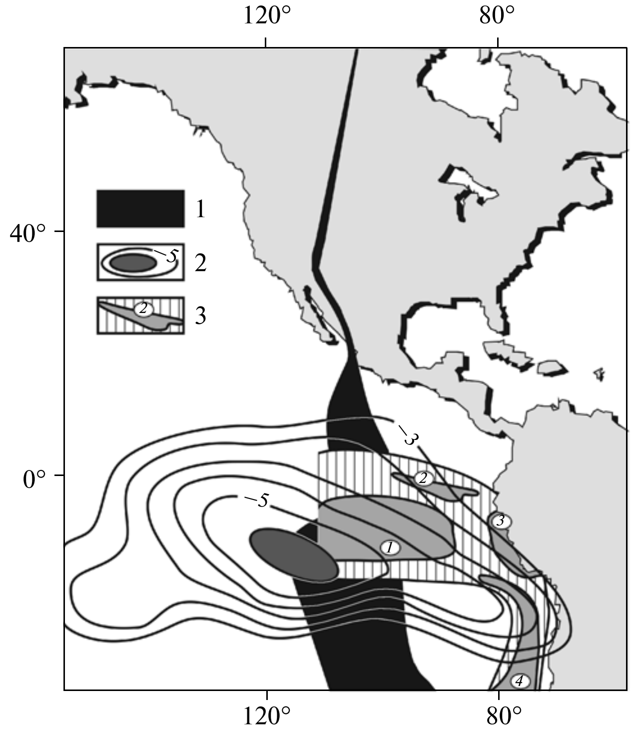


Fig. 24. Rift, ozone anomaly, and radiolarians from the Eastern Pacific: (1) East Pacific Rift Belt (after Syvorotkin, 1994); (2) center of ozone anomaly above the East Pacific Uplift in January, 1998 (satellite data, processed in the Central Aerogeological Laboratory of the town of Dolgoprudnyi) (Syvorotkin, 1998); (3) distribution of radiolarians in subtropical and equatorial surface deposits in the Eastern Pacific (Molina-Cruz, 1977): (*1*) "subtropical association," connected with subtropical surface waters and southern equatorial current, (*2*) "equatorial deepwater association," connected with reduced trade winds and Southern Equatorial Current (El Niño), (*3*) "association of the Peruvian Current," connected with the Peruvian Upwelling, (*4*) "association of the Chilean Current," connected with the water temperature in the northern part of the Chilean Current.

To explain mass accumulations of the fossil fauna, alternating with the periods of complete absence of the fauna, in particular, in deposits of the Domanik type, it is possible to use the model of Syvorotkin (1994, 2002). This model was developed in the course of the analysis of El Niño and it helps to explain abnormal productivity of local sites of the sea and periodic, rapid, and mass extinction of the biota.

El Niño is a warm current which sometimes develops near the coasts of Peru and Chile.

El Niño develops above one of the most active areas of the world rift system, Eastern Pacific Uplift (Fig. 24), the axial zone of which shows a very high thermal flow from the magmatic centers of the mantle.

The rift system is a degassing zone, which provides the oceanic bottom and water column with huge amount of chemical compounds, including the elements of life, nitrogen and phosphorus. The mechanism of transportation of nutritive matter from the bottom relieving region of hydrothermal sources to the oceanic surface consists of floating to the surface of gas bubbles. This column of gas bubbles is accompanied throughout its extent from the bottom to the surface by increased bioproductivity of organisms, which are not always typical of appropriate depths (Goryainov et al., 1996).

Most of the gases in the degassing zone are reduced gases, such as methane, hydrogen sulfide, hydrogen, and ammonia. Therefore, the oxygen content is very low over most of the water column. However, the surface layer (20–30 m thick) is enriched with oxygen from the atmosphere. Above the fracture zones (source of nutritive matter of endogenous nature), this layer provide unique conditions for the development of life.

During the El Niño Time, when degassing is amplified, hydrogen, which rises from the oceanic bottom of the rift valley, reacts with oxygen of surface water. Thus, oxygen disappears; thermal energy is produced and water becomes warmer. As a result, solubility of carbon dioxide decreases and it passes to the atmosphere; the ozone hole in the stratosphere is formed due to the influence of hydrogen.

On the other hand, as reduced gases are blown through the water, this medium becomes unfavorable for the aerobic biota. Stinking odor of hydrogen sulfide

Explanation of Plate 32

Acritarchs (1–5) and tentaculites (6–10).

Figs. 1 and 2. *Acritarcha* sp. 502: (1) specimen PIN, no. 5311/089271; scale bar, 30 μm; (2) specimen PIN, no. 5311/502–12306; scale bar, 21 μm.

Fig. 3. *Acritarcha* sp. 505, specimen PIN, no. 5311/12309; scale bar, 32 μm.

Figs. 4 and 5. *Acritarcha* sp. 504, specimen PIN, no. 5311/08924, (4) scale bar, 21 μm; (5) fragment, scale bar, 10 μm.

Fig. 6. *Tentaculita* sp. 604, specimen PIN, no. 5311/10017; scale bar, 89 μm.

Fig. 7. *Tentaculita* sp. 603, specimen PIN, no. 5311/08909; scale bar, 167 μm.

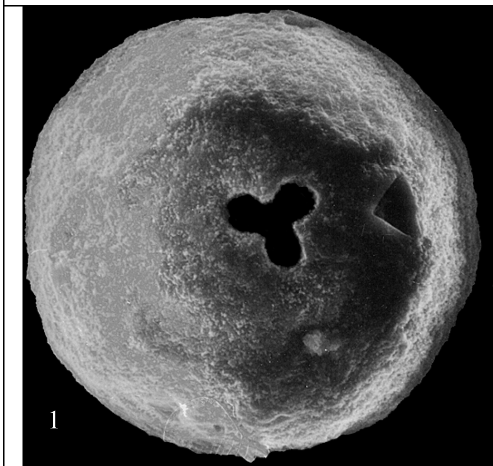
Fig. 8. *Tentaculita* sp. 608, specimen PIN, no. 5311/08913; scale bar, 170 μm.

Fig. 9. Scattered tentaculite skeletons on the surface of a layer of black siliceous shale; scale bar, 8 mm.

Fig. 10. Microlamination in tentaculite siliceous–clayey limestones produced by the number (0–70%) and orientation of tentaculite skeletons, thin section; scale bar, 1.5 mm.

Upper Devonian: (1, 4–10) Middle Frasnian Substage, Domanik Formation; (2, 3) Lower Frasnian Substage. Timan–Pechora Basin: (1, 4, 5) borehole Shuda-Yag-1003 (98–99 m of depth), sample 40; Chut River, outcrop 7: (2, 3) sample 0', (9) sample 7d; (6) Lyaiol River, outcrop 1904, sample 6; (7, 8) borehole Ukhtinskaya-3B (98.7–99.1 m of depth), sample 121; (10) Domanik River, 250 m upstream from the mouth, sample 2.

Plate 32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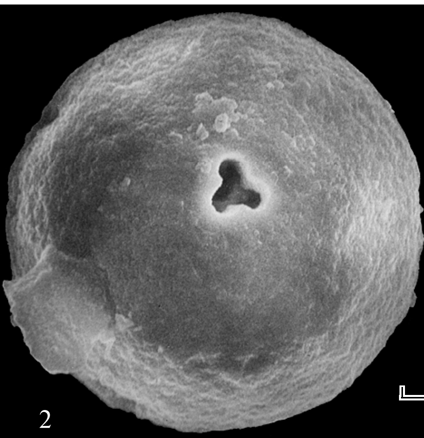
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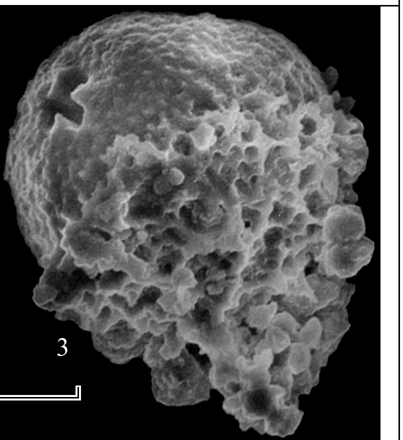
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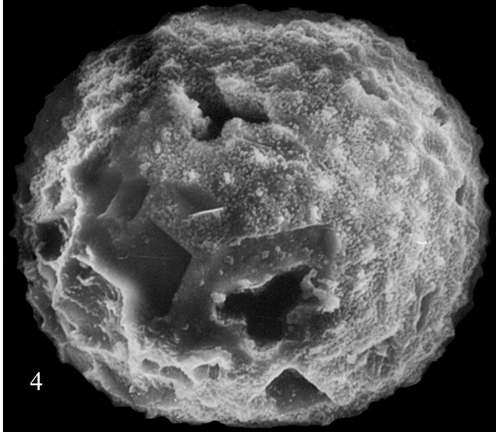
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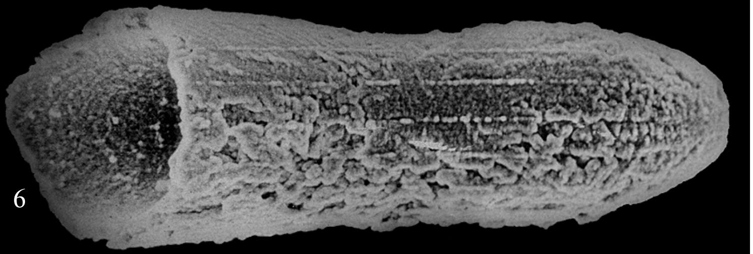
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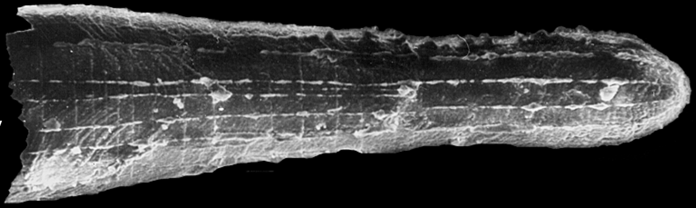
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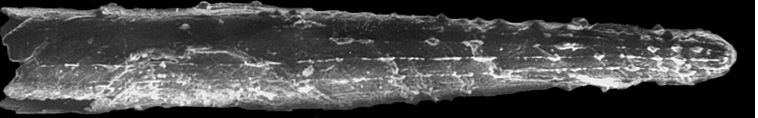
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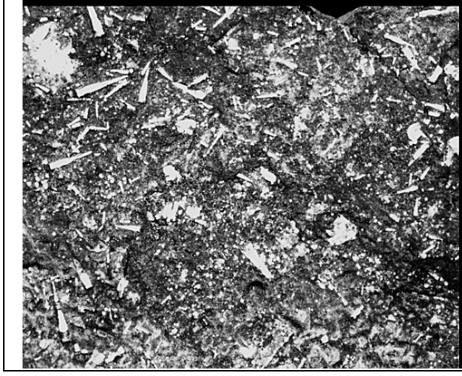
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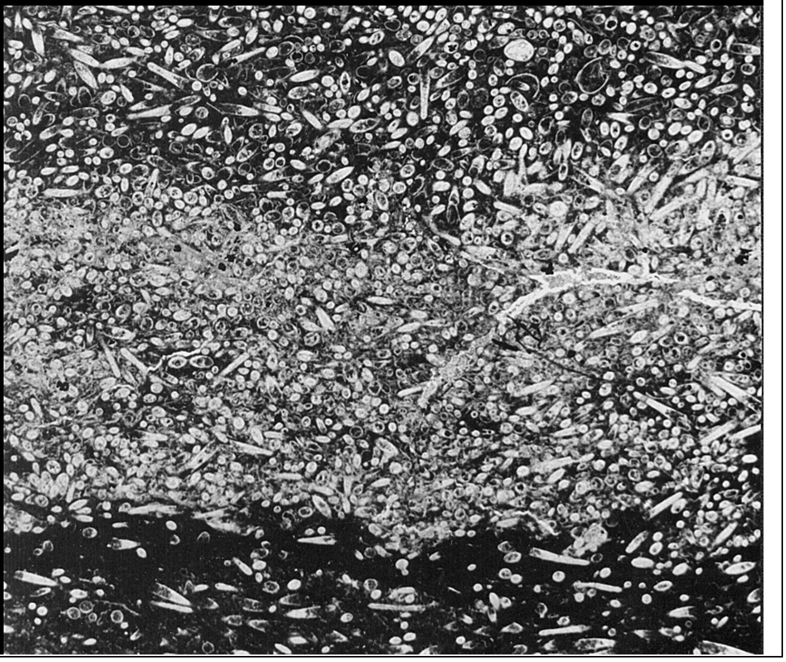
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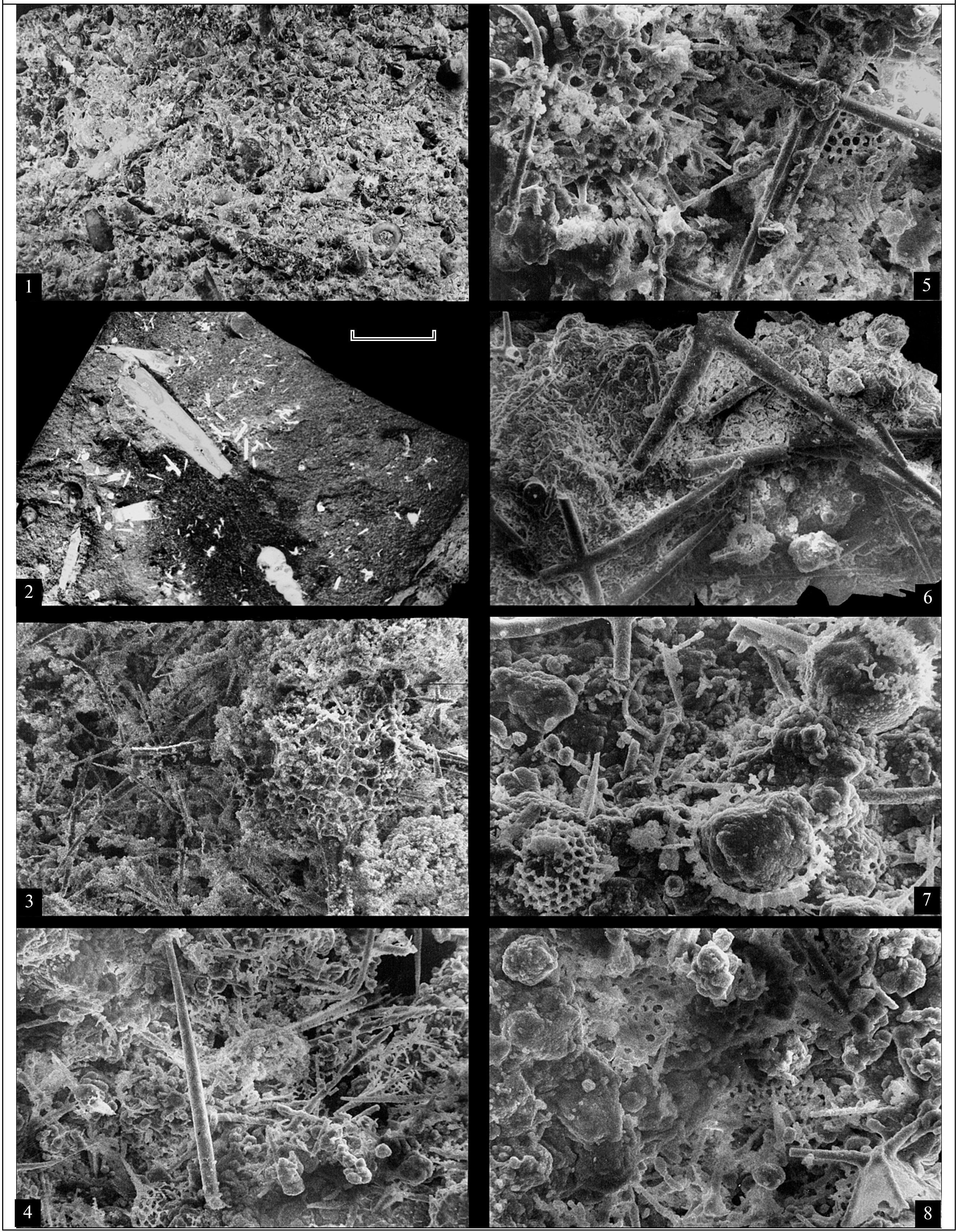
Plate 33



expands widely. Mass extinction of organisms caused by poisonous gases begins.

However, even after mass extinction of the aerobic biota, surprisingly vigorous development of life continues. In the water deprived of oxygen and rich in poisonous gases, the red tide caused by the development of Dinoflagellata begins. The ocean as though returns to the geological "preoxygen" past. The term *red tide* was introduced because these conditions are only favorable for strongly colored algae, which intensely developing change the color of marine water. The color of algae provides protection from ultraviolet; it was acquired as early as the Proterozoic, when the ozone layer was absent and the water surface was exposed to intense ultraviolet radiation (Syvorotkin, 1994, 2002).

Thus, El Niño has two biological aspects: (1) mass extinction of marine organisms and (2) abnormally high bioproductivity.

Traditional explanation of this phenomenon is upwelling, which lifts cold water enriched with nutritive components from the depth. However, during El Niño, upwelling processes are interrupted, the inflow of deep water rich in nutritive matter stops, and the productivity in the upper layers sharply falls.

The key to the resolution of points of abnormally high biological productivity of the ocean in the El Niño Time is the confinement of "spots" of extreme bioproductivity to degassing zones of the Earth's interior above the most active sites of the world rift system, which provide the oceanic bottom and water with huge amount of chemical compounds, including the elements of life, nitrogen and phosphorus (Syvorotkin, 1994, 2002).

Particular Recent areas of accumulation of rich radiolarian silts are drawn to the zones of fracture and ozone anomalies. The region of the East Pacific Rift Belt and ozone anomaly above the East Pacific Uplift are particularly indicative (Fig. 24) (Syvorotkin, 1994, 2002). They are connected with the distribution of radiolarians in subtropical, tropical, and equatorial surface deposits of the eastern Pacific (Molina-Cruz, 1977):

- "the subtropical association" is connected with the penetration of subtropical superficial waters and the Southern Equatorial Current;
- "the equatorial deepwater association" is connected with reduced trade winds and Southern Equatorial Current (phenomenon El Niño);
- "the association of the Peruvian Current" is connected with the Peruvian upwelling;
- "the association of the Chilean Current" is connected with the temperature of waters in the northern part of the Chilean Current.

Within the Russian Platform, lowered concentration of ozone occurs in the Ural–Caspian Rift System, which remains an intense degassing zone of the planet (Syvorotkin, 1994, 2002). During almost all the Paleozoic, this region was within the equatorial belt and, less often, in the tropical belts. As all known radiolarian localities of the Paleozoic are imposed on the map of aulacogens of the Russian Platform, it is seen that distribution of rich radiolarian assemblages surprisingly coincides with the area of the Ural–Caspian Rift System (Fig. 25). It determines the zone of distribution of Domanik rocks, which are rich in organic matter (Afanasieva, 2000a).

Perhaps, the Timan–Pechora Domanik Basin with an abnormal mode of hydrosulphuric contamination developed above one of the most active sites of ancient aulacogens (Fig. 25) (Klevtsova and Afanasieva, 1998; Klevtsova, 2000). In this region, as in the case of the modern El Niño, degassing and disruption of the ozone layer occurred. Apparently, the marine snow also occurred; however, diatoms were probably replaced by the widespread acritarchs and timanites.

Consequently, the development of zones of increased radiolarian bioproductivity is under control of climatic and tectonic factors; above the deepwater fractures of rift zones and aulacogens (sources of nutritive matter of endogenous nature), unique conditions for life are formed within the equatorial and tropical belts.

Hydrosulphuric Contamination of Bottom Waters

In the section of the Domanik Formation of the Timan–Pechora Basin, two main deposit variants alternate: on the one hand, black bituminous rocks rich in organic matter, but completely deprived of skeletal remains and, on the other hand, limestone beds overfull of skeletons of various organisms, but

Explanation of Plate 33

Organogenic limestones and cherty limestones with faunal remains.

Fig. 1. Organogenic, whole-shell, "boundary" limestone, with ammonoids and orthoceratoids, PIN, no. 5311/001; scale bar, 1.3 mm.

Fig. 2. Black cherty limestone, with orthoceratoids, ammonoids, and gastropods, PIN, no. 5311/004; scale bar, 1.3 mm.

Figs. 3, 4, 7, and 8. Sponge–radiolarian limestone: (3) PIN, no. 5311/14229; scale bar, 89 μm; (4) PIN, no. 5311/14106; scale bar, 72 μm; (7) PIN, no. 5311/14110; scale bar, 44 μm; (8) PIN, no. 5311/14102; scale bar, 44 μm.

Figs. 5 and 6. Radiolarian–sponge limestone: (5) PIN, no. 5311/14218 (= 44 μm; (6) PIN, no. 5311/13414; scale bar, 200 μm.

Upper Devonian: (1) Lower Frasnian Substage, Ust'-Yarega Formation; (2–5, 7, 8) Middle Frasnian Substage, Domanik Formation; (6) Upper Frasnian Substage. Timan–Pechora Basin: (1) Chut River, outcrop 7, sample 0'; (2) sample 4; (3) outcrop 8, sample 7d; (4, 7, 8) Domanik River, outcrop 21, sample 3a; (5) Ukhta River, point 3, sample 1681; (6) borehole Vapovskaya-2056 (72 m of depth), sample 11. Samples were treated with 15% acetic acid.

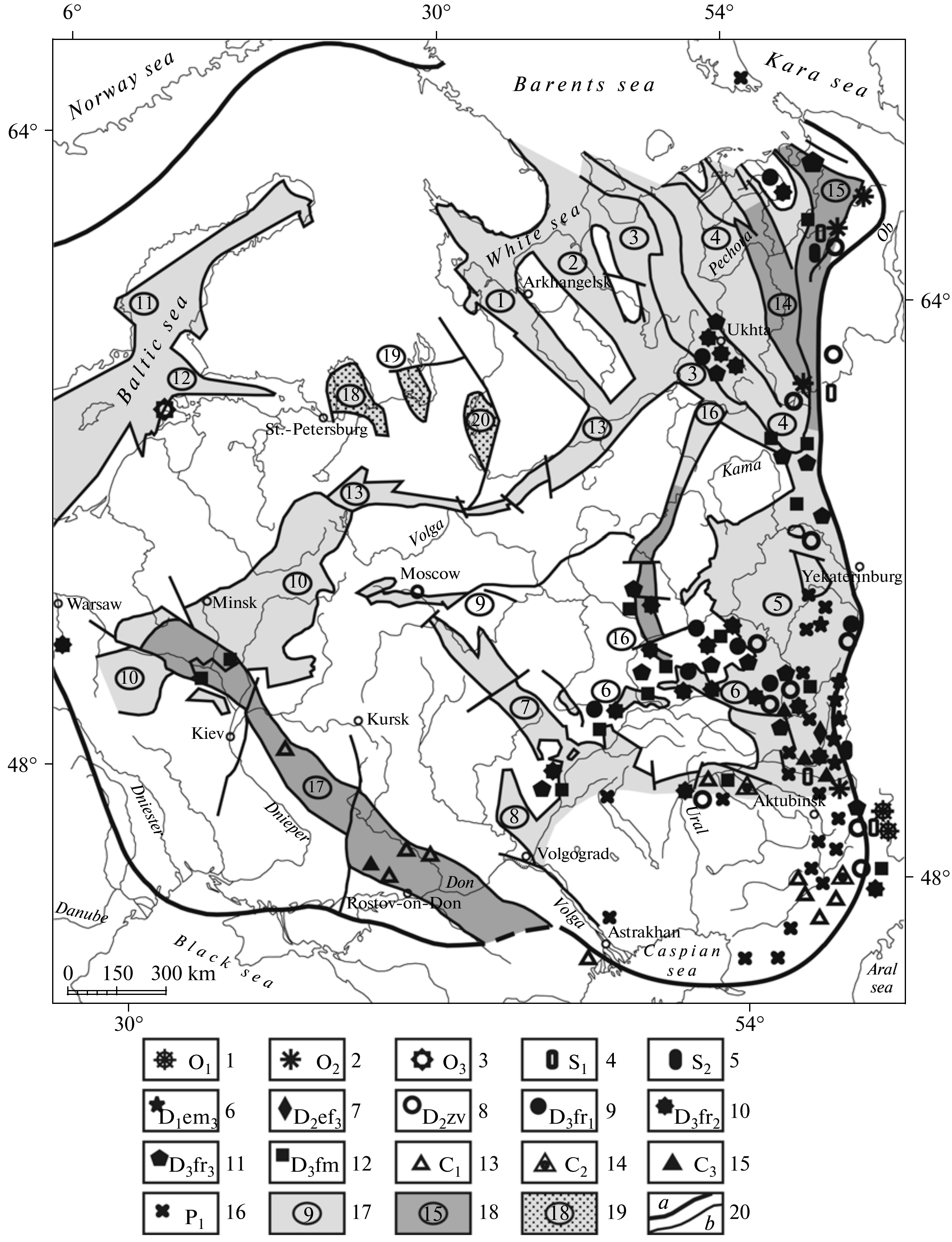


Fig. 25. Radiolarian localities of the Paleozoic and aulacogens of the Russian Platform: (1–14) radiolarian localities of the Paleozoic: (1–3) Ordovician: (1) Lower, (2) Middle, and (3) Upper; (4, 5) Silurian: (4) Lower, (5) Upper; (6) Lower Devonian, Upper Emsian Substage; (7, 8) Middle Devonian: (7) Upper Eifelian Substage, (8) Givetian Stage; (9–12) Upper Devonian: (9) Lower Frasnian Substage, (10) Middle Frasnian Substage, (11) Upper Frasnian Substage, (12) Famennian Stage; (13–15) Carboniferous: (13) Lower, (14) Middle, (15) Upper; (16) Lower Permian; (17, 18) aulacogens: (17) Baikalian (1–12) and Baikalian–Caledonian (13), (18) Baikalian–Hercynian (14–15) and Hercynian (16, 17); (19) grabens (18–20): (1) Kandalaksha–Dvina, (2) Mezen, (3) Timan, (4) Timan–Izhma, (5) Kama–Ufa, (6) Sernovodsk–Abdulin, (7) Pachelma, (8) Don–Medveditsa, (9) Moscow, (10) Volyn'–Orsha, (11) Botnichskii–Baltic, (12) Finnish, (13) Central Russia, (14) Pechora–Kolvin, (15) Varandei–Adzvinsk, (16) Vyatka–Kazan–Sergiev, (17) Pripyat–Dniepr–Donets, (18) Onega, (19) Ladoga, (20) Vozhe–Lacha; (20) boundaries of (*a*) platform and (*b*) aulacogens (after Valeev, 1978; Klevtsova, 2000).

with a low content of C_{org}. This is interbeds of organogenic limestone, and "sprinkle" (scattering) of organisms and their imprints on the surface of cherts, siliceous shale, or silicides, which lack fauna because it is merely not preservation (?) or abruptly disappeared in the course of burial.

An important factor controlling the ration of organic matter and skeletons of various organisms in deposits is the bottom hydrosulphuric contamination. It forms special conditions with the prevalence of reduction reactions from the very beginning of fossilization of organic matter.

Hydrosulphuric contamination is evidence of the absence of vertical circulation in the basin and, hence, impossibility of lifting waters rich in phosphorus from the depth. The change in phosphorus content disturbs the balance between phosphorus and nitrogen and, hence, increases the organic component; this, in turn, increases hydrosulphuric contamination in anoxic conditions. The formation of hydrosulphuric poisoning of the bottom zones of the basin is only possible in normal marine medium, because anaerobic bacteria receive oxygen for breathing by decomposition of sulfate with the discharge of the widespread pyrite. This phenomenon is evidenced by pyritization of some interbeds of Domanik rocks and spicules of sponges, tentaculites, and radiolarian skeletons; it turned out that fine latticed skeletons consist of pyrite, which has replaced silica (Pl. 35) (Afanasieva, 2000a; Afanasieva et al., 2005d).

Hydrosulphuric contamination promotes accumulation of organic matter produced by siliceous organisms and, simultaneously, destroys material (skeletal) evidence of the existence of these organisms. However, the more organic matter is in deposits the worse crystallization of siliceous rocks is observed. The deposits formed under these conditions are characterized by huge amount of organic matter, with a considerable contribution of carbohydrates of marine algae (acritarchs and timanites in the Paleozoic and diatoms in the Meso–Cenozoic). This is sapropel inseparably linked with oil.

Strakhov (1937) was the first to pay attention to the dependence of accumulation of reduced sulfur (ΣSH_2S or S_{pyrite}) on the content of organic matter in marine deposits. A general law for the rate of burying organic matter and reduced sulfur in marine deposits is the fact that they reach maximum in the coastal marine zone, i.e., in the area of the maximum sedimentation rate. However, in strongly reduced deposits, which contain $C_{org} > 3\%$ and, usually, free hydrogen sulfide, the absence of correlation between S_{pyrite} and C_{org} is marked. The loss of correlation between organic matter and sum of derivatives of hydrogen sulfide in these conditions is caused by the fact that, in strictly anaerobic conditions provided by the appearance of free H_2S in silt waters, the processes of bacterial sulfate reduction are strongly slowed and even almost stop. The last is connected with exhaustion of capacity of deposits for binding bacterial hydrogen sulfide. Thus, in deposits with high content of C_{org}, its potential for reduction of sulfate is used incompletely and the content of the sum of H_2S derivatives (and the main component, S_{pyrite}) is determined there by the concentration of reactive compounds of iron (Volkov, 1995).

Pyritization of Skeletons

Under conditions of hydrosulphuric contamination, the primary amorphous opal of radiolarian skeletons is occasionally replaced by pyrite (Pl. 35, figs. 3–10).

The study of radiolarians from the Upper Devonian, Middle Frasnian, Domanik deposits of the Timan–Pechora Basin and analysis of the skeleton structure have shown that the secondary pyrite, with characteristic copper–yellow luster, completely replaces silica in the skeleton (Pl. 35, figs. 3–8, 10) or only in its initial part (Pl. 35, fig. 9). Apparently, pyritization of skeletons could have begun in living organisms or just before the death (Afanasieva, 2000a).

The assumption that secondary pyrite was formed in skeletons of living radiolarians, imposes certain restrictions on the time and place of its formation. It is improbable that pyritization conditions included burial of radiolarian skeletons deep in deposits and long geological time. Moreover, the formation of petroleogenic Domanik rocks (Middle Frasnian), which contain pyritized skeletal remains of radiolarians and other organisms, could only develop in anoxic conditions.

Hydrosulphuric contamination of bottom waters forms conditions with the dominance of strictly reduction reactions from the very beginning of fossilization of organic matter. Hydrosulphuric poisoning of the bottom zones is only possible in a normal marine environment, because anaerobic bacteria receive oxygen for breathing due to decomposition of sulfate with extraction of the widespread pyrite. In the Domanik Time, this phenomenon is evidenced by pyritization of particular interbeds (Pl. 35, figs. 11, 12), spicules of sponges (Pl. 35, fig. 1), tentaculites (Pl. 35, fig. 2), and radiolarian skeletons: it turned out that fine latticed skeletons consist of pyrite, which has replaced silica (Pl. 35, figs. 3–10).

According to the data of Betekhtin (1950, p. 277), the formation of pyrite in sedimentary rocks "is connected with decomposition of fossils in the absence of free oxygen in the deeper sites of the water basin." Pyrite frequently forms pseudomorphoses based on various fossil organisms. These pseudomorphoses are probably formed under the influence of H_2S on minerals. It is noteworthy that the formation of pyrite by reduction reactions of sulfates and other sulfur-bearing compounds with organic matters follows the scheme:

$$2FeSO_4 + 2H_2SO_4 - 7O_2 = 2FeS_2 + 2H_2O.$$

Then, Betekhtin (1950, p. 278) reported on a very interesting experiment dealing with "a mouse placed in a glass with iron sulfate was replaced by pyrite in several years. Apparently, there was decomposition of proteins, which resulted in the formation of hydrogen sulfide. Pyrite appeared through the reaction of sulfur ions and iron." In addition, there is evidence of lifetime pyritization of shells in marine bivalves (Clark and Lutz, 1980).

Our concept of pyritization, which implies that primary skeletal opal of living radiolarians is replaced by pyrite, is rather incomplete. And the best support for the character of pyritization is provided by partially pyritized radiolarian skeletons, i.e., secondarily pyritized spherical part of the skeleton (Pl. 35, figs. 9, 10) and primarily siliceous spine ends (Pl. 35, fig. 9). It is possible to assume that pyritization developed on the organic matrix of the primary skeleton of living radiolarians. The recrystallization began from the initial internal part of the skeleton and gradually expanded to the peripheral ends of spines. Secondary skeletal pyrite of radiolarians and other organisms differs considerably from classical crystals or framboid pyrite observed in the rock (Pl. 35, fig. 11). In skeletons, pyrite is represented by very small granules, which are united in a massive skeleton with characteristic pyrite luster and color. The orientation of pyrite granules is probably similar to that of primary opal granules in radiolarian skeletons.

From the paleontological point of view, the most important assumption is that pyrite begins to replace skeletal opal in living radiolarians. Although this process is still insufficiently understood, it seems probable that pyritization develops at biomineralogical boundaries and along growth directions of the skeleton. This agrees with observations and illustrations of partial and complete pyritization of radiolarian and tentaculite skeletons, spicules of sponges, and other organisms (Pl. 35, figs. 1–10).

Model of Cyclic Changes in Ecological Conditions of Basins of the Domanik Type

The reconstruction of ecological conditions in the Timan–Pechora Basin in the Domanik Time allowed the development of a model for cyclic formation of rocks of the Domanik Type under conditions of hydrosulphuric contamination (Fig. 26) (Afanasieva and Mikhailova, 1998; Afanasieva, 2000a).

Periodic emissions of large amount of endogenous nutritive matter at faults in thermophilic aquatic conditions of the tropical sea occasionally promoted "bursts" of general bioproductivity of unicellular algae (Acritarcha and Tasmanaceae) and radiolarians as well as various ammonoids, many tentaculites, ostracodes, buchias, lingulids, and fishes (Fig. 26a).

After natural biological death of organisms, organic sediments are rapidly oxidized by oxygen in the bottom water layer due to vital activity of aerobic bacteria. If amount of organic matter is limited it is decomposed completely. In this case, a complex community of benthic organisms is formed. As hydrogen sulfide is oxidized by oxygen in the water to sulfur, it leaves reaction and contamination is not observed.

On the contrary, if there is great amount of organic matter, i.e., it prevails over the mineral component of deposits, hydrogen sulfide, not having time to oxidize, poisons the bottom layer of stagnant water and the boundary between oxidizing and reducing media passes high above the deposits (Fig. 26b).

Mass algal blooms, involving phytoplankton (possibly, acritarchs and timanites) in these stagnant water bodies probably produced huge amount of carbohydrate compounds of marine algae and caused fabulous bloom of zooplankton, particularly, radiolarians. Organisms die, not being consumed by others, their remains are accumulated at the bottom, giving rise to radiolarian algal taphocoenoses.

However, on the other hand, mass phytoplankton blooms and wide development of zooplankton (including radiolarians) in the upper aerated and well-lighted water layers restrict aeration of deeper water layers. This causes periodical temporal extinction of benthic forms and suppression of vital activity of aerobic bacteria.

At the same time, some organisms are probably capable of surviving in these conditions. This is probably true of radiolarians. Recent radiolarians survive in poorly lighted water due to symbiosis with unicellular algae serving as a reserve source of energy in adverse conditions (Anderson and Matsuoka, 1992; Afanasieva et al., 2005d). Perhaps, in anoxic conditions of deep water layers of the Domanik Sea, radiolarians could have existed due to symbionts.

At the same time, under conditions of hydrosulphuric contamination, anaerobic bacteria capable of reducing sulfates and gaining energy for life from this reaction become widespread.

Nevertheless, a favorable ecological situation is gradually restored; living forms renew progressive development, mass blooms of phytoplankton return again, and this is again continued by hydrosulphuric contamination and extinction of organisms. Such "waves of life" disappear as rapidly as appear (Vernadsky, 1926, 1983). Thus, we see natural cyclic replacement of rich associations of various marine organisms by radiolarian–algal assemblages, corresponding to alternating natural environments of organisms in the Middle Frasnian Domanik Sea.

Ecology of Radiolarians in the Domanik Sea

Morphological features of radiolarian shells and the character of their assemblages are tightly connected with the environment and change from the surface to relatively deepwater and, particularly, benthic habitats.

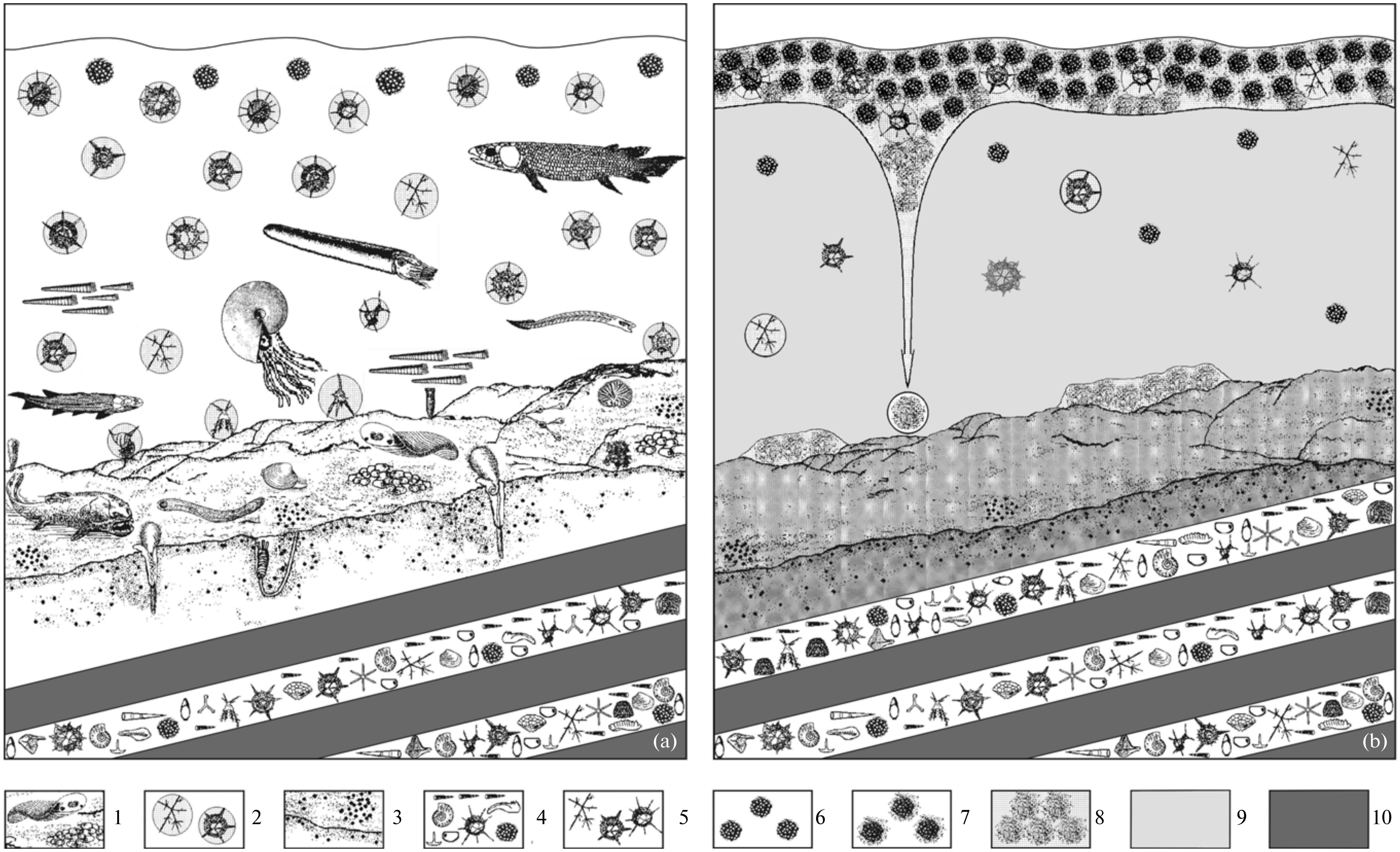
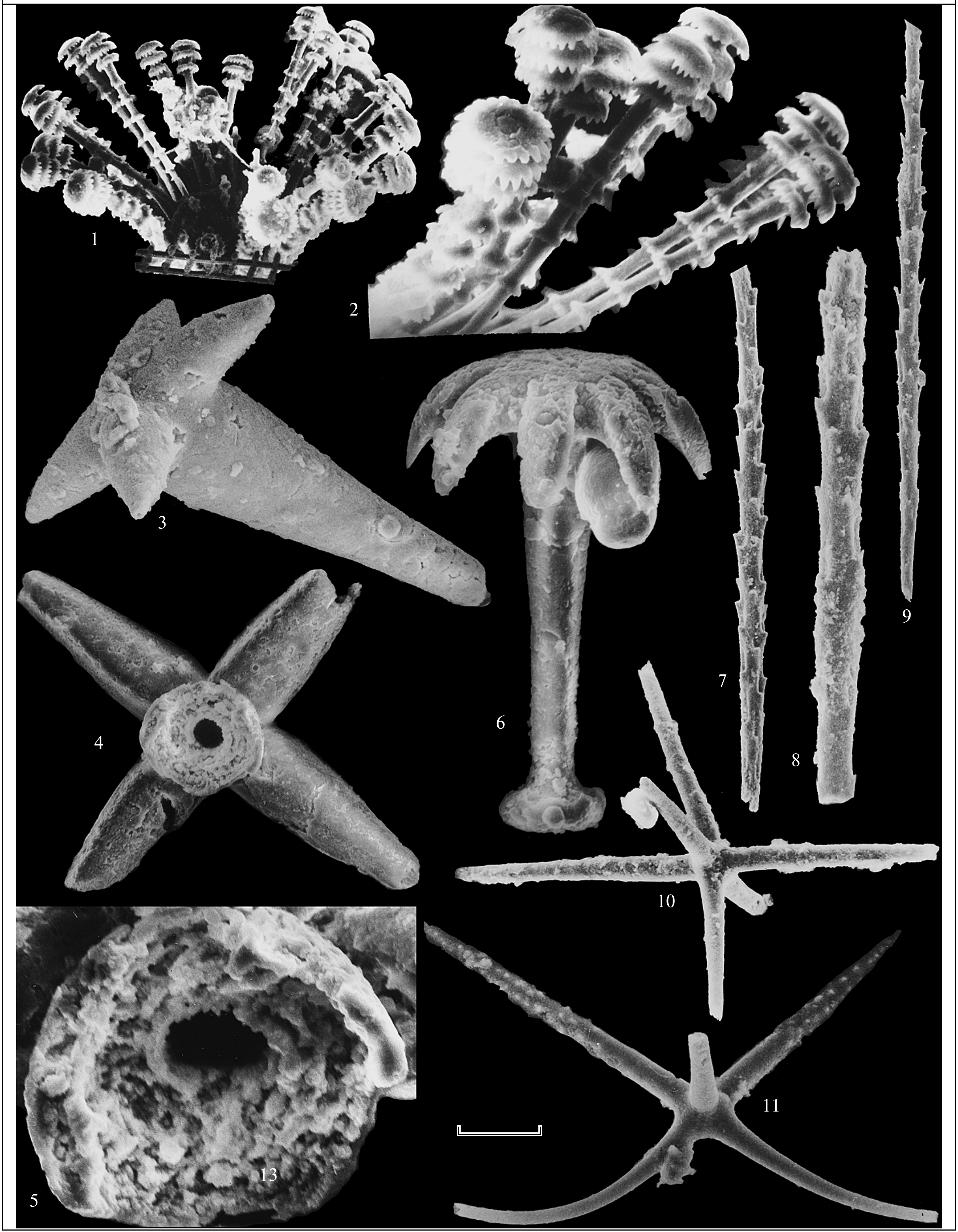


Fig. 26. Reconstruction of a basin of the Domanik type (a) stage of flourishing of the biota and lifestyle of some marine organisms, (b) stage of hydrosulphuric contamination. Designations: (1) some inhabitants of the Domanik Sea, (2) living radiolarians, (3) bacteria, (4) limestones and oryctocoenosis, (5) radiolarian skeletons, (6) algae (Acritarcha and Tasmanaceae), (7) algae and extracellular organic matter, (8) "sea snow," (9) hydrosulphuric contamination, and (10) cherty limestones, rich in organic matter. The size ratios of particular organisms are not natural. Figures of Devonian organisms are cited from (*Paleontologiya bespozvonochnykh*, 1962; Nazarov, 1988; Mikhailova and Bondarenko, 1997; Rich et al., 1997.

Plate 34



Among Domanik radiolarians from the Middle Frasnian of the Timan–Pechora Basin, two morphological groups are recognized, i.e., spherical members of the classes Sphaerellaria and Spumellaria (**S**) and spiny forms of the class Aculearia (**A**), which are distinguished by the selective confinement to different zones of the sea and types of deposits. It is noteworthy that the range of changes in diversity of spiny Aculearia in the lower and upper parts of the section of the Domanik Formation is approximately the same, ranging from 7–8 to 16–18 species (Fig. 27; Table 10). On the contrary, the number of spherical Sphaerellaria and Spumellaria changes very sharply; the lower part of the section has yielded 14–26 species; in the middle part, they evidently play a subordinated role (1–7 species); in the upper part of the section, their abundance and diversity sharply increase (up to 40 species). Apparently, the ecological situation in the middle of the Domanik Time provided predominant development of relatively cold-resistant spiny Aculearia, which became dominants of the radiolarian association.

Based on changes in the ratio of morphological groups of radiolarians, the paleoclimatic coefficient **PC = S/A** is established, according to which the prevalence in deposits of spiny radiolarians over spherical taxa is evidence of colder waters in radiolarian habitats (**PC ≤ 1**) and vise versa (Fig. 27) (Afanasieva, 2000a).

The prevalence of spiny Aculearia over spherical Sphaerellaria and Spumellaria is probably evidence of relatively cold conditions.

The Rdm-1 Subassemblage is characterized by a relatively low general species diversity of spherical Sphaerellaria and Spumellaria (45 species) and spiny Aculearia (23 species). At the same time, spiny radiolarians play a significant role in paleobiocoenosis of the Early Domanik Time, reaching 61% of the total number of individuals (Fig. 27; Table 7).

The Rdm-2 Subassemblage displays an extremely low general species diversity of both spherical taxa (12 species) and spiny Aculearia (ten species) (Fig. 27; Table 7).

Conditions of the ancient sea in the middle of the Domanik Time were probably far from favorable for the development of the organic world of the basin. Probable fall in temperature near the boundary of the lower and middle radiolarian subassemblages resulted in the inversion of the ratio of spherical and spiny radiolarians in favor of Aculearia. Apparently, the ecological situation in the middle of the Domanik Time provided the development of only relatively cold-resistant spiny Aculearia, which developed against a background of inflow of cold water from melted snow and became dominants in these conditions (Fig. 27). Adverse environmental conditions are probably evidenced by *Entactinia bifida* Afanasieva and *Moskovistella mira* Afanasieva (Pl. 11, figs. 3, 4). These radiolarian species are distinguished by the development of bifurcating or, on the contrary, pulled together, coupled spines, which are probably abnormalities providing additional support for the idea of adverse ecological conditions in the Middle Domanik Time.

The Rdm-3 Subassemblage displays a very large proportion of Sphaerellaria and Spumellaria, represented by 88 species (Fig. 27; Table 7). In the lower part of the section, spherical radiolarians are represented by 45 species; in the middle part, by only 12 species.

In the upper part of the Domanik section, spiny Aculearia are represented by 33 species, that is, approximately the same number as in the Rdm-1 Subassemblage (23 species); however, it is three times as great as in the middle part of the section, with ten species (Fig. 27; Table 7).

General climatic warming, which occurred at the end of the Domanik Time, probably caused stabilization of warm sea conditions (Tikhii, 1975). The change in environments at the end of the Domanik Time was accompanied by a sharp increase in the total number of radiolarian individuals (more than 1000 specimens per 1 g of rock) (Table 10).

COEVOLUTION OF FRASNIAN RADIOLARIANS, AMMONOIDS, AND OTHER ORGANISMS IN THE TIMAN–PECHORA BASIN

Recently, great attention has been paid to the study of combined influence of various abiotic and biotic factors on the development of ecosystems in the geological past. Afanasieva, Nikolaeva, and Konovalova (Nikolaeva et al., 2008; Afanasieva et al., 2010) ana-

Explanation of Plate 34

Spicules of sponges.

Figs. 1 and 2. *Triaxonida?* sp. 401, specimen PIN, no. 5311/04320: (1); scale bar, 67 μm; (2) fragment, scale bar, 33 μm.

Figs. 3–5. *Triaxonida?* sp. 403: (3) specimen PIN, no. 5311/12512; scale bar, 56 μm; (4, 5) specimen PIN, no. 5311/12513: (4) scale bar, 59 μm; (5) fragment, scale bar, 21 μm.

Fig. 6. *Triaxonida?* sp. 402, specimen PIN, no. 5311/12518; scale bar, 33 μm.

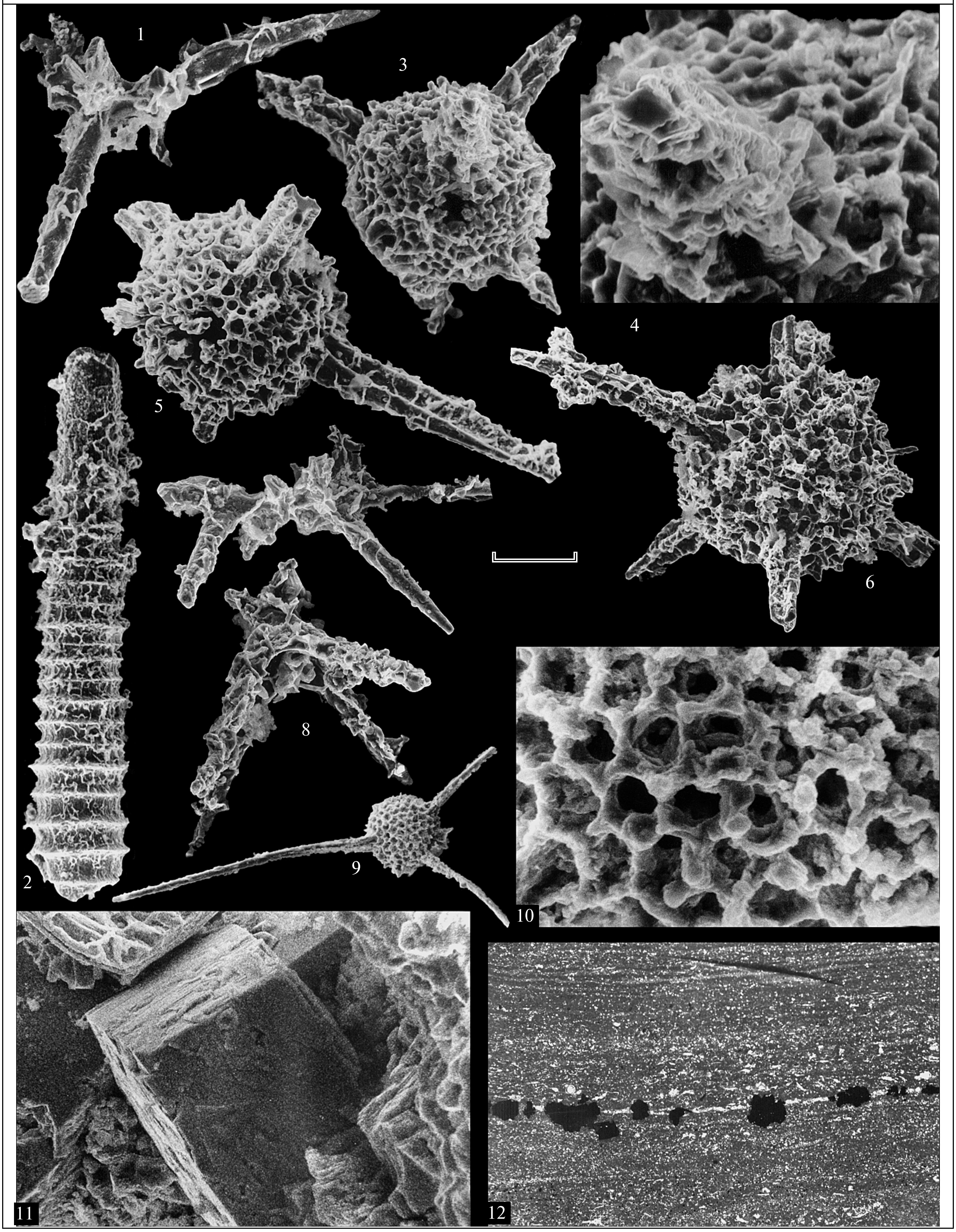
Figs. 7–9. *Triaxonida?* sp. 404: (7) specimen PIN, no. 5311/12418; scale bar, 125 μm; (8) specimen PIN, no. 5311/12403; scale bar, 63 μm; (9) specimen PIN, no. 5311/12404; scale bar, 125 μm.

Fig. 10. *Triaxonida?* sp. 407, specimen PIN, no. 5311/04612; scale bar, 43 μm.

Fig. 11. *Triaxonida?* sp. 405, specimen PIN, no. 5311/09312; scale bar, 33 μm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin: borehole Shuda-Yag-1003: (1, 2) sample 29 (105.0–106.0 m of depth); (10) sample 56 (81.6–83.0 m of depth); Domanik River: (3–6) quarry 2, sample 5; (7–9) outcrop 21, sample 49; (11) borehole Ukhtinskaya-3B, sample 114 (104.2–104.7 m of depth).

Plate 35



lyzed the structure of the pelagic biota of radiolarians, ammonoids (Fig. 28), and other organisms of the Timan–Pechora Basin in the Frasnian Age of the Late Devonian.

Thy study was based on published data (Bogoslovsky, 1969; Lyashenko, 1973; Ivanov, 1990; Orlov and Fokin, 1991; Ovnatanova and Kuzmin, 1991; Menner et al., 1992; Yatskov and Kuzmin, 1992; Yudina, 1994, 1997; Kuzmin, 1995; Kuzmin et al., 1997; Kuzmin and Yatskov, 1997; Becker et al., 2000; Barskov et al., 2008) and original collections of ammonoids, radiolarians, tentaculites, acritarchs, and spicules of sponges (Afanasieva, 2000a) from the Ust'-Yarenga, Domanik, and Lyaiol formations of the Frasnian Stage, which were collected (1) in the southern Timan–Pechora Basin in boreholes Ukhtinskaya–3B, Shuda-Yag-1002, Shuda-Yag-1003, Vapovskaya-2056, and many localities situated on the banks of the Ukhta, Yarega, Chut, Domanik, Lyaiol, Sedyu, and Vega-Vozh rivers; (2) in the northern Timan–Pechora Basin in borehole Zapadnaya Vissertynskaya-1 (Figs. 6, 14).

The ecological situation in the Timan–Pechora Basin in the Frasnian Age was under control of global eustatic fluctuations and local tectonic events (Tikhomirov, 1967, 1995; Tikhii, 1975; Menner et al., 1991, 1992; Belyaeva et al., 1998).

The changes considered in paleobiogeographic conditions in the Timan–Pechora Basin during the Frasnian Age are evidence of connection between eustatic and local tectonic events with the evolution, migration, and extinction of radiolarians, ammonoids, and other organisms.

Early Frasnian, Ust'-Yarenga Time

The Ust'-Yarenga Formation was formed under conditions of increasing transgression. During the Early Frasnian, diversity of radiolarians and ammonoids was relatively low (Fig. 28). The biota of the Timan–Pechora Basin was formed under conditions of a shallow shelf, at most 50 m of depth (Tikhomirov, 1967, 1995; Tikhii, 1975; Menner et al., 1991, 1992; Belyaeva et al., 1998) (Fig. 12a).

Radiolarians. The radiolarian assemblage of the Early Frasnian in the southern Timan–Pechora Basin consists of a few (seven species of four genera), mostly spherical porous Sphaerellaria (Pl. 9, figs. 1–4, 6–8): *Astroentactinia biaciculata* Nazarov, *A. paronae* (Hinde), *Borisella bykovae* Afanasieva, *B. maksimovae* Afanasieva, *Entactinia patorovaria* Afanasieva, *E. bogdanovi* Afanasieva, and *Moskovistella deorsiacus* (Nazarov and Ormiston); only one species of spherical spongy Spumellaria, *Meschedea crassicortex* Won (Pl. 9, fig. 5); and one spiny Aculearia, *Ceratoikiscum spinosiarcuatum* Foreman (Pl. 9, fig. 9).

In the northern Timan–Pechora Basin, radiolarians are represented by abundant, but uniform discoidal forms (two species of two genera), *Palaeodiscaleksus punctus* (Hinde) and *Palaeotripus patella* (Hinde) (Pl. 9, figs. 10–12).

Ammonoids. The earliest Frasnian ammonoids are known in the Timan–Pechora Basin from the middle part of the Ust'-Yarenga Formation, which is composed of gray and green–gray clays, with interbeds of marls and fine-grain limestones. This is a zonal species, with narrow, oxycone, involute shell, *Hoeninghausia nalivkini* Ljaschenko. In the middle and upper parts of the formation (*Timanites keyserlingi* Zone) (Fig. 28), *Timanites keyserlingi* Miller, *Tornoceras typum* (Sandberger), and *Manticoceras* sp. have been recorded (Yatskov and Kuzmin, 1992; Kuzmin and Yatskov, 1997; Becker et al., 2000).

The appearance of the genus *Timanites* was a prominent event in the Frasnian history of ammonoids. This genus was widespread during the global transgression ("event *Timanites*") from Australia to the Timan–Pechora Basin, Novaya Zemlya, and Canada (Becker, 1993, 2000; Becker et al., 1993, 2000). At the same time, *Timanites* is absent in the areas far from the equator in Western Europe, North Africa, eastern

←

Explanation of Plate 35

Pyritized skeletons of sponges (1), tentaculites (2), radiolarians (3–9), and pyrite in domanik deposits (11, 12).

Fig. 1. *Triaxonida* (?) sp. 407, specimen PIN, no. 5311/407–09101; scale bar, 37 μm.

Fig. 2. *Tentaculites* cf. *semilukianus* G. Ljaschenko, 1965, specimen PIN, no. 5311/09028; scale bar, 89 μm.

Figs. 3 and 4. *Ornatoentactinia* cf. *solita* Afanasieva, 2000, specimen PIN, no. 5311/09123: (3) scale bar, 40 μm; (4) fragment, scale bar, 17 μm.

Fig. 5. *Bientactinosphaera* cf. *variacanthina* (Foreman, 1963), specimen PIN, no. 5311/09035; scale bar, 55 μm.

Fig. 6. *Bientactinosphaera* cf. *grandis* (Nazarov, 1975), specimen PIN, no. 5311/09119 (77 μm.

Fig. 7. *Ceratoikiscum* cf. *ukhtensis* Afanasieva, 2000, specimen PIN, no. 5311/09129; scale bar, 48 μm.

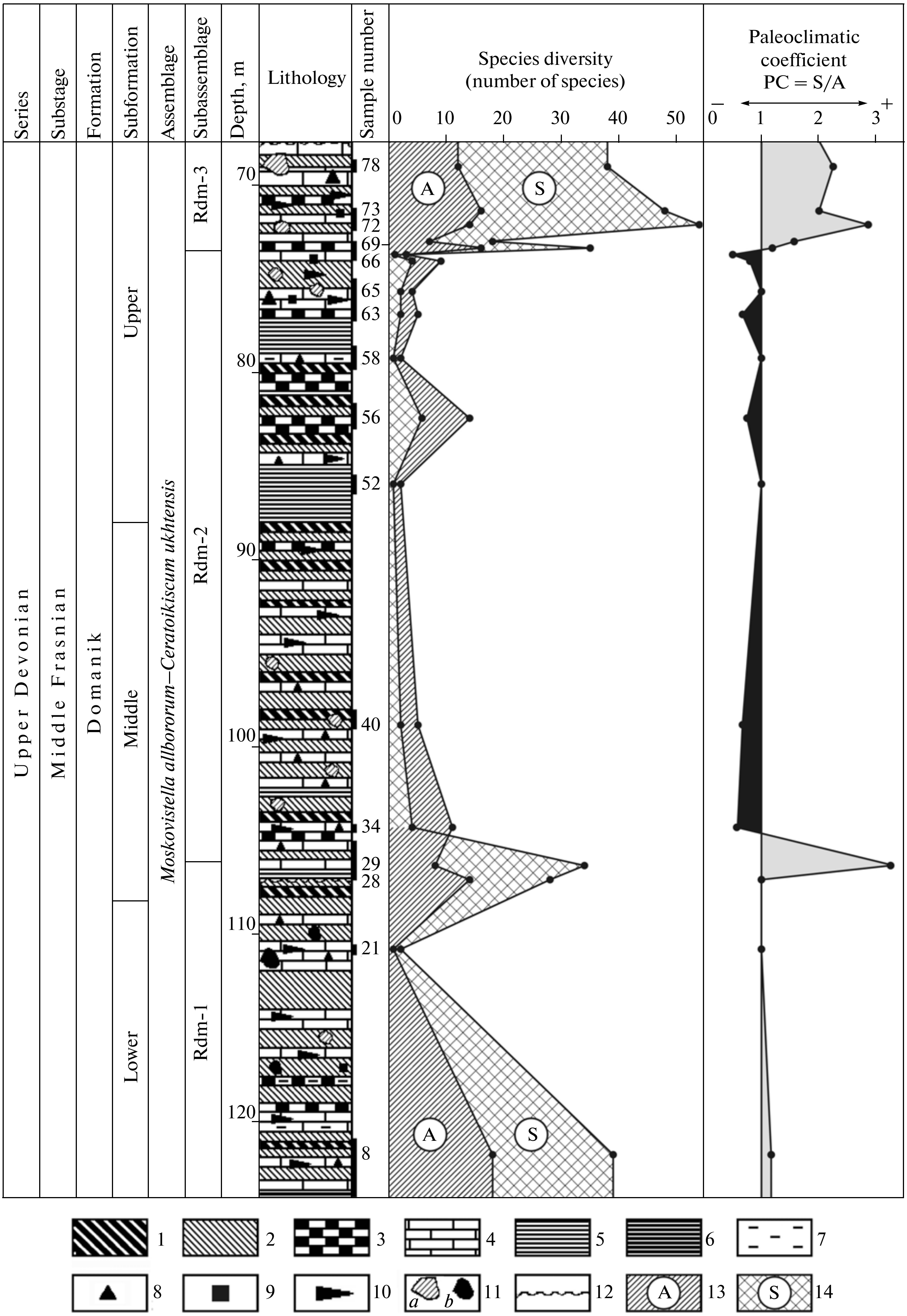
Fig. 8. *Palaeoscenidium* cf. *cladophorum* Deflandre, 1953, specimen PIN, no. 5311/09135; scale bar, 38 μm.

Figs. 9 and 10. *Borisella maksimovae* Afanasieva, 2000, specimen PIN, no. 5311/04302: (9) scale bar, 89 μm; (10) fragment, scale bar, 15 μm.

Fig. 11. Impregnation with cubic pyrite crystals in the rock: specimen PIN, no. 5311/14211; scale bar, 33 μm.

Fig. 12. Thin-layer bituminous cherty limestone, with admixture of carbonate detritus and layer-by-layer extraction of pyrite growths: specimen PIN, no. 5311/005, section; scale bar, 1.5 mm.

Upper Devonian, Middle Frasnian Substage, Domanik Formation; Timan–Pechora Basin: (1–8) borehole Ukhtinskaya-3B (104,2–104,7 m of depth), sample 100; borehole Shuda-Yag-1003: (9, 10) sample 28 (106–107 m of depth); (12) sample 29 (105–106 m of depth); (11) Chut River, outcrop 3, sample 12A.


Series
Substage
Formation
Subformation
Assemblage
Subassemblage
Depth, m
Lithology
Sample number
Species diversity (number of species)
0
10
20
30
40
50
Paleoclimatic coefficient PC = S/A
–
0
1
2
3
+
Upper Devonian
Middle Frasnian
Domanik
Upper
Middle
Lower
Moskovistella allbororum–Ceratoikiscum ukhtensis
Rdm-3
Rdm-2
Rdm-1
70
80
90
100
110
120
78
73
72
69
66
65
63
58
56
52
40
34
29
28
21
8
A
S
A
S
1
2
3
4
5
6
7
8
9
10
a
b
11
12
A
13
S
14

North America, and the shelf of the Siberian Craton (Novosibirsk Islands).

In the upper part of the Ust'-Yarenga Formation, a relatively rich ammonoid assemblage is known, including *Manticoceras* sp., *Komioceras stuckenbergi* (Holzapfel), *Tornoceras typum* (Sandberger), *Domanikoceras timidum* (Becker et House), *Timanites* sp., and *Phoenixites keyserlingi* (Müller) (Bogoslovsky, 1969; Yatskov and Kuzmin, 1992; Kuzmin and Yatskov, 1997). The ammonoid assemblage characterizes the *Komioceras stuckenbergi* Zone (Fig. 28); the genera *Komioceras* and *Domanikoceras* are endemic to Timan, and other genera are recorded in all known Frasnian basins.

The ammonoid community was characterized by the presence of two main morphotypes, with a narrow oxycone shell (*Hoeninghausia, Komioceras, Timanites*) and pachycone involute shell (*Domanikoceras, Phoenixites, Tornoceras*). These forms were probably characteristic of different adaptive zones (planktonic and quasinanoplanktonic/nectobenthic) (Barskov et al., 2008).

Coevolution of faunal diversity in the Ust'-Yarenga Sea. In the Lower Frasnian Ust'-Yarenga Formation, radiolarians and ammonoids are accompanied by other pelagic and benthic faunal groups.

The ichthyofauna from the lower member of the Ust'-Yarenga Formation is rather rich, with the prevalence of *Psammosteus* and *Bothriolepis.* These groups are characteristic of shallow-water deposits and widespread in deposits of the same age of the Main Devonian Field and Middle Timan. In the middle part of the Ust'-Yarenga Formation, the ichthyofauna is poor and represented by rare ptyctodontids and palaeoniscids. In the upper member of the formation, many ptyctodontids, palaeoniscids, and arthrodirs (*Eastmanosteus, Plourdosteus*) appeared, which are characteristic of deep shelf conditions (Ivanov, 1990; Kuzmin et al., 1997).

Ostracodes from the Ust'-Yarenga Formation are represented by 32 genera (Orlov and Fokin, 1991). Ostracodes of the lower and middle members are mostly shallow-water. The ostracode assemblage of the upper member of the Ust'-Yarenga Formation shows almost complete disappearance of shallow-water forms, except for one species of the genus *Acratia.* The prevalence in the oryctocoenosis of micronektonic (*Polenovia, Eocypridina, Entomorimitia*) and deepwater creeping ostracodes (*Franklmella*) is evidence of relatively deepwater conditions of sedimentation at the end of the Ust'-Yarenga Time.

Hinged brachiopods are represented in the Ust'-Yarenga Formation by more than 50 species, although, near the roof of the formation, they are only represented by individual specimens (Lyashenko, 1973; Kuzmin et al., 1997).

Conodonts in the lower subformation of the Ust'-Yarenga Formation are only represented by rare species of the genus *Polygnathus***,** which is characteristic of shallow-water conditions (Ovnatanova and Kuzmin, 1991; Kuzmin, 1995; Kuzmin, et al., 1997). In the middle part of the formation, conodont assemblages correspond in composition to the more deepwater ancyrodellan–polygnathid conodont biofacies. Near the roof of the Ust'-Yarenga Formation, about half of conodont taxa are deepwater *Mesotaxis*; *Palmalolepis transitans* Muller appears for the first time. At the same time, in limestones of the Upper Ust'-Yarenga Subformation, the proportion of *Palmatolepis* is in general at most 1–2% (Ovnatanova and Kuzmin, 1991; Kuzmin, 1995; Kuzmin, et al., 1997).

The analysis of faunal diversity of the Timan–Pechora Basin in the Ust'-Yarenga Time has shown an unidirectional pattern in the development of various groups of planktonic and benthic organisms in varying conditions of the deepening paleosea.

At the beginning of the Ust'-Yarenga Time, the shallow-water ichthyofauna, ostracodes, and hinged brachiopods were widespread. Conodonts are represented by rare shallow-water forms. Ammonoids and radiolarians are absent.

In the paleosea of the middle of the Ust'-Yarenga Time, the ichthyofauna was poor. Shallow-water ostracodes were widespread and more deepwater conodonts appeared. The first most ancient Frasnian ammonoids appeared, including the genus *Timanites.* Abundant discoidal radiolarians in the northern Timan–Pechora Basin are evidence of normal marine, but probably not favorable for radiolarians relatively shallow-water conditions of the paleosea.

The end of the Ust'-Yarenga Time was marked by the appearance of a rich ichthyofauna characteristic of deepwater shelf conditions, the prevalence of micronektonic and deepwater ostracodes, and almost complete disappearance of hinged brachiopods. About half of the conodont assemblage is formed of deepwater forms.

The diversity of radiolarians and ammonoids increased somewhat at the end of the Ust'-Yarenga Time under conditions of increasing transgression. In the Ust'-Yarenga Formation on the Chut River (Fig. 23) in the southern Timan–Pechora Basin, nine radiolarian species have been recorded; from a layer of organogenic limestone (Pl. 33, fig. 1), the roof of which is regarded as the lower boundary of the

Fig. 27. Distribution of spiny (A) and spherical (S) radiolarian taxa in the Domanik Formation of the Timan–Pechora Basin, using an example of the section of borehole Shuda-Yag-1003: (1) massive flint, (2) flinty slate, (3) cherty limestone, (4) limestone, (5) clay, (6) claystone, (7) clayey matter, (8) silicification, (9) pyrite, (10) bituminosity; (11) nodules: (a) carbonate, (b) siliceous; (12) erosion surface, (13–14) radiolarians: (13) spiny Aculearia (A), (14) spherical Sphaerellaria and Spumellaria (S).

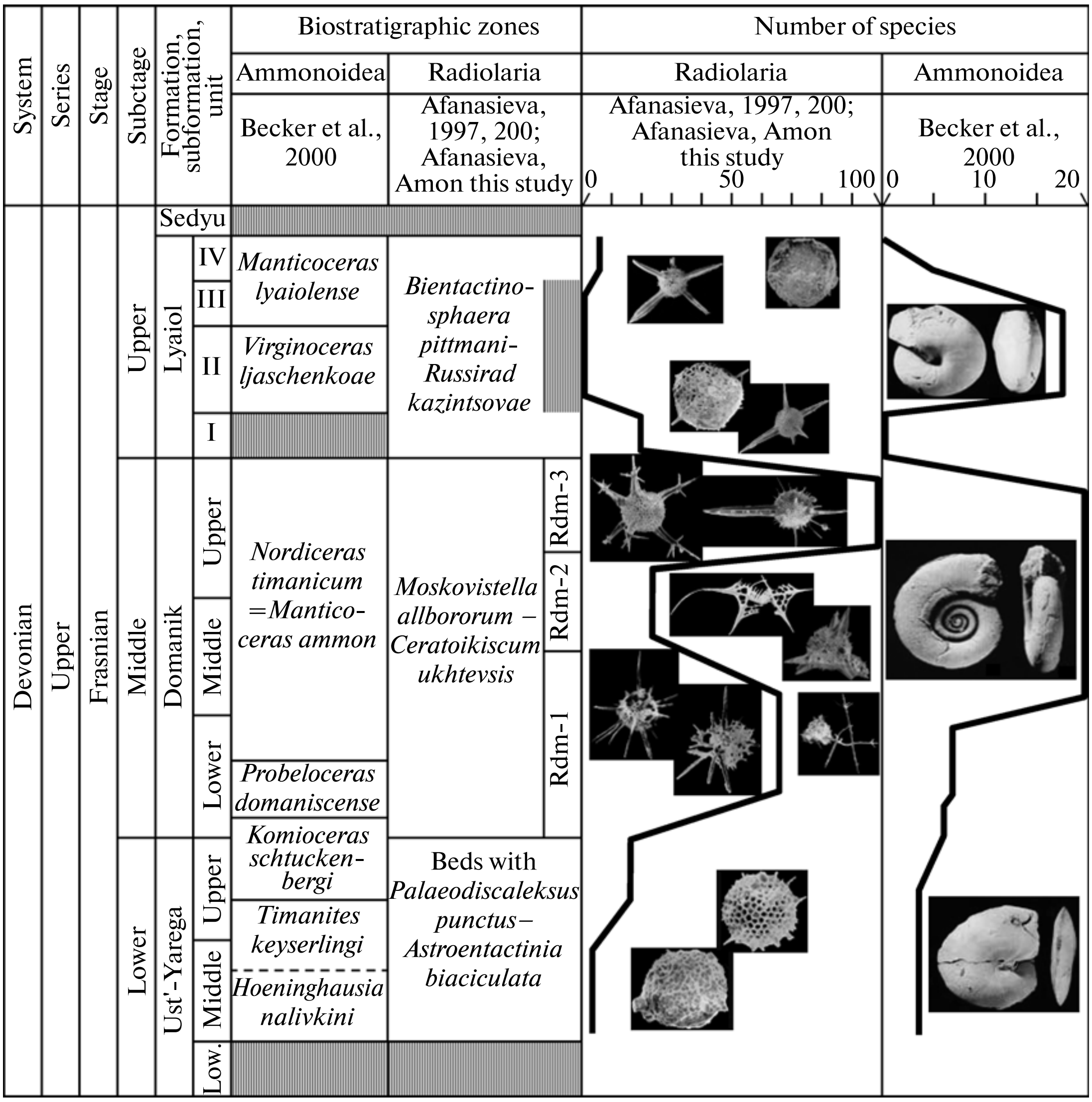


Fig. 28. Coevolution of radiolarians and ammonoids in the Frasnian of the Timan–Pechora Basin.

Domanik Formation (Fig. 23), a rich ammonoid assemblage has been described (Fig. 28).

These changes in the biota were undoubtedly caused by gradual deepening of the basin and expansion of food relationships.

Middle Frasnian, Domanik Time

The paleobiogeographic situation apparently changed at the boundary of the Ust'-Yarenga and Domanik. At the end of the Ust'-Yarenga, the basin gradually became deeper, and the onset of the Domanik was marked by the maximum transgression of the Frasnian marine basin; this resulted in significant rearrangement of the relief of the marine bottom (Tikhomirov, 1967, 1995; Tikhii, 1975; Menner et al., 1991, 1992; Belyaeva et al., 1998) (Fig. 12b).

At that time, the area investigated was a strongly dissected shelf, with shallow zones of carbonate accumulation and sites of noncompensated deepwater flexure with siliceous carbonate sedimentation. The boundaries between these zones were linear and reef massifs were formed along them (Menner, 1989; Menner et al., 1992; Veimarn et al., 1996).

In addition, it was proposed that, in the region of the Timan–Pechora Sea (Fig. 12b), the climate was warm, tropical and paleomagnetic equator in the Frasnian Age passed through the eastern part of the Russian Platform close to the meridian 50° E (Tikhii, 1975). This hypothesis developed by Nalivkin (1956) is based on the presence of the barrier reefs in the Ural Paleobasin. The development of reefs is evidence of a strong surf, clean water, and tropical climate, with the mean annual temperature up to 20°C. The stabilization of the tropical climate is confirmed by extreme diversity of radiolarians in the final phase of the development of the Domanik Sea at the end of the Middle Frasnian.

A general increase in sea level in the Domanik Time and increase in the area of deep shelf as well as periodic emission of a large amount of nutrients of endogenous nature and highly siliceous waters at fractures of the rift system gave rise in warm conditions of the tropical Timan–Pechora Sea to "bursts" of total bioproductivity and prosperity of pelagic organisms, including radiolarians and ammonoids.

On the other hand, topographical isolation of relatively deepwater sites of the external shelf caused in the Domanik Time changes in water circulation, with the formation of anoxic conditions of hydrosulphuric contamination near the marine bottom. The development of anoxic conditions near the bottom resulted in changes in communities of planktonic and benthic organisms. In conditions of hydrosulphuric contamination of bottom waters, benthic fauna is completely absent. At the same time, during oxygen shortage in bottom waters, radiolarians and ammonoids probably occupied the middle and upper pelagial of the eutrophic Domanik basin.

Apparently, the combination of all the above factors resulted in essential changes at the boundary of the Ust'-Yarenga and Domanik formations in the taxonomic composition of associations of various planktonic and benthic organisms. The Late Devonian peak of taxonomic diversity of radiolarians and ammonoids coincided with the maximum transgression, hydrosulphuric contamination of bottom waters, and the peak of eutrophication in the Middle Frasnian.

Fauna of the Domanik Sea. Faunal assemblages of the Domanik Formation of the Timan–Pechora Basin are very unusual and essentially differ from overlying and underlying beds: the Domanik biota is mostly represented by planktonic forms. Normal marine benthos is absent there. Against a general pulsating background of the evolution of the Domanik basin, several peaks of sharp changes in species and quantitative composition of radiolarian and ammonoid assemblages (Fig. 28), abundance of ostracodes, brachiopods, conodonts, fishes, tentaculites, and spicules of sponges have been recorded.

This problem was considered for the first time by Maksimova (1970, 1975). However, works performed during the last 20 years have shown new features and patterns in the development of various groups (Ivanov, 1990; Orlov and Fokin, 1991; Ovnatanova and Kuzmin, 1991; Menner et al., 1992; Yatskov and Kuzmin, 1992; Yudina, 1994, 1997; Kuzmin, 1995; Afanasieva, 1997a, 2000a; Kuzmin et al., 1997; Kuzmin and Yatskov, 1997; Becker et al., 2000; Barskov et al., 2008; Nikolaeva et al., 2008; Afanasieva et al., 2010).

The Domanik Sea, with a pulsating mode of hydrosulphuric contamination, demonstrates precise dependence of organisms on trophic and oxygen factors of environments. The Domanik Formation is characterized by alternation of two main rock variants:

(1) black bituminous shales rich in organic matter, but completely lacking skeletal remains, even radiolarian skeletons and siliceous spicules of sponges, which are resistant to disruption;

(2) limestones literally overfull of skeletons of diverse organisms, but with a low content of C_{org}. At the same time, monoorganogenic formations are frequently observed (Pls. 32, 33), including linguloids, buchias, goniatites nautiloid, tentaculites, spheroids (most likely, algal acritarchs, additional rich accumulations of green unicellular algae, *Timanites*), radiolarians–sponges, and sponges–radiolarians.

The lower subformation is interbedding strata of limestones and cherty limestones with silicides (Fig. 14) (Afanasieva, 2000a; Afanasieva and Mikhailova, 2001). They include three massive limestone layers rich in shells of ammonoids, orthoceratoids, tentaculites, buchias, gastropods, and fishes. Tentaculites sometimes form interbeds of tentaculite limestones. Spicules of sponges and skeletons of Tentaculita, Radiolaria, and Acritarcha are also recorded there (Pls. 32–34).

The middle subformation is more siliceous. In contrast to other parts of the Domanik section, the Middle Subformation has poor faunal remains, which occur in individual limestone interbeds, considerably smaller in size, and very thin-walled.

The upper subformation is characterized by an increase in carbonate content of rocks and diversification of various fossils, including acritarchs, spicules of sponges, ammonoids, and radiolarians (Fig. 28).

In warm tropical sea, periodic emissions at fractures of abundant nutritive matter of endogenous nature apparently promoted success of unicellular algae and radiolarians, which provided ample "pastures" for abundant tentaculites, ostracodes, buchias, lingulids, and fishes. Conodonts and gastropods are rare.

The considerable species diversity and abundant shells of ammonoids, which are frequently very large in size, are evidence of favorable conditions for the development of ammonoids, which probably inhabited the middle and upper pelagial of a rich eutrophic basin. However, the main role is played by radiolarians and sponges, i.e., organisms with a siliceous skeleton, which form radiolarian–sponge and sponge–radiolarian ecosystems (Pl. 33, figs. 4–8).

Sponges are of great significance for estimation of paleoecological conditions in the Domanik Sea. However, in early studies, spicules of sponges were either only mentioned in the Domanik beds (Kushnareva, 1959, 1963) or the opportunity of development of sponges in the Domanik Sea was put in doubt (Maksimova, 1970). Comprehensive studies of microfossils and Domanik rocks have shown for the first time the presence in the Domanik Sea of four-rayed siliceous spicules of sponges, which are characterized by a specific skeletal growth and presence of the central canal (Afanasieva and Mikhailova, 1998, 2001; Afanasieva, 2000a) (Pl. 34). Morphological features of spicules (Koltun, 1961) suggest that, in the Domanik Time, sponges existed at great depths (about 200 m).

Ostracodes were represented in the Domanik Basin by micronektonic *Polenovia* and *Entomorimitia* and deepwater creeping *Franklmella*. Only the upper subformation of the Domanik Formation contains a new group of deepwater bottom ostracodes, including *Nehdengtomis, Nandania*, and *Richterina* appeared (Orlov and Fokin, 1991; Kuzmin et al., 1997).

Brachiopods. Hinged brachiopods are absent in deposits of the Domanik Sea; only scarce *Caryurhynchus* sp. are sometimes recorded. At the same time, some interbeds contain shells of hingeless lingulids (Yudina, 1994).

Conodonts. At the boundary between the Ust'-Yarenga and Domanik formations, the composition of conodont assemblages and species composition of the genera *Ancyrodella, Mesotaxis*, and *Palmatolepis* change substantially. In particular, in the "boundary" limestone, the proportion of *Palmatolepis* sometimes reaches 20% (Ovnatanova and Kuzmin, 1991; Kuzmin, 1995; Kuzmin, et al., 1997).

The lower subformation of the Domanik Formation is characterized by the following conodont assemblage: *Ancyrodella soluta* Ziegler, Sandberg et Bultynk, *A. mouravieffi* Garcia-Lopez, *A. gigas* Youngquist, *Mesotaxis falsiovalis* Ziegler, Sandberg et Bultynk, *M. johnsoni* Klapper, Kuzmin et Ovnatanova, *Klapperina ovalis* (Ziegler et Klapper), *Palmatolepis transitans* Muller, *P. punctata* (Hinde), *P. keyserlingi* Kuzmin, *P. roptundilobata* Kuzmin, *P. triguetra* Kuzmin, *P. maximovae* Kuzmin, *P. gutta* Kuzmin, *Polygnathus anguslidiscus* Youngquist, *Pol. lanei* Kuzmin, *Pol. webbi* Stauffer, *Pol.* aff. *xylus* Stauffer, *Pol. strictus* Kuzmin et Yurchenkova, *Pol. dubius* Hinde, *Pol. brevilamifonnis* Ovnatanova, *Pol. timanicus* Ovnatanova, *Pol. vialovi* Zvereva, and *Pol. elegantulus* Klapper et Lane (Kuzmin, et al., 1997).

Conodont assemblages from the middle and upper subformations of the Domanik Formation are dominated by species of the genus *Palmatolepis* (Menner et al., 1992; Kuzmin, et al., 1997).

The ichthyofauna of the Domanik Sea consists of taxa characteristic of the deep shelf. The lower subformation is rich in placoderms and palaeoniscids; acanthodeans and chondrichthians are occasionally recorded (Palaeonisci, Ptyctodontidae, *Plourdosteus, Eastmanosteus, "Acanthodes,"* Symmoriidae). Upward in the section, the proportions of chondrichthians and acanthodeans increase, while the proportion of placoderms decreases. In the upper part of the section, rare crossopterygians also occur: Ptyctodontidae, *Plourdosteus, Eastmanosteus, "Acanthodes,"* Coccosteidae, Protacrodontidae, Ctenacanthidae, Chondrichthyes, and Osteolepididae (Kuzmin et al., 1997).

Tentaculites are particularly widespread in deposits of the Domanik Sea. They occur throughout the section of the Domanik Formation in almost all rock types. *Tentaculita* often forms interbeds of tentaculite limestones and are usually oriented following the lamination (Kushnareva, 1963; Afanasieva, 2000a; Afanasieva and Mikhailova, 2001) (Pl. 32, figs. 6–10).

Tentaculites sometimes form on the surface of combustible shales continuous "pannose" cover or rich scattering; however, they are completely absent inside the strata. On the contrary, inside limestone layers, chaotic accumulation of *Tentaculita* skeletons are usually observed. In limestones, the content of tentaculites reaches 85–95%. At the same time, tentaculite layers are relatively thin, at most 5–6 cm thick, or, frequently, several millimeters thick or even thinner. Chaotic conglomerates in bottom deposits of skeletal remains of *Tentaculita*, with a minor admixture of oozy material, are probably evidence of abrupt mass extinction of organisms.

Radiolarians. The tropical climate, a high content of organic matter and silicic acid promoted intense development of radiolarians. The Domanik beds have yielded 128 radiolarian species of 32 genera of perfect preservation (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2001). The assemblage characterizes the *Moskovistella allbororum–Ceratoikiscum ukhtensis* Regional Zone. The Domanik Zone of radiolarians is divided into three subzones: Rdm-1, Rdm-2, and Rdm-3 (Fig. 28).

The Rdm-1 Subzone corresponds to the *Ponticeras domanicense* Ammonoid Zone and the lower part of the *Nordiceras timanicum* Zone. The radiolarian assemblage is characterized by relatively small total number and low species diversity; spherical forms are represented by 45 species; spiny Aculearia, by 23 species; and discoidal Stauraxonaria, by only two species (Pl. 10).

The Rdm-2 Subzone corresponds to the middle part of the *Nordiceras timanicum* Ammonoid Zone. The radiolarian assemblage from the Rdm-2 Subzone displays a decrease in the total number of radiolarians in deposits to individual specimens and low species diversity of both spherical (12 species) and spiny taxa (11 species) (Pl. 11). In addition, an inverse ratio of spherical and spiny radiolarians in favor of species of Aculearia is observed.

The Rdm-3 Subzone corresponds to the upper part of the *Nordiceras timanicum* Ammonoid Zone and shows the greatest radiolarian diversity, 123 species. The assemblage is dominated by spherical taxa, represented by 88 species; spiny Aculearia comprise 33 species; and discoidal Stauraxonaria, only two species (Pls. 12, 13).

During oxygen shortage, in bottom waters of the epicontinental seas of present and past, radiolarians display from ecosystems normal marine benthic and planktonic organisms: foraminifers, ostracodes, goniatites, and tentaculites and are only associated with sponges and acritarchs. Moreover, foraminifers are in general not characteristic of the Domanik beds (Bykova, 1955). The assumption that foraminifers existed in such a basin of sedimentation, although their shells were dissolved is highly improbable, since calciferous skeletons of other organisms are perfectly preserved.

Apparently, only important biological differences between these groups could have caused this short-term, but distinct dominance of radiolarians and complete absence of foraminifers. The point is that the life cycle of foraminifers includes alternation of sexual and asexual generations. During sexual reproduction, gametes fall on the marine bottom for subsequent development, which would be impossible in the absence or shortage of oxygen. On the contrary, radiolarians reproduce by asexual cell fission and are independent of oxygen conditions in bottom waters (Ormiston, 1993). On the one hand, it has been shown experimentally that axopods support the organism in marine water in suspended condition. However, during sporogenesis, radiolarians lose ectoplasm and axopods; therefore, central capsules at once fall on the bottom (Cachon and Cachon, 1984). However, on the other hand, radiolarians of the past, like Recent radiolarians (Anderson and Matsuoka, 1992), probably had stable symbiosis with unicellular algae, which allowed them to survive even in anoxic conditions of hydrosulphuric contamination of basins.

Apparently, these ontogenetic features promoted life success of radiolarians in specific ecological conditions of basins of the Domanik type. Hence, the abundance of radiolarians (organisms with siliceous skeletons) and the absence of foraminifers (protists with calciferous shells) in the Domanik beds of the epicontinental seas of the past are probably evidence of an oxygen minimum in bottom waters. The shortage of oxygen could have facilitated the preservation of neutral reaction in waters of paleoceans and the formation of acid products of metabolism at the cellular level. These factors interfered with the formation of calcitic and phosphate skeletons in living creatures. However, the same conditions could be optimum for the development of skeletons formed of opal, gel of orthosiliceous acid.

This minor point in the life of radiolarians helps to gain an insight into the causes of the absence of foraminifers (protists with calciferous shells) and success of radiolarians (organisms with siliceous skeletons) in specific ecological conditions of basins of the Domanik type.

The analysis of changes in morphological features of radiolarians in the Domanik Time in the Timan–Pechora Basin has shown that the biotic crises in the evolution of radiolarians reflect ecological changes in environments:

- in adverse crisis situations, aberrant species frequently appear; in particular, this is recorded in adverse conditions of hydrosulphuric contamination of the Middle Domanik, where *Entactinia bifida* Afanasieva and *Moskovistella mira* Afanasieva, with bifurcating or, on the contrary, coupled spines, occur (Pl. 11, figs. 3, 4);

- only spherical, primitive, having nothing remarkable species (*species vulgaris*), which usually form a general background of an assemblage, successfully survive critical points in the evolution;

- possibly, these are just *species vulgaris* which give rise to new species, as favorable ecological conditions return.

Ammonoids. Global transgression and eutrophication of the basin at the beginning of the Domanik Time resulted in a substantial increase in taxonomic diversity of ammonoids (during the Domanik Time, 17 species and at least five genera appeared).

The lower subformation of the Domanik Formation contains an assemblage of the *Ponticeras domanicense* Ammonoid Zone (Fig. 28), including species of the genera *Ponticeras, Uchtites, Chutoceras, Manticoceras, Mixomanticoceras, Tornoceras*, and *Linguatornoceras*, the majority of which appeared at that time.

The middle and upper subformations of the Domanik Formation contain an ammonoid assemblage of the *Nordiceras timanicum* [=*Manticoceras ammon* (pars.)] Ammonoid Zone (Becker et al., 2000) (Fig. 28). The endemic genus *Nordiceras* and new species of the genera *Lobotornoceras* and *Phoenixites* appeared. The taxonomic composition, morphological pattern, and ecological structure of ammonoid communities remained approximately the same as in the basal Domanik. Communities lack species of the genus *Probeloceras*, which are known from the beds of the same age in many other areas of the world.

Assemblages of the Domanik Formation are dominated by various ponticeratids (*Ponticeras* and the endemic genus *Uchtites*). These taxa with evolute thin-discoidal shell with many whorls and flattened living chamber were incapable of active swimming, although, having a large phragmocone, they probably could move vertically in the water column; therefore, they are regarded as a planktonic living form (Barskov et al., 2008). Ponticeratids evolved rapidly, remaining within the planktonic adaptive zone; in the Domanik Time, nine ponticeratid species appeared. Ponticeratids reached the maximum range during the phases of the greatest flooding, which are recognized in the section as “ponticeratid beds.”

Tornoceratids are represented in the Domanik Formation by involute, least specialized pachycone forms (Barskov et al., 2008). Tornoceratids were probably confined to the nectobenthic adaptive zone and, therefore, were not clearly connected with the maxima of the sea level.

Late Frasnian, Lyaiol Time

At the beginning of the Late Frasnian, in the Lyaiol Time, after a significant regression, a new transgression from the east began (Fig. 17a). The Lyaiol Formation is divided into four members (Fig. 28). Two lower members are treated as basin facies, and two upper members, as slope facies (Ovnatanova et al., 1999).

The fauna of the Lyaiol Formation consists of radiolarians, ammonoids, brachiopods, ostracodes, and fishes. Late Frasnian ammonoids and radiolarians occur in the most deepwater depressive and slope deposits of the Lyaiol Formation.

Radiolarians. In the Lyaiol Time of the Late Frasnian, the taxonomic composition of radiolarians decreased to 30 species of 15 genera; morphological diversity and general abundance in deposits are also reduced (Fig. 14). The assemblage characterizes the *Bientactinosphaera pittmani–Polyentactinia circumretia* Radiolarian Zone and corresponds to the *Virginoceras ljaschenkoae* and *Manticoceras lyaiolense* ammonoid zones (Fig. 28). The radiolarian assemblage from the first, lower member of the Lyaiol Formation is most diverse and includes 29 species of 14 genera. The assemblage is dominated by taxa with a spherical skeleton (23 species), among which forms with two differently directed main spines are of particular interest, i.e., *Bientactinosphaera egindyensis* Nazarov, *B. obtusa* (Hinde), and *B. pittmani* (Hinde). Typical and relatively frequent taxa are *Borisella maksimovae* Afanasieva, *Bientactinosphaera variacanthina* (Foreman), *Polyentactinia kossistekensis* Nazarov, and *P. rudihispida* Nazarov et Ormiston. Spiny Aculearia are only represented by six species, with the prevalence of species of the genus *Ceratoikiscum* (Pls. 17, 18).

In the second and third members of the Lyaiol Formation, radiolarians are absent (Fig. 14).

In the fourth member, an impoverished radiolarian assemblage is recorded; it includes rare spherical *Bientactinosphaera variacanthina* (Foreman), *Entactinia* sp., and *Astroentactinia* sp. and spiny *Palacantholithus stellatus* Deflandre. In the upper layers of the fourth member, on a background of individual spherical *Entactinia* sp., discoidal *Palaeodiscaleksus punctus* (Hinde) and *Primaritripus patella* (Hinde) occur; this suggests that the paleobasin became shallow again (Pl. 18, figs. 14, 15).

In the northern Timan–Pechora Basin, in a section on the Unya River (Nazarov, 1988) (Fig. 6), a mixed radiolarian assemblage of Frasnian and Famennian forms has been recorded. The assemblage includes taxa known from the Frasnian and Famennian stages and the species *Tetrentactinia barysphaera* Foreman, which is only characteristic of the Famennian.

Ammonoids. In the first member of the Lyaiol Formation, which corresponds to a regressive phase, ammonoids are absent.

The most diverse ammonoids occur in the second member, which corresponds to a maximum transgression (*Virginoceras ljaschenkoae* Zone) (Fig. 28). The majority of taxa of this zone are cosmopolites, which probably came from peri-Gondwanan areas. In abundance and species diversity, the assemblage is dominated by species of the genus *Manticoceras*, some of which are very large. Virginoceratids (species of the genera *Virginoceras* and *Carinoceras*) are present; they probably occupied newly appearing niches in the distal shelf. Among tornoceratids, members of *Tornoceras* and *Phoenixites* replaced species of the genera *Linguatornoceras* and *Aulatornoceras.* Morphological changes in this group only slightly concerned the shell shape, whorls became somewhat narrower.

In the ammonoid assemblage from the third and fourth members (*Manticoceras lyaiolense* Zone), species diversity of ammonoids is reduced; species of *Manticoceras* prevail. The lowest diversity of ammonoids is in the fourth member. Species with an oxycone shell gradually became extinct and completely disappeared at the end of the Lyaiol Time (Becker et al., 2000).

A decrease in morphological diversity of ammonoids and radiolarians in the Late Frasnian occurred against a background of a gradual decrease in sea level and filling of deepwater depression, which resulted in reduction of the deep shelf. The end of the Late Frasnian Age was marked in the Timan–Pechora Basin by general regression of the sea; this resulted in a crisis in communities of radiolarians and ammonoids. In shallow-water beds of the Sedyu Formation of the Upper Frasnian, which overlie the Lyaiol Formation, ammonoids and radiolarians have not been recorded (Fig. 28).

CHAPTER 5. PALEOBIOGEOGRAPHY OF DEVONIAN RADIOLARIANS

The major morphological novelties in historical development of various groups of organisms arose during crises, when “impossible becomes possible.” Under these conditions, genetic search and a sharp increase in variation range occur.

The evolution of radiolarians in the Phanerozoic was very diverse. In this situation, it is impossible to simulate biological processes without taking into account the effect of external factors. The origin, major evolutionary patterns, and great biotic crises in the development of radiolarians during the Phanerozoic were closely connected with the geological history of the Earth. The evolution of communities was under the influence of climatic evolution; in turn, climatic changes reflect a number of geological, geophysical, and space processes.

The global falls in temperature in the Paleozoic and Cenozoic and warm climate of the Mesozoic played a special role in the evolution of life on the Earth (Chumakov, 2001; Dobretsov, 2003), including radiolarians (Afanasieva and Amon, 2006a). Periodic pulsations, alternation of fall in temperature and warming were the driving force which made the biota continuously adapted to varying conditions (Dobretsov, 2003).

A decrease in the concentration of carbon dioxide in the atmosphere is one of the main factors of paleoclimatic changes, which resulted in strong fall in temperature and glaciations. Paleolevels of atmospheric carbon dioxide in the Phanerozoic (Berner and Kothavala, 2001) show (1) very high concentration of carbon dioxide during the Early Paleozoic, (2) a significant decrease at the end of the Devonian, in the Carboniferous, and Permian, (3) high concentration in the Early Mesozoic and a gradual decrease during late Cretaceous and Cenozoic (Fig. 29).

Increased interglacial diversity of radiolarians established by Matul (2007; Matul et al., 2009) for Quaternary radiolarians is also traced in radiolarians throughout the Phanerozoic (Afanasieva et al., 2005d, 2009; Afanasieva and Amon, 2006a, 2006b). Radiolarians, which disappeared at transitions to glaciation or during glacial phases, were common during warm phases of interglacials (Fig. 29). Most of new radiolarian species appeared during warm periods, and sharp fall in abundance occurred during falls in temperature (Afanasieva et al., 2005d, 2009; Afanasieva and Amon, 2006a, 2006b; Kovalev, 2007; Matul, 2007; Matul et al., 2009).

The general pattern of growth of interglacial biodiversity of radiolarians in the Phanerozoic is determined by (1) stabilization of climate, (2) increase in productivity of the food base, (3) complication of habitats of specialized species confined to particular ecological niches (Pianka, 1994).

STAGES OF RADIOLARIAN EVOLUTION AND GALACTIC SEASONS

Seasonal rhythmics of the galactic year is reflected in evolutionary stages of radiolarians (Afanasieva and Amon, 2006a, 2006b, 2010a). The galactic year is a complete turn of the Sun around the Galaxy center (Parenago, 1952). The following names of the galactic year have been proposed for Phanerozoic (Fig. 29): Phosphatian comprises Cambrian–Devonian; Phitonian is Carboniferous–Jurassic, and Noetian is Cretaceous–Quaternary. The galactic year is divided into seasons, which approximately correspond to the periods of the Phanerozoic (Fig. 29): spring, summer, winter, and autumn. (Kulikova and Kulikov, 2000).

The boundaries of galactic years at the transition from spring to summer are preceded by peaks of radiolarian abundance in the spring periods (Fig. 29); transition from the year Phosphatian to Phitonian is accompanied by an explosive increase in abundance in the Late Devonian; transition from the year Phitonian to Noetian, by an explosive increase in number in the Late Jurassic.

The seasons of galactic years are characterized by approximately the same pattern of dynamics of radiolarian biodiversity: appearance of new taxa was replaced by progressive development and, then, extinction. Many great extinctions occurred at the boundaries of seasons (Fig. 29).

Phosphatian

The first stage of radiolarian evolution (Cambrian–Silurian) combines two steps and the first three seasons of the year Phosphatian (Fig. 29): step 1 (Cambrian–Middle Ordovician) comprises “summer” and beginning of “autumn”; step 2 (Late Ordovician–Silurian) comprises the end of “autumn” and “winter.” Within the first three seasons of galactic year (“summer,” “autumn,” “winter”), the biodiversity dynamics remained the same: at first, slow gradual growth of the number of taxa, then, a peak of diversity and, then, decrease in number.

The phylum Radiolaria emerged in the Early Cambrian, beginning of the summer of the year Phosphatian. In the Cambrian, “summer” of the year Phosphatian, the five radiolarian classes and the overwhelming majority of higher taxa appeared. They include 11 radiolarian orders, 24 families, 18 subfamilies, 59 genera, and 223 species. The rate of speciation of radiolarians at the first evolutionary stage ranged from 0.3 to 3.0 species/m.y., on average 1.6 species/m.y. (Fig. 30).

At the end of “winter” of the year Phosphatian, at the Silurian–Devonian boundary, there was the first radical turn in the evolution of radiolarians. Sea regression and long geocratic epoch at the end of the Silurian and beginning of the Devonian resulted in the disappearance of typical Early Paleozoic taxa and changes in the taxonomic composition of radiolarians at the levels of species, genera, and particular families and orders (66.1% of Early Paleozoic radiolarian genera and 91.0% of species became extinct) (Fig. 29).

The second stage of radiolarian evolution (Devonian–Early Carboniferous) covers the final season of the year Phosphatian (“spring”) and beginning of “summer” of the year Phitonian. Sea transgression in the Middle–Late Devonian and Early Carboniferous promoted rapid development of radiolarians. At that time, 90 radiolarian genera with 317 species are known. The rate of speciation of radiolarians at the second evolutionary phase ranged from 1.3 to 7.9 species/m.y., on average 3.3 species/m.y. (Fig. 30).

“Spring” of the year Phosphatian displays different biodiversity dynamics of radiolarians than in the previous seasons. In this season, radiolarian biodiversity and the rate of speciation reached the Paleozoic maximum (up to 317 species and 7.9 species/m.y., respectively); the peaks of the taxonomic number and rate of speciation were shifted to the end of the season (Fig. 29).

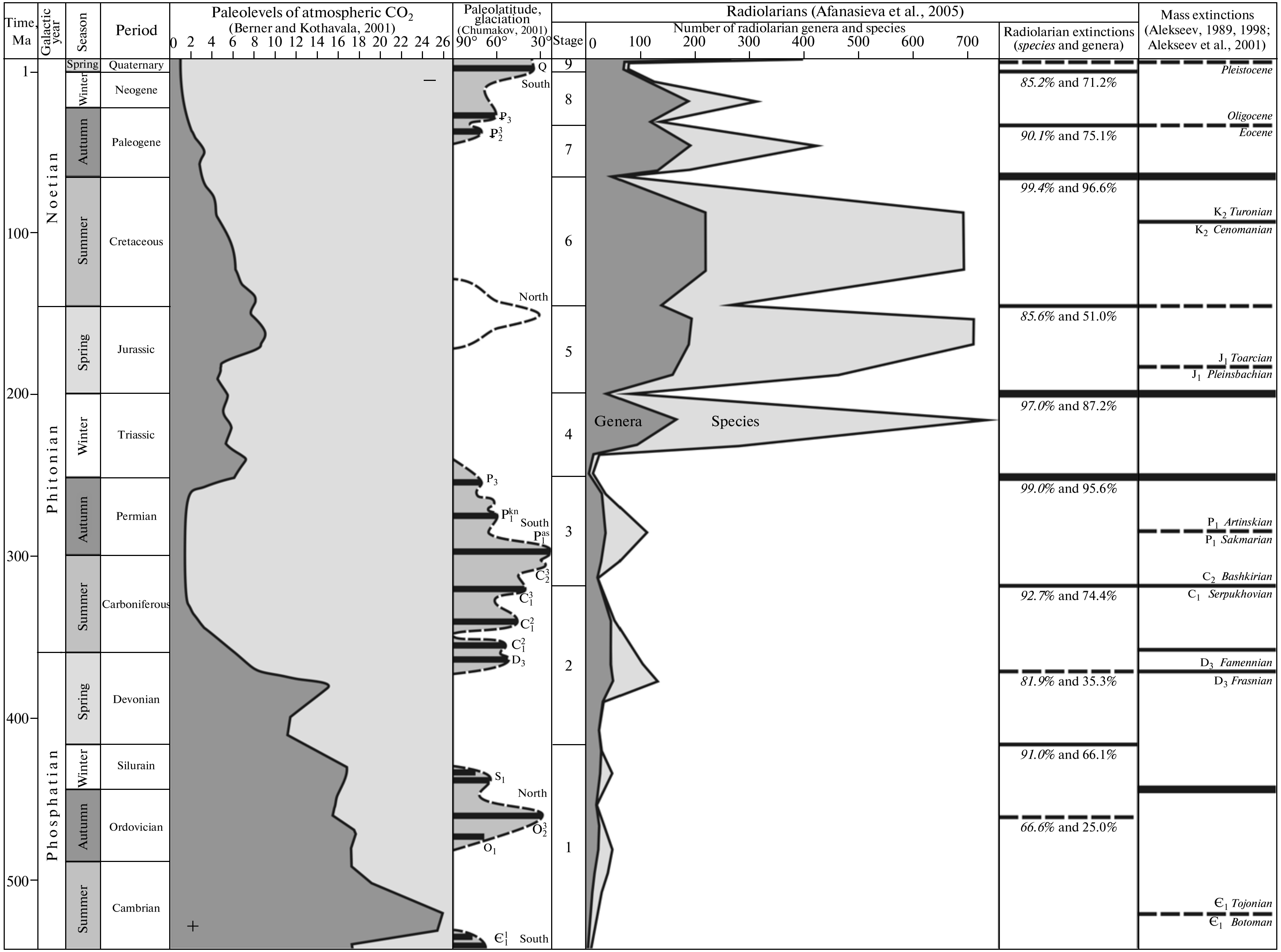


Fig. 29. Dynamics of radiolarian taxonomic diversity in the Phanerozoic.

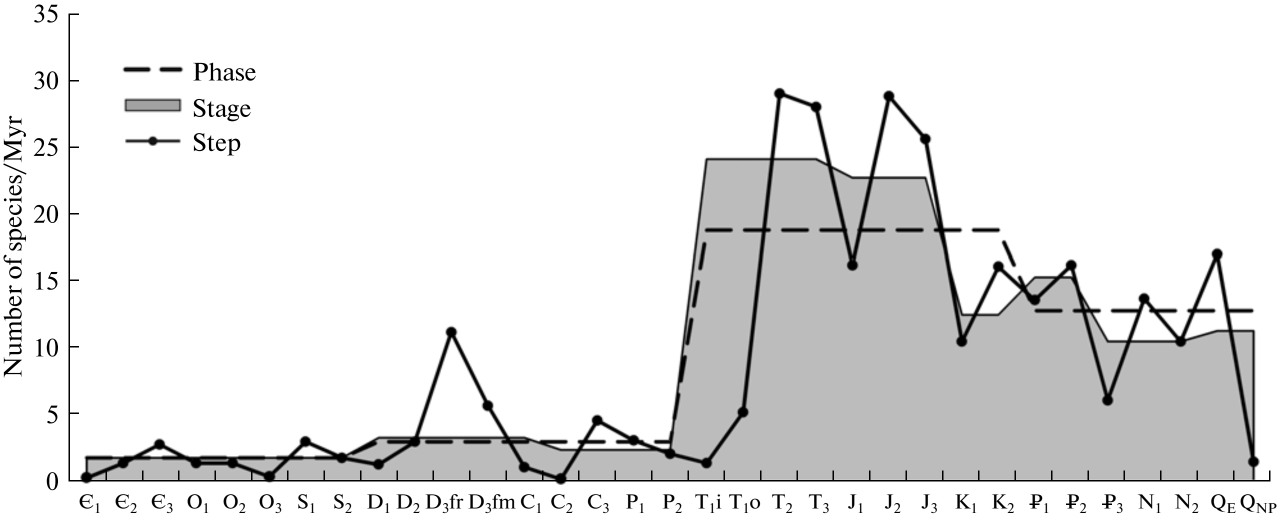


Fig. 30. Speciation rate in Phanerozoic radiolarians.

Phitonian

In the middle of "summer" of the year Phitonian, evolutionary development changed drastically; mass extinction of taxa began, which stopped at the boundary between the Early and Middle Carboniferous. Sweeping development and distribution of Devonian–Early Carboniferous radiolarians was interrupted by the onset of a global fall in temperature and glaciation in the Middle Carboniferous–Permian. This second crucial point in radiolarian evolution was marked by the disappearance of 74.4% of radiolarian genera and 92.7% of species (Fig. 29).

The third stage of radiolarian evolution (Middle Carboniferous–Permian) corresponds to the second half of summer and autumn of the year Phitonian (Fig. 29). In the Middle Carboniferous–Permian, 52 radiolarian genera and 202 species have been recorded. The general species diversity changed from 25 species in the Middle Carboniferous to 112 in the Early Permian and 37 in the Late Permian. The rate of speciation of radiolarians at the third evolutionary stage ranged from 0.1 to 4.6 species/m.y., on average 2.3 species/m.y. (Fig. 30).

At the end of the Permian, a long cold period of the Paleozoic accompanied by global glaciations was over. In addition, after the transgression in the Late Carboniferous–Early Permian, a long geocratic epoch began and covered almost the entire Late Permian and Triassic. As a result, the end of the Permian, the boundary between "autumn" and "winter" of the year Phitonian, was marked by a mass extinction of 95.6% of Paleozoic radiolarian genera and 99.0% of species (Fig. 29).

After the cold Paleozoic climate, the warm Mesozoic Era began. It comprised "winter" and "spring" seasons of the year Phitonian and "summer" season of the year Noetian.

The fourth stage of radiolarian evolution (Triassic) corresponds to "winter" of the year Phitonian. Only seven Paleozoic genera continued into the Triassic.[18] The total number of radiolarians sharply increased to 227 genera and 967 species (Bragin, 2002). The rate of speciation in the Triassic, "winter" of the year Phitonian, sharply increased from 1.4 to 29.0 species/m.y., on average 15.9 species/m.y. (Fig. 30).

At the same time, at the end of "winter," 97.0% of Triassic radiolarian species became extinct (Fig. 29).

The fifth stage of radiolarian evolution (Jurassic) coincides with "spring" of the year Phitonian (Fig. 29). The total number of Jurassic radiolarian genera is 286. The rate of speciation in the Jurassic ranged from 16.2 to 28.8 species/m.y., on average 23.5 species/m.y. (Fig. 30).

Jurassic "spring" of the year Phitonian has much in common with Devonian "spring" of the year Phosphatian, i.e., the average rate of speciation increased, reaching a maximum in the Mesozoic (23.5 species/m.y.); the greatest Mesozoic and even Phanerozoic species diversity was reached, 1486 radiolarian species; as in the Devonian, the peaks of diversity and speciation rate were shifted to the end of the season.

However, at the end of Jurassic "spring," 85.6% of Jurassic radiolarian species became extinct (Fig. 29).

Noetian

The sixth stage of radiolarian evolution (Cretaceous) corresponds to "summer" of the year Noetian (Fig. 29). In the Cretaceous, the total number of radiolarian species was 1118. The sixth stage of radiolarian

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[18] Statistical analysis of changes in radiolarian biodiversity in the Mesozoic and Cenozoic was performed based on the database "RADBASE," compiled by Agarkov (1998, 1999, 2004; Agarkov; Afanasieva et al., 2005a, 2005d).

evolution resembles somewhat "summer" of the year Phitonian: the developmental trend also changed towards a decrease in number and gradual lowering of speciation rate from 10.5 to 16.1 species/m.y. In "summer" of the year Noetian, the average rate of speciation decreased to 13.3 species/m.y., i.e., it was almost half that of Jurassic "spring" of the year Phitonian (23.5 species/m.y.) and approximately the same as in the Triassic "winter" of the Phitonian (15.9 species/m.y.) (Fig. 30). At the same time, the total number of Cretaceous radiolarian genera is 281, i.e., similar to that in the Triassic (227 genera) and Jurassic (286 genera).

Tectonic activity at the Cretaceous–Paleogene boundary, fall in temperature and glaciation, which began in the Eocene, promoted the establishment of the geocratic epoch of the Cenozoic. As a result, at the end of "summer" of the year Noetian, there was a new radical turn in evolution and mass extinction of 96.6% of Mesozoic radiolarian genera and 99.4% of species (Fig. 29). At the beginning of the Paleogene, only 21 species of Mesozoic radiolarians remained; they were the basis for historical development of Cenozoic radiolarians.

The seventh stage of radiolarian evolution (Paleocene–Eocene) coincides with "autumn" of the year Noetian (Fig. 29). "Autumn" of the year Noetian is similar in diversity dynamics to "autumns" of the years Phitonian and Phosphatian.

However, "autumn" of the year Noetian differs from the Cretaceous "summer" in a decrease in the total number of radiolarians to 537 species against a background of approximately the same average rate of speciation (14.9 species/m.y.). The rate of speciation in "autumn" of the year Noetian ranged from 13.6 to 16.2 species/m.y. (Fig. 30).

The maximum generic diversity was in the Eocene, 193 genera. The total number of radiolarian genera of the seventh stage is 213, i.e., similar to that of the Mesozoic stages: 227 genera in the Triassic, 286 in the Jurassic, and 281 in the Cretaceous.

At the same time, at the end of the seventh stage, 90.1% of radiolarian species and 75.1% of genera disappeared (Fig. 29).

The eighth stage of radiolarian evolution (Oligocene–Pliocene) falls on the end of "autumn" and "winter" of the year Noetian (Fig. 29). In general, this phase is characterized by a decrease in the development of radiolarians. "Winter" of the year Noetian in radiolarian development differs substantially from the previous "winters" of the years Phitonian and Phosphatian. The total number of radiolarian species decreased to 420 species. The rate of speciation ranged from 6.1 to 13.7 species/m.y., and the mean rate of speciation decreased to 10.1 species/m.y. (Fig. 30).

The eighth stage of radiolarian evolution is distinguished by a decrease in radiolarian diversity to 120 genera in the Oligocene and 127 genera in the Pliocene versus a small increase in diversity in the Miocene (up to 187 genera). The total number of radiolarian genera in the Oligocene–Pliocene was 215, i.e., similar to that of stages 4–7 (Fig. 29).

At the end of the Neogene, 83.5% of Cenozoic radiolarian genera and 93.1% of species became extinct (Fig. 29).

The ninth stage of radiolarian evolution (Quaternary), "spring" of the year Noetian, is a special epoch in the development of radiolarians, which covers a very short period. The first step of the Quaternary (Eopleistocene and Neopleistocene) displays a sharp fall of radiolarian diversity to 79–80 species. During the second step of the Quaternary, in the Holocene, about 400–600 new radiolarian species appeared (Fig. 29). However, 10–30% of the total number of living radiolarians are empty skeletons. In loose deposits, the number of radiolarian skeletons is several dozen times as great as in consolidated rock (Petrushevskaya, 1986; Zasko, 2004). Consequently, in the very distant future, the Holocene beds will contain at most 30–60 radiolarian species, i.e., the number comparable with the data on the Eopleistocene (79 species) and Neopleistocene (80 species) (Afanasieva et al., 2005d; Afanasieva and Amon, 2006a, 2006b).

MASS EXTINCTIONS

During the Phanerozoic, there were periods of relatively quiet evolutionary development of the biota, alternating with several short-term mass extinctions, when the rate and level of extinction increased by many times compared with a background extinction level (Alekseev, 1989, 1998; Alekseev et al., 2001). The intensity of extinction in particular groups of phyto- and zooplankton differs for organisms with calciferous and siliceous skeletons. In radiolarians and silicoflagellates, the intensity of extinction at the generic level is 0.33–0.2 of that in planktonic foraminifers and nanoplankton, although the background level of extinction is approximately the same.

Sharp changes in environment and climate affect the initial stages of the formation of new aromorphoses and result in irreversible extinction of unsuccessful forms (Kanygin, 2001).

Species diversity of Phanerozoic radiolarians ranges from 5450 to 5650 species, among which Polycystina comprise about 5000 species (excluding polycystine radiolarians of the Holocene). The number of Recent species of polycystine radiolarians ranges from 400 to 600 (Kruglikova, 1995; Boltovskoy, 1998), the number of Collodaria is about 45 species and Pheodaria, about 105 species (Reshetnyak, 1966; Strelkov and Reshetnyak, 1971; Dumitrica, 1973).

Transition from a cold climate of the Paleozoic to a warm climate of the Mesozoic was marked by the disappearance at the Permian–Triassic boundary of 95.6% of radiolarian genera and 99.0% of species (Fig. 29). The Permian–Triassic extinction changed the course of the development of radiolarians. All classes of Polycystina responded to these catastrophic events in the Mesozoic–Cenozoic by explosion of taxonomic diversity:

- Spumellaria (Pz) 57 genera, (Mz–Cz) 81 genera;
- Sphaerellaria (Pz) 24 genera, (Mz–Cz) 107 genera;
- Stauraxonaria (Pz) 32 genera, (Mz–Cz) 156 genera;
- Collodaria (Mz–Cz) 15 genera.

An exception is provided by the spiny radiolarians Aculearia, which are represented in the Paleozoic by 45 genera and gradually decrease in number in the Mesozoic–Cenozoic to 21 genera.

The class Nassellaria shows the greatest taxonomic diversity among all polycystine radiolarians. In the Paleozoic, nassellarians are only represented by 20 genera of the order Pylomariata; however, in the Mesozoic and Cenozoic, Nassellaria are represented by 574 genera versus 366 genera of all other classes of Polycystina.

Transition from a warm climate of the Mesozoic to a cold climate of the Cenozoic was accompanied by extinction of 96.6% of Mesozoic radiolarian genera and 99.4% of species. The beginning of the Holocene displays a sharp extinction of 98.2% of Cenozoic radiolarian genera and 99.2% of species, that is, comparable to the data on the Paleozoic and Mesozoic (Fig. 29).

In the Paleozoic, 158 radiolarian genera and 701 species appeared; the average rate of speciation is 2.2 species/m.y.: in the Early Paleozoic (Cambrian–Silurian), 59 radiolarian genera and 223 species appeared, with the average rate of speciation 1.6 species/m.y.; in the Late Paleozoic (Devonian–Permian), 119 genera and 496 species are known, which emerged at the mean rate 2.8 species/m.y. The Mesozoic is characterized by the greatest number of known radiolarians, 625 genera and 3328 species, and the maximum mean rate of speciation is 17.9 species/m.y. In the Middle Triassic and Middle Jurassic, the rate of speciation was maximum in radiolarian history, 29 species/m.y. In the Cenozoic (excluding Recent), the total number of radiolarians decreased to 385 genera and 922 species; the mean rate of speciation decreased to 11.2 species/m.y. (Fig. 30). In the Holocene, 377 radiolarian genera and about 400–600 species are known.

The major changes in taxonomic diversity and extraordinary extinctions of radiolarians completely coincide with the major mass extinctions of the biota in the Phanerozoic established by Alekseev (1989, 1998; Alekseev et al., 2001): Frasnian–Famennian, Serpukhovian–Bashkirian, Permian–Triassic, Triassic–Jurassic, Jurassic–Cretaceous, Cretaceous–Paleogene, and Pleistocene–Holocene (Fig. 29).

In the Late Devonian, the mean rate of speciation of radiolarians was 7.9 species/m.y., i.e., the maximum for the Paleozoic. The Paleozoic maximum of the rate of speciation, 11.2 species/m.y., was in the Frasnian Age.

Geological events at the Frasnian–Famennian boundary (Veimarn et al., 1997) had effect on radiolarian development. At the Frasnian–Famennian boundary, the taxonomic composition of radiolarians strongly changed (Fig. 29); 118 (81.9%) species and 18 (35.3%) genera became extinct. In addition, in the Famennian Age, the rate of speciation became half that of the Paleozoic maximum, 5.7 species/m.y. (Fig. 30). At the same time, the change in the taxonomic composition of radiolarians was not accompanied by a sharp shift of the total number of taxa, because extinct Frasnian species and genera were at once replaced by new taxa; in the Famennian, 87 (77.0%) radiolarian species and 17 (34.0%) genera appeared.

At the Jurassic–Cretaceous boundary, a mass extinction of radiolarians occurred. However, Alekseev (1989, 1998; Alekseev et al., 2001) put this in doubt, because, at this boundary, the marine fauna as a whole underwent only minor changes. The level of extinction of marine genera and families was at most 30 and 5%, respectively (Sepkoski, 1996). At the same time, at the end of the Jurassic, 13 (18.3%) radiolarian families and subfamilies, 57 (28.9%) genera, and 497 (69.9%) species became extinct (Fig. 29).

At the same time, mass extinctions at the Botoman–Tojonian, Ordovician–Silurian, Devonian–Carboniferous, and Cenomanian–Turonian boundaries, are not seen in the history of radiolarians (Fig. 29). On the other hand, mass extinctions of radiolarians at the Silurian–Devonian and Neogene–Quaternary boundaries are not seen in the general scale of mass extinctions of the biota (Fig. 29). However, at the Silurian–Devonian boundary, 91.0% of Early Paleozoic radiolarian species and 66.1% of genera disappeared and, at the Neogene–Quaternary boundary, 93.1% of Cenozoic radiolarian species and 83.5% of genera became extinct.

Catastrophic mass extinctions in the Phanerozoic at the Permian–Triassic and Cretaceous–Paleogene boundaries were connected with the end or beginning of autumn (Fig. 29). At these boundaries, the structural pattern of skeletons and the taxonomic composition of radiolarians changed (Afanasieva and Amon, 2006a, 2006b, 2010a).

The peaks of taxonomic diversity occurred in "spring" seasons, which terminated galactic years (Fig. 29).

Devonian "spring" of the year Phosphatian was marked by an outburst of radiolarian biodiversity (Fig. 29); in the Late Devonian, the taxonomic diversity of radiolarians reached the Paleozoic maximum, 231 species. In the Frasnian, the rate of speciation became several times greater, 11.2 species/m.y.

Jurassic "spring" of the year Phitonian displays unprecedented diversity of radiolarians; in the Late

Jurassic, 1486 species have been recorded; the maximum rate of speciation was 29.0 species/m.y.

Recent "spring" of the year Noetian is characterized by strong changes in taxonomic composition and a sharp increase in radiolarian diversity in the Holocene, up to 400–600 species, and a striking rate of speciation.

Thus, "springs" of galactic years provided extremely favorable conditions for successful development of radiolarians:

- many biotopes became free due to the previous catastrophes and glaciations;
- oceanic water contained abundant silica and biogenic elements;
- the systems of paleoceanic currents favored expansion of radiolarian populations and adaptation to new biotopes.

As a result of changes and improvement of ecological situation, the formation of new radiolarian morphotypes accelerated.

SYMBIOSIS IN THE LIVE AND EVOLUTION OF RADIOLARIANS

The community structure at the initial stages of the development was relatively simple, allowed for the establishment of various relationships between species. However, as communities developed, more and more interspecific relationships were stabilized and fixed. New species constantly appeared in both favorable and adverse environments (Chernykh et al., 2007; Kovalev et al., 2007). "Therefore, it is incorrect to take changes in climatic conditions for the factor of general deterioration of environments of all species. Crisis for some of them is a chance for others" (Kovalev et al., 2007, p. 142).

The features of habitats, bioproductivity, and vertical and horizontal distribution of radiolarians in various ecological zones of oceans and seas are caused by biotic and abiotic factors (Afanasieva et al., 2005b, 2005c, 2005d).

One of the major biotic factors directly influencing the life of radiolarians and patterns of their vertical and horizontal distribution in the water body is symbiosis with unicellular algae and bacteria, in which radiolarians play the role of hosts.

The life of photosynthesizing microalgae even in radiolarian cytoplasm is directly connected with day time light, which has a significant effect on vertical distribution of organisms in the basin. Symbiotic bacteria can be located along the axopods of radiolarians or on the cell margin. In turn, radiolarians use symbionts as a reserve source of food in adverse conditions, for example, in oligotrophic ocean waters (Anderson and Matsuoka, 1992; Matsuoka, 1992).

On the other hand, the most probable physical agents of distribution of new genetic information among asexual radiolarians were bacteria and unicellular algae, which are both symbionts of radiolarians and capable of dwelling in a "wild" environment (Dumitrica and Guex, 2003; Afanasieva and Amon, 2010b).

The distribution of genetic information between organisms of one conditional generation (without taxonomic restrictions) through living viruses and endosymbionts is termed *lateral transfer*, in contrast to *vertical transfer* in a descending series of generations. The distribution of genetic information by lateral transfer through living endosymbionts is characteristic of all living creatures (Kordyum, 1982; Khesin, 1984; Gvozdev, 1998; Golubovsky, 2000; Nazarov, 2005). Unfortunately, this biotic factor is underestimated by modern researchers, although it could have promoted the formation and distribution in asexual radiolarians of new morphological designs and processes of evolution (Afanasieva and Amon, 2010b).

Morphological novelties in historical development of radiolarians arose during crises, when there were conditions for genetic search and a sharp increase in variability. Lateral transfer of genes was probably a mechanism for distribution of innovations in ecosystems.

The mechanism for distribution in radiolarians of genetic innovations by living agents of gene transfer could have been as follows (Afanasieva and Amon, 2010b):

(1) New formations which appeared in structural genes of individual radiolarians could have been received by a bacterial or dinoflagellate genome by means of transfer through viruses and mobile genetic elements.

(2) Subsequently, these innovations became widespread in the "wild" environment of free microorganisms, without any influence on them.

(3) Then, innovations could have been introduced in genomes of bacteria and dinoflagellates, which inhabited remote water areas.

(4) After that, innovations could have been introduced in genome of the symbiont host in remote populations.

Thus, a new character very rapidly appeared not only in the geographical range of the mutating population, but also in the entire water area inhabited by radiolarians (in extreme case, over the whole of the World Ocean). In addition, according to the data of modern genetics, for protists, one or two generations are enough to provide the distribution of a mutant character and stabilization of its phenotypic manifestation (Nazarov, 2005). However, on the other hand, eukaryotes have a complex, multilevel, highly efficient system for protection against mutations (Kordyum, 1982; Nazarov, 2005).

At the same time, on geological time scale, innovations could have been distributed almost instantly over the whole water area of the World Ocean inhabited by radiolarians (theoretically, during 100 years), like virus invasion . It is noteworthy that bacteria participated in

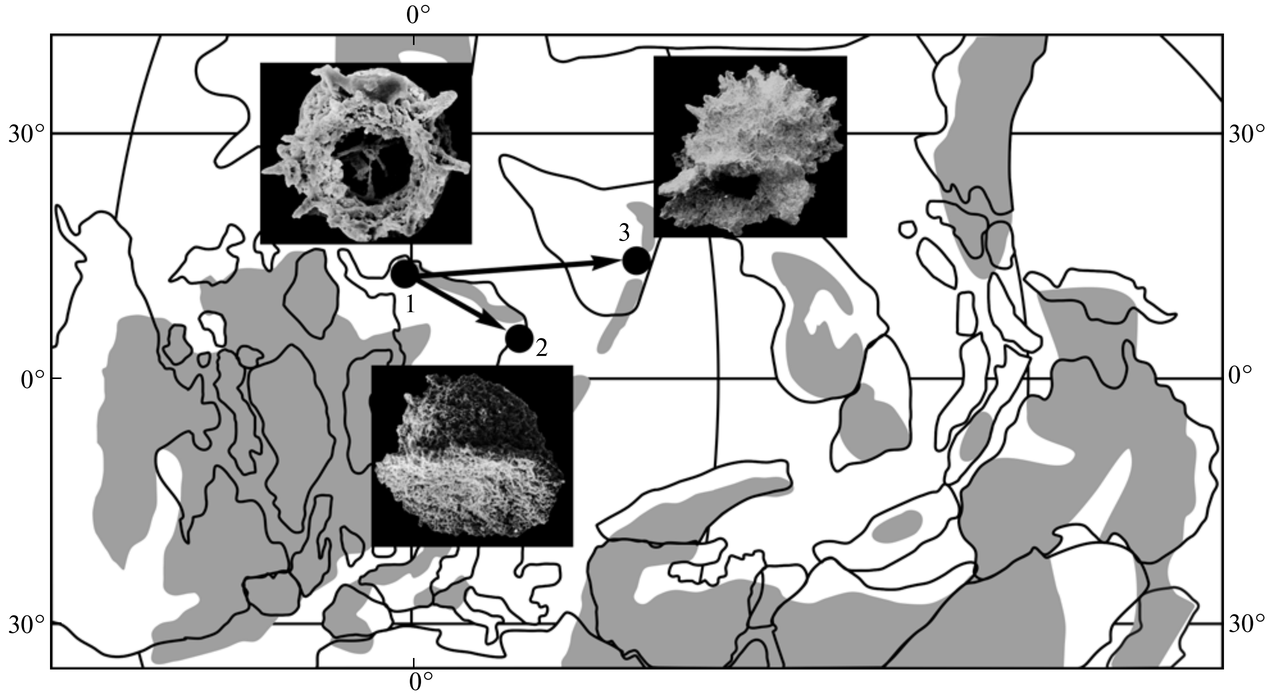

Fig. 31. Migration routes of the genus *Caspiaza* in the Late Devonian and Early Carboniferous (Afanasieva, 1986, 1993, 2000b): (1) Polar Urals, Late Devonian, Early Famennian; (2) North Caspian Region, Early Carboniferous; (3) Tien Shan, Early Carboniferous.

historical development of radiolarians from their origin in the Early?–Middle Cambrian and dinoflagellates from the Middle Triassic or even earlier.

The evolution of radiolarians in the Phanerozoic was very diverse. On the one hand, general development of radiolarians was under control of strict rhythmics, with the cyclic character, so that epochs of appearance of new taxa alternated with epochs of flourishing and, then, extinction. On the other hand, the general morphological patterns of radiolarian evolution consist of almost parallel formation of properties determining the general body plan of various higher taxa, and improvement of particular skeletal structures (Afanasieva et al., 2005d; Afanasieva and Amon, 2006a).

The analysis of synchronous morphological changes in radiolarian skeletons has shown that they could have been caused (particularly in closely related groups) by lateral transfer of genes, with participation of symbiotic bacteria and unicellular algae (Afanasieva and Amon, 2010b).

The development of radiolarians in the Phanerozoic provides various examples of rapid distribution of certain morphological structures in radiolarian communities inhabiting different, frequently rather remote areas of the World Ocean (De Wever et al., 2001; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a).

Expansion of the radiolarian morphotype with pylome of the genus *Caspiaza* at the Devonian–Carboniferous boundary is an example of rapid distribution of a morphological character for a large distance (Fig. 31). The genus *Caspiaza* appeared for the first time in the Famennian Age as endemic to the Polar Urals. In the Early Carboniferous, descendants of *Caspiaza* expanded more widely and have been recorded in the northern Caspian Region and Tien Shan (Afanasieva, 1986, 1993, 2000a).

The Tithonian Age of the Late Jurassic was a crucial point in the development of Phanerozoic radiolarians, when the radiolarian biota was considerably reduced. At the same time, some lineages showed prominent outbursts of speciation and formation of new genera. This was particularly strongly pronounced in pylomate radiolarians of the subfamily Vallupinae, which existed only in the Tithonian (Fig. 32) (Yang and Pessagno, 1989, Matsuoka, 1995; De Wever et al., 2001).

Among pylomate radiolarians, the Vallupinae are relatively close in morphology to the subfamilies Pylentoneminae and Archocyrtiinae. The morphology of Pylentoneminae and Vallupinae is characterized by the formation of two spheres in the skeleton. The development of massive main spines around the pylome connect members of the Archocyrtiinae and Vallupinae. In addition, the genera *Allocyrtium* and *Vallupus* are distinguished by the development of laminate skeletal tissue on three main spines framing the pylome. The appearance in the Early Silurian of such shells among Archocyrtiinae was probably an attempt of benthic organisms to adapt to at least heminanoplanktonic lifestyle in bottom waters. In the Late Jurassic, this attempt was repeated by members of the family Vallupinae.

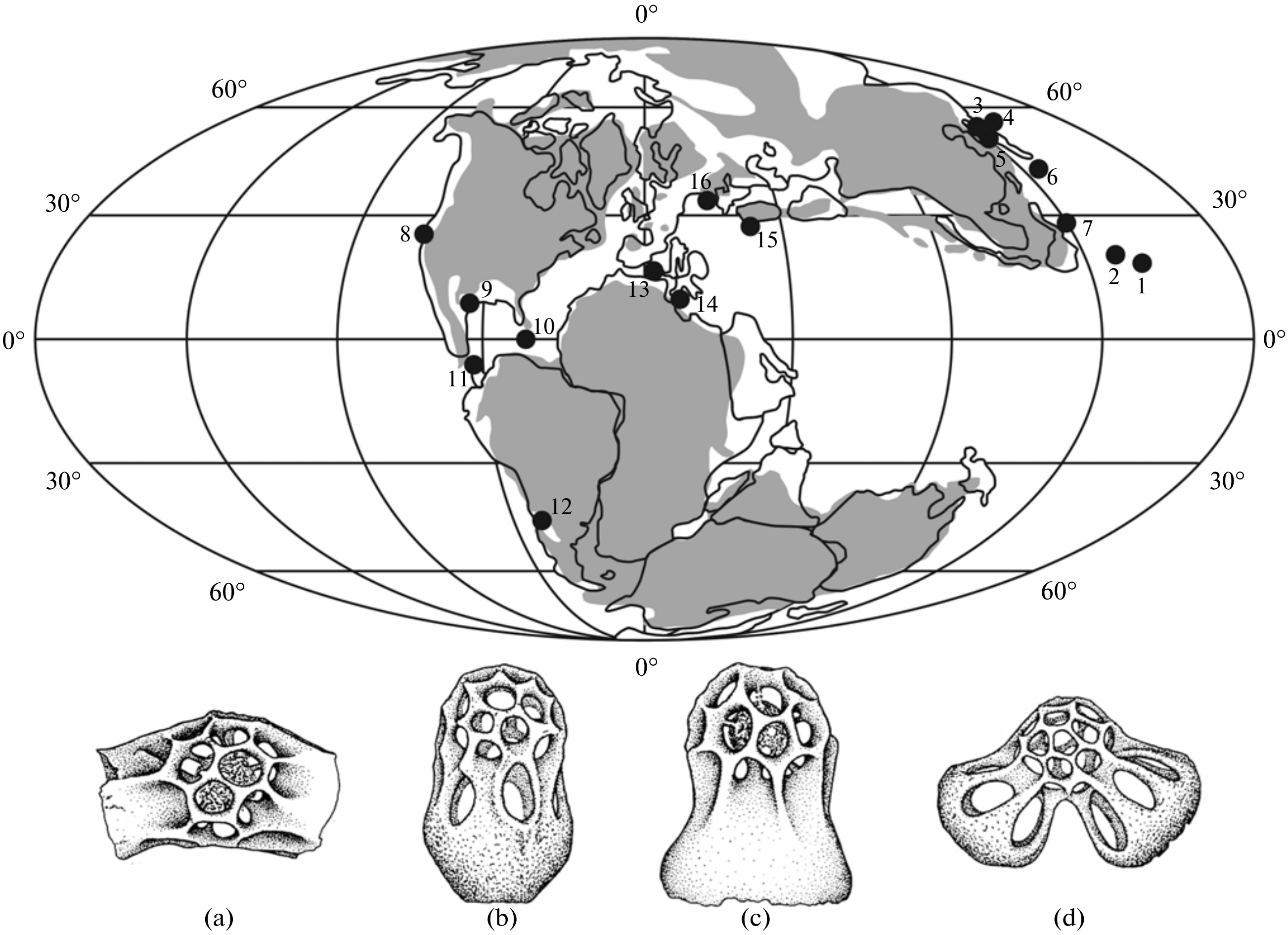

Fig. 32. Distribution of the radiolarian subfamily Vallupinae in the Tithonian of tropical and subtropical belts (Yang and Pessagno, 1989, Matsuoka, 1995; De Wever et al., 2001): (a) *Bivallupus mexicanus* Pessagno et MacLeod, 1987; (b) *Neovallupus modestus* Yang et Pessagno, 1989; (c) *Vallupus hopsoni* Pessagno et Blome, 1986; and (d) *Supervallupus haeckeli* Yang et Pessagno, 1989: (1) Pacific Ocean, Pifagetta Basin, ODP Site 801; (2) Mariana Trench; (3–6) Japan: (3, 4) central Hokkaido, (5) eastern Hokkaido; (6) Ie Island, Okinawa; (7) Philippines, Busuanga Island; (8) California, Alamo Canyon; (9) eastern and central Mexico; (10) Lesser Antilles, island of La Désirade; (11) Costa Rica; (12) Argentina, southern Andes; (13) Italy, Sicily; (14) Greece, Argolis Peninsula; (15) Turkey; and (16) Romania. Radiolarian localities are mapped in global reconstruction of continents and oceans in the Late Jurassic (McKerrow and Scotese, 1990; Scotese, 1997).

The time distribution of the Pylentoneminae (Late Devonian–Early Carboniferous) and Archocyrtiinae (Silurian–Middle Triassic) shows that an important set of morphological characters, i.e., the presence of one or two spheres with a large pylome, was absent from the fossil record of radiolarians for 94.2 m.y. (from the Middle Triassic to the end of the Jurassic).

At the end of the Jurassic, during a great evolutionary crisis and stress experienced by the radiolarian biota of that time, which resulted in a catastrophe, this set of characters appeared again in Vallupinae and rapidly expanded (Fig. 32) over the tropical and subtropical belts of the World Ocean (Matsuoka, 1995). It is possible to assume that the main carrier of this character (preserved in genetic memory or restored again?) was the species *Vallupus hopsoni*, which showed the greatest geographical range among the Vallupinae. The time of the appearance of this mutation is estimated as the Early Tithonian, lasting for 2.9 m.y.

It is only possible to explain the fact of instantaneous (on the geological time scale) appearance and global distribution in the Late Jurassic of the family Vallupinae from the point of view of lateral transfer of genes through living viruses and endosymbionts (Fig. 32) (Afanasieva and Amon, 2008c).

A prominent example of expansion of new morphotypes and the dynamics of biological explosion in the zone of invasion is the scenario of wave expansion in the Devonian of evolutionary innovations in the morphologically extraordinary radiolarian group with two porous walls and one main spine (Afanasieva and Amon, 2009b).

TYPES OF INTERACTION BETWEEN SPECIES AND TRENDS IN ADAPTATION TO ENVIRONMENTS

Invasion of a species in a new ecological system and adaptation to a new niche are regarded as *two different phases* of the existence of populations. The phase of invasion is a unique event of a *solitary population wave*, established by Kovalev and Vechernin (1986) and confirmed by our studies of Paleozoic radiolarians (Afanasieva and Amon, 2009b). The event of a *solitary population wave* is universal in character as an evolutionary factor of expansion of invasive species. The population growth of alien taxa follows the hyperbolic pattern and is accompanied by exclusively wide phenotypic diversity (Kovalev and Vechernin, 1986, 1989; Afanasieva and Amon, 2009b).

However, the capability of forming solitary population waves is only manifested in phylogenetically young *"juvenile taxa"* (Kovalev, 1994, 2004, 2007). Juvenile taxa are initial stages in the evolution of superspecies taxa and have a high activity of mobile genetic elements (Kovalev, 2007). They provide a rapid filling of free ecological niches (Kovalev, 1994, 2004; Markov and Naimark, 1998). In the evolutionary process, they are coenophobes, which retain an unstable state of genome during invasion in a new geographic range (Kovalev, 2007). Biological explosion of a young invasive species is characterized by "critical mass," i.e., the minimum population number, below which the population of new species is suppressed by the ecosystem. If the population density of invasive species is greater that the critical value, "explosion" occurs. The quantitative dynamics of such a biological explosion in the zone of introduction of alien taxon is characterized by a very rapid growth of population density following the hyperbolic pattern. Therefore, the introduced species gains advantages in struggle against the ecological system, which impedes introduction, and occasionally has a profound effect on further development of this ecosystem (Kovalev, 2007).

In the ecosystem, two interaction types between species (coenophilic and coenophobic) are supposed to exist, depending on the way of adaptation to environments (Kovalev et al., 2007).

Coenophilic type. A coenophile adapts within a certain community of coenophilic species, which directly depend on each other and are connected by rigid relationships. Changes connected with one species necessarily have effect on its partner.

Coenophobic type. A coenophobe adapts to environment independently. It survives only if independently adapts to the requirements of new environment and occupies in the ecosystem all possible ecological niches. In the case that environment is worsened, so that the species becomes inadaptive, coenophobic species changes.

Thus, in the course of natural selection, coenophobic species struggle for niches against a coenophilic system (Kovalev et al., 2007).

In the model of the biosphere evolution developed by Kovalev (1994, 2004, 2007), the formation of a new ecosystem begins when the most mobile species from boundary areas try to adapt to other's territory with particular ecological conditions. These species get into environment which is distinct from their previous environment. Therefore, new conditions are adverse for these species, since they have not yet adapted to them. However, in this period, coenophobic species with essentially new properties may appear, because evolution is directed to adaptation to new conditions. Thus, the time of coenophobes comes.

Subsequently, as species adapt to changed conditions, further adaptation cease to have significance, environment becomes favorable and the process of coenophilization begins. Living organisms try to occupy all possible ecological niches. However, species appearing in the ecosystem acquire features only slightly differing them from their neighbors in the ecosystem. The appearance of species with essentially other characters is highly improbable, because, having other features, these species would most likely be removed by community. The time of coenophobes is replaced by the time of coenophiles.

Intense speciation in a coenophilic system existing in favorable environments continues until sharp changes in natural conditions begin, which may result in complete extinction of the ecosystem, providing free space for mobile coenophobic species coming from boundary regions.

The cycle is closed. The time of coenophobes comes again, which is then replaced by the time of coenophiles (Kovalev, 1994; Chernykh et al., 2007).

In the evolutionary process, coenophobes retain unstable state of genome and are capable of expansion into a new geographic range. However, in stable environments, under the control of ecological systems, species sometimes remain constant over unlimited time. From this point of view, it is possible to regard the evolution of ecosystems as a process of punctuated equilibrium, so that coenophilic stages, during which species with similar features increase in number, are possible to interpret as the time of stabilization or even stagnation, and stages of coenophobes, which come because of profound changes in climatic conditions and mark key alteration in the course of biological evolution (Chernykh et al., 2007).

This treatment of biological evolution implies that the history of establishment of new radiolarian species is history of coenophobes, because species surviving after global environmental changes only weakly depend on the ecosystem. Otherwise, they would become extinct along with species connected with them.

We pay particular attention to juvenile taxa and solitary population wave (Kovalev, 1994, 2004, 2007; Kovalev and Vechernin, 1986, 1989), division of species into coenophobes and coenophiles (Kovalev et al., 2007), and the model of biosphere evolution of Kovalev (1994) because they are directly connected with the character of radiolarian evolution as a whole and, in particular, the appearance in the Devonian basins of the radiolarian morphotype with two porous spheres and one main spine (Afanasieva and Amon, 2009b, 2009c, 2009e, 2009f).

APPEARANCE AND DISTRIBUTION OF DEVONIAN RADIOLARIANS WITH TWO POROUS SPHERES AND ONE MAIN SPINE

The development of radiolarians of the Phanerozoic abounds in various examples of rapid or instantaneous distribution of certain morphological structures among radiolarian communities inhabiting various, frequently remote areas of the World Ocean.

The appearance and distribution of radiolarians with two porous spheres and one main spine in the Devonian basins of the Ural Mountains, Russian Platform, Europe, Rudny Altai, China, Australia, and North America (Fig. 33) are a vivid example of a synchronous new formation and almost global distribution of this morphotype in conditions of a very warm climate of the Devonian.

It should be noted that morphological novelties of coenophobic species developed under conditions of a general stress of the Early Devonian, which is usually referred to as the geocratic epoch in the development of the Earth. According to the concept of solitary population waves of Kovalev–Vechernin (Kovalev and Vechernin, 1986, 1989; Kovalev, 2004, 2007), new coenophobic species expanded in the Devonian for large distances, reaching remote areas of the World Ocean.

The new data provide more detailed paleogeographic characteristics of sedimentation conditions in the Devonian Period, which abounded in geological events, display for the first time features of the establishment of radiolarians in the Early, Middle, and Late Devonian, and give some insight into the formation of Devonian radiolarian faunas.

Early Devonian

In the Early Devonian (Emsian Age), the speciation centers of radiolarians with two porous spheres and one main spine appeared synchronously during at most 5 m.y. in three remote regions: Japan, New South Wales of Australia, and the Southern Urals (Fig. 33).

In southwestern Japan, in the Kurosegawa Fold Belt, Umeda described ten Emsian radiolarian species and established one (Umeda, 1998b) and, then, three (Umeda, 2002) radiolarian zones: *Trilonche (?)* sp. *A* (Lower Emsian), *Glanta fragilis* (Middle Emsian), and *Protoholoeciscus hindea* (Upper Emsian). The species with two porous spheres and one main spine *Trilonche trifoliolata* Umeda was included in the list of Early Emsian radiolarians of the *Trilonche (?)* sp. *A* Zone (Fig. 33).

Middle Emsian radiolarians of eastern Australia were described for the first time by Aitchison and coauthors (Metcalfe et al., 1997; Stratford and Aitchison, 1997) from interbedding tuffogenic siliceous shale and limestones and clayey shale of the Gemilaroi terrane (New England Range, New South Wales). The radiolarian assemblage is characterized by 13 species, in which the species with two porous spheres and one main spine *Trilonche echinata*[19] appeared for the first time (Hinde, 1899a) (Fig. 33).

Late Emsian radiolarians were recorded for the first time and described by us (Afanasieva and Amon, 2008b) on the Southern Urals, in a section of Kamennaya Gora on the Tanalyk River near the town of Buribai, Bashkiria (Fig. 1). The Late Emsian radiolarian assemblage of the Southern Urals is represented by 20 species of 11 genera (Table 2), including spherical Sphaerellaria (*Astroentactinia, Bientactinosphaera, Entactinia, Radiobisphaera*) and Spumellaria (*Spongentactinia*), discoidal (*Palaeodiscaleksus, Primaritripus, Theodiscus, Trochodiscus*) and spindle-shaped (*Pseudospongoprunum*) Stauraxonaria, and spiny Aculearia (*Palacantholithus*) (Pls. 1, 2).

In the Early Devonian radiolarian assemblage, the species *Radiobisphaera rozanovi* Afanasieva et Amon pays is of particular importance; it is distinguished by the skeleton with two porous spheres and one massive, three-bladed, relatively short main spine (Fig. 33; Pl. 1, figs. 2, 3). Radiolarians with this structural type of the skeleton appeared for the first time in the Lower Devonian of the Southern Urals and are possibly ancestral to all radiolarians with two porous spheres and one main spine from the eastern Russian Platform and Rudny Altai (Fig. 33).

Middle Devonian

Eifelian Age. Late Eifelian radiolarians with two porous spheres and one main spine are presently known in two localities, in the Prague Basin (Budil, 1995a, 1995b; Čejchan, 1987, 2006; Braun and Budil, 1999; Afanasieva and Amon, 2009d) and Southern Urals (Afanasieva and Amon, 2009a).

We found Late Eifelian radiolarians in the Southern Urals in Bashkiria in a section on the southeastern slope of Karyukmas Mountain (Fig. 1) (Afanasieva and Amon, 2009a). The Upper Eifelian assemblage is represented by 17 radiolarian species of 11 genera (Table 2): discoidal Stauraxonaria (*Palaeodiscaleksus, Primaritripus, Theodiscus, Trochodiscus*), pylomate radiolarians of the order Pylomariata (*Hozmadia*), spiny Aculearia (*Palacantholithus*), and spherical

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[19] See Footnote 9.

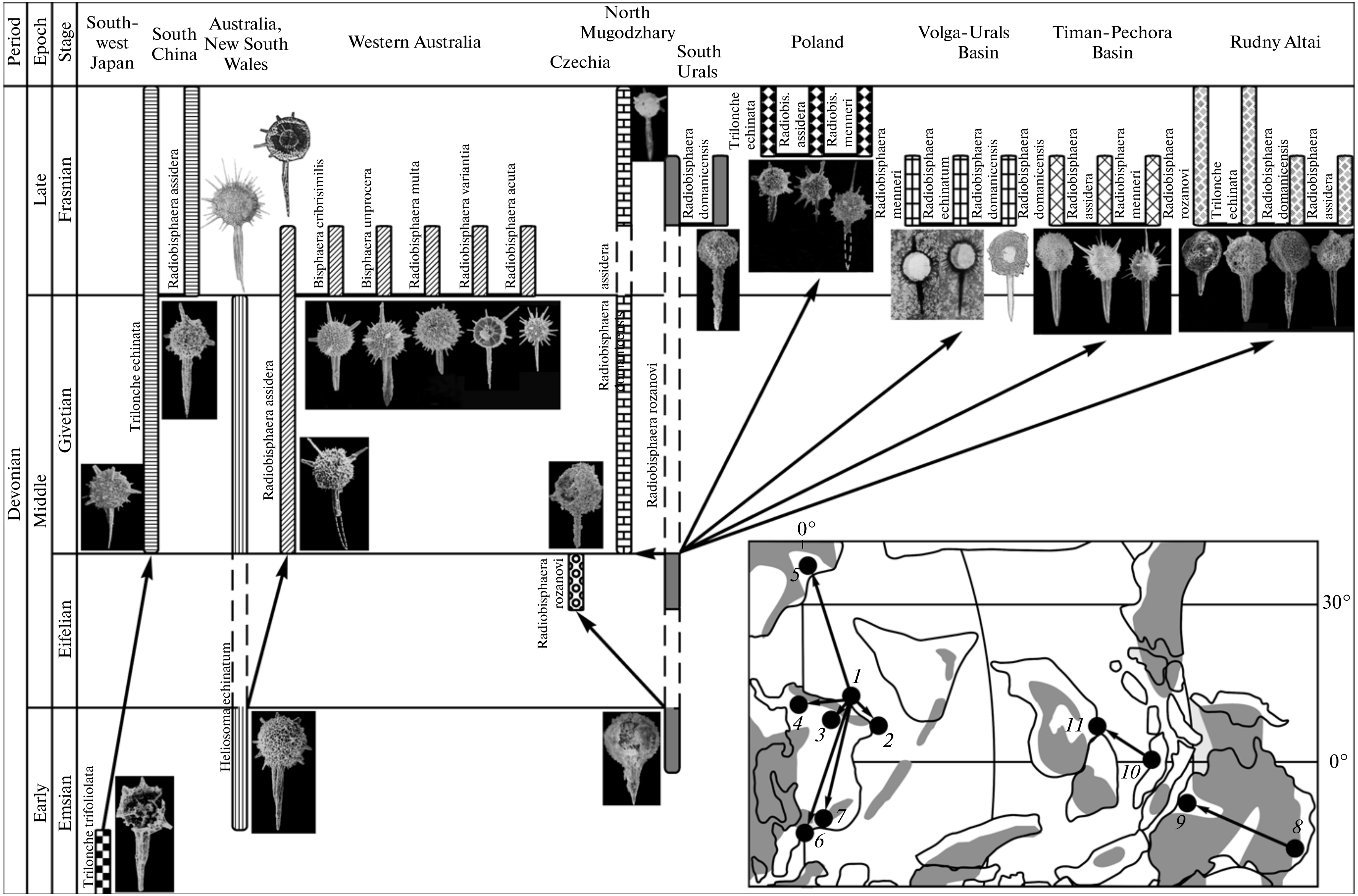

Fig. 33. Phylogeny of radiolarians with two porous spheres and one main spine. Radiolarian locality: (1) Southern Urals, (2) Northern Mugodzhary, western Kazakhstan, (3) Volga–Ural Province, (4) Timan–Pechora Basin, (5) Rudny Altai, (6) Czechia, (7) Poland, (8) New South Wales of Australia, (9) western Australia, (10) southwestern Japan, and (11) southern China. Arrows show directions of radiolarian expansion. Hatching show temporal distribution of radiolarians in various regions. Radiolarian localities are shown in the global reconstruction of continents and oceans for the Early Devonian (McKerrow and Scotese, 1990; Scotese, 1997).

Sphaerellaria (*Astroentactinia, Bientactinosphaera, Entactinia, Radiobisphaera*) and Spumellaria (*Spongentactinia*) (Pls. 3, 4). In this assemblage, radiolarians with two porous spheres and one main spine, *Radiobisphaera rozanovi* Afanasieva et Amon, are relatively abundant (Fig. 33; Pl. 3, figs. 3, 4).

Our new study of radiolarians from limestones of the Chotec Formation of the Prague Basin of Czechia (Fig. 7) has shown the presence of a diverse assemblage comprising 30 species of 13 genera (Table 4): spherical porous Sphaerellaria (*Astroentactinia, Bientactinosphaera, Entactinia, Radiobisphaera*), spherical spongy Spumellaria (*Pluristratoentactinia, Polyentactinia, Spongentactinella, Spongentactinia*), and spiny Aculearia (*Ceratoikiscum, Nazarovites, Palacantholitus, Palaeoscenidium, Palaeothalomnus*) (Pls. 5, 6). In this assemblage, the morphotype with two porous spheres and one main spine is revealed for the first time: *Radiobisphaera rozanovi* Afanasieva et Amon (Fig. 33; Pl. 5, fig. 13).

Givetian Age. In the Givetian Age, the geographic ranges of radiolarians with the skeleton type under consideration expanded, covering, on the one hand, Northern Mugodzhary and, on the other hand, western Australia and southern China (Fig. 33).

Nazarov (1975, 1988) recognized for the first time the *Spongentactinella windjanensis–Bientactinosphaera nigra* radiolarian assemblage in syngenetic lenticular limestone interbeds in jasper, siliceous, and siliceous–clayey units of the Shuldak Formation in the Zakir-Sai gorge of Western Mugodzhary. The assemblage includes 32 species of eight genera, among which the species *Entactinosphaera assidera*[20] Nazarov with two porous spheres and one main spine is of particular interest (Fig. 33; Pl. 7, fig. 7).

Nazarov dated this radiolarian assemblage based on co-occurrence of radiolarians with the conodonts *Polygnathus* ex gr. *pseudofoliatus* Witt. and *P.* aff. *linguiformis* (Hinde); therefore, siliceous rocks with limestone lenses of the Shuldak Formation were assigned to the Upper Eifelian–Givetian (Nazarov, 1988, 1989). At the same time, the analysis of geological data on the Southern Urals and Western Mugodzhary allows us to conclude that it is possible to restrict this assemblage to the Givetian (Afanasieva and Amon, 2009a).

At the end of the 19th century, Hinde (1899a) described a diverse (54 species) radiolarian association from the chert limestone lenses of the volcanogenic–siliceous Tamworth Series on the New England Fold Belt of New South Wales in Australia (Fig. 33) and dated it to the Devonian (in the broad sense). A century later, Aitchison (1988a, 1988b, 1990) and Aitchison and Stratford (1997) revised the data on the Gemilaroi Terrane of the New England Fold Belt and dated this radiolarian assemblage to the Givetian.

Among Givetian radiolarians of New South Wales, Hinde (1899a, p. 50, pl. IX, figs. 1, 2) found for the first time and described the radiolarian with two porous spheres and one main spine *Heliosoma echinatum* (Fig. 33).

Nazarov et al. (1982) established an analogue of the Givetian *Spongentactinella windjanensis–Bientactinosphaera nigra* assemblage at the base of a terrigenous–shale section with limestone interbeds of the Middle–Upper Devonian of Western Australia in the Canning Basin. In this locality, radiolarians with two porous spheres and one main spine, *Entactinosphaera assidera* Nazarov (Fig. 33; Pl. 7, fig. 7), appeared for the first time.

At the beginning of the 21st century, Givetian radiolarian assemblages were described in Guangxi (Luo et al., 2002) and Yunnan (Wang et al., 2003) provinces of China. Radiolarians of perfect preservation include forms with two porous spheres and one main spine, *Trilonche echinata* (Hinde) (Fig. 33).

Late Devonian

Frasnian Age

In the Early Frasnian, radiolarians with two porous spheres and one main spine occurred in southern China and were very diverse in western Australia (Fig. 33).

In southern China, this morphotype is represented in the Frasnian siliceous beds of Yunnan and Guangxi provinces by the species *Entactinosphaera assidera* Nazarov (Li and Wang, 1991) and *Trilonche echinata* (Hinde) (Wang et al., 2003) (Fig. 33).

In western Australia, in the Canning Basin, from the lower part of the Gogo Formation, which is represented by clayey–shale deposits with limestone interbeds, lenses, and nodules of the Frasnian Stage, Aitchison (1993) described mostly spiny radiolarians (57 species). Won (1997a, 1997b) described 84 species and subspecies of predominantly spherical radiolarians from the same beds.

Among rich and diverse associations of Early Frasnian radiolarians of western Australia, the species *Entactinosphaera assidera* Nazarov, 1975 continued to develop (Aitchison, 1993) and a burst of speciation and establishment of new radiolarian genera with two porous spheres and one main spine were marked: *Bisphaera*[21] *cribrisimilis* Won, *B. uniprocera* Won, *Radiobisphaera multa* Won, *R. varianta* Won, and *R. acuta* Won (Won, 1997a) (Fig. 33).

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[20] Hereinafter, we use the name *Entactinosphaera assidera*, because it is used in works of other researchers, although it should be noted that the analysis of morphological features of this species suggests to assign it to the genus *Radiobisphaera* Won, 1997 (Afanasieva, 2000).

[21] The generic name *Bisphaera* (Won, 1997a, p. 344) is preoccupied. The senior homonym is the genus *Bisphaera* Birina (Birina, 1948, p. 129), established for foraminifers from the boundary beds of the Devonian and Carboniferous of the Russian Platform; thus, the genus *Bisphaera* Won is a junior homonym. Therefore, according to the principle of homonymy (*International Code ...,* 1999, article 52.1), the generic name *Bisphaera* Won should be replaced.

In the Middle Frasnian the picture changed. In the Middle–Late Frasnian of Australia, radiolarians with two porous spheres and one main spine have not been recorded.

Morphological diversity of Middle Frasnian spherical radiolarians with one spine from the Southern Urals, Northern Mugodzhary, Volga–Ural Province, Rudny Altai, and, particularly, from the Domanik beds of the Timan–Pechora Basin considerably surpasses that of southern China, where the species *Entactinosphaera assidera* Nazarov and *Trilonche echinata* (Hinde) occur (Li and Wang, 1991; Wang et al., 2003) (Fig. 33).

Among Middle Frasnian radiolarians of Northern Mugodzhary, representatives of *Entactinosphaera assidera* Nazarov still exist (Nazarov, 1975, 1988) (Fig. 33).

On the southern slope of Argagan Mountain in the Southern Urals, Bashkiria (near the village of Sultantemirovo, south of the town of Baimak), we discovered a new Middle Frasnian radiolarian locality (Afanasieva and Amon, 2009a). The radiolarian assemblage of the Middle Frasnian of the Southern Urals consists of 13 species of eight genera of spherical porous Sphaerellaria (*Astroentactinia, Bientactinosphaera, Radiobisphaera*), discoidal Stauraxonaria (*Palaeodiscaleksus, Primaritripus, Trochodiscus*), and spiny Aculearia (*Palacantholithus*). The morphotype with two porous spheres and one main spine is of particular importance; it is observed in *Radiobisphaera domanicensis* (Bykova) and *R. rozanovi* Afanasieva et Amon (Fig. 33; Pl. 14, figs. 1, 5).

The first Middle Frasnian radiolarians of the Volga–Ural Basin were described by Bykova (1955) in thin sections of siliceous–carbonate rocks of the Domanik Formation of Tatarstan, Bashkortostan, and the western slope of the Ural Mountains (Fig. 13). Among Domanik radiolarians, Bykova established for the first time two radiolarian species with two porous spheres and one main spine: *Dorysphaera domanicensis* Bykova and *Xiphosphaera echinatum* (Hinde). The analysis of morphological features of these species suggests that they belong to the genus *Radiobisphaera* Won, and some representatives of the species *Xiphosphaera echinatum* (Bykova, 1955, pl. XXII, fig. 4) are assigned to the species *Radiobisphaera menneri* Afanasieva (Afanasieva, 2000a) (Figs. 17k–17m).

However, the richest localities of Middle Frasnian radiolarians are known in Russia from the deposits of the Timan–Pechora Basin and Rudny Altai.

The Domanik stratotype in the southern Timan–Pechora Basin is of particular interest. Here, radiolarians are literally conserved in carbonate nodules among siliceous differences of rocks (Afanasieva, 1997a, 2000a; Afanasieva and Mikhailova, 1998, 2001). The Middle Frasnian radiolarian assemblage of the Timan–Pechora Basin displays an extremely high diversity, including 127 species of 35 genera (Table 7), among which there are three radiolarian species with two porous spheres and one main spine: *Radiobisphaera domanicensis* (Bykova), *R. assidera* (Nazarov), and *R. menneri* Afanasieva (Fig. 33; Pl. 10, fig. 7; Pl. 12, figs. 16–18).

Morphological diversity of radiolarians from the Middle Frasnian of the Rudny Altai (Fig. 22) includes 39 species of 16 genera of spherical, discoidal, and spiny forms (Afanasieva et al., 2008, 2009). The radiolarian taxa recorded are similar to radiolarians from the Domanik assemblage of the Middle Frasnian of the Timan–Pechora Basin. Radiolarians of the Rudny Altai include three species with two porous spheres and one main spine (Fig. 33): *Radiobisphaera domanicensis* (Bykova), *R. assidera* (Nazarov), and *R. rozanovi* Afanasieva et Amon (Pl. 29, figs. 6–8).

Obut et al. (2007) recorded a less diverse radiolarian assemblage in a Middle Frasnian section near the village of Gornyak of the Rudny Altai (Fig. 22); it includes a species with two porous spheres and one main spine, *Trilonche echinata* (Hinde) (Fig. 33).

In the Late Frasnian of Guangxi Province of southern China (Li and Wang, 1991) and Northern Mugodzhary (Nazarov, 1975, 1988), the latest Late Frasnian representatives of *Entactinosphaera assidera* Nazarov have been recorded; in Yunnan and Guangxi provinces of southern China (Wang et al., 2003), *Trilonche echinata* (Hinde) continued development (Fig. 33).

In the Rudny Altai (Fig. 22, d-442), we have recorded morphological diversity of Late Frasnian radiolarians (Afanasieva et al., 2008, 2009), represented by 12 species of six genera, including one radiolarian species with two porous spheres and one main spine, *Radiobisphaera rozanovi* Afanasieva et Amon (Fig. 33; Pl. 29, fig. 7).

Obut et al. (2007) studied radiolarians from the Upper Frasnian of the Rudny Altai positioned higher in the section and revealed a more diverse radiolarian assemblage, which includes one species with two porous spheres and one main spine, *Trilonche echinata* (Hinde) (Fig. 33).

At the Frasnian–Famennian boundary, the taxonomic composition of radiolarians essentially changed (Afanasieva et al., 2005d; Afanasieva and Amon, 2006a, 2006b). In sections of the Rudny Altai (Obut and Iwata, 2005) and central Poland (Vishnevskaya et al., 1997, 2002), the transition from the Upper Frasnian to the Lower Famennian is characterized by an intricate mixture of Frasnian and Famennian elements.

In the Holy Cross Mountains of central Poland, at the Frasnian–Famennian boundary (*linguiformis*–*crepida* conodont zones), many radiolarians (34 species 12 genera) have been recorded (Vishnevskaya et al., 1997, 2002; Racki, 1999). Morphological diversity of the morphotype considered in central Poland is relatively wide and represented by three species (Vish-

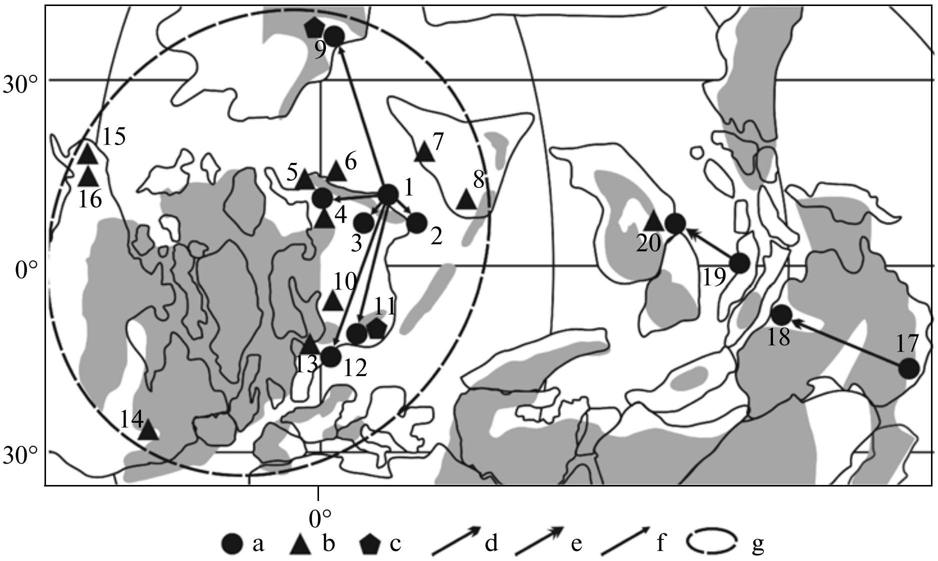

Fig. 34. Expansion waves of radiolarians with two porous spheres and one main spine. Designations: (a–c) radiolarian localities: (a) Emsian–Frasnian deposits; (b) sections of the Famennian Stage; (c) Frasnian–Famennian boundary beds; (d–g) waves of radiolarian expansion: (d) first wave, (e) second wave, (f) third wave, and (g) fourth wave: (1) Southern Urals, (2) Northern Mugodzhary, western Kazakhstan, (3) Volga–Ural Province, (4) Timan–Pechora Basin, (5) Polar Urals, (6) Northern Urals, (7) eastern slope of the Middle Urals, (8) eastern Kazakhstan, Chara Zone, (9) Rudny Altai, (10) Belarus, Pripyat Depression, (11) Poland, (12) Czechia, (13) Germany, (14) United States, Ohio, Lake Erie, (15) central Alaska, (16) eastern Alaska, (17) New South Wales of Australia, (18) western Australia, (19) southwestern Japan, and (20) southern China. Radiolarian localities are mapped in the global reconstruction of continents and oceans for the Early Devonian (after McKerrow and Scotese, 1990; Scotese, 1997).

nevskaya et al., 1997, 2002b): *Trilonche echinata* (Hinde), *Radiobisphaera menneri* Afanasieva, and *R. assidera* (Nazarov) (Fig. 33).

Famennian Age. The history of Famennian radiolarians is characterized by a decrease in morphological diversity of radiolarians with two porous spheres and one main spine. In the Famennian of Yunnan and Guangxi provinces of southern China, this morphotype is only described in one species, *Trilonche echinata* (Wang et al., 2003).

An Early Famennian radiolarian assemblage containing 27 species of 16 genera was investigated by Afanasieva (2000a) from siliceous–carbonate rocks of the Saremboi–Lekkeyaga Swell of the northeastern part of the Timan–Pechora Basin (Fig. 6; Table 7). Early Famennian radiolarians of the northeastern Timan–Pechora Basin, one species of the morphotype considered has been recorded, *Radiobisphaera rozanovi* Afanasieva et Amon (Pl. 24, fig. 12).

We investigated a very rich and diverse association of Early Famennian radiolarians from the Lemvin Zone of the Polar Urals (Fig. 6). In Early Famennian radiolarians of the Polar Urals, this morphotype is represented by the species *Radiobisphaera assidera* (Nazarov), *R. domanicensis* (Bykova) (Pl. 25, figs. 14, 16), and *Radiobisphaera rozanovi* Afanasieva et Amon (Pl. 25, fig. 17). In addition, a new species with the morphotype considered have been recorded, *Radiobisphaera palimbola* (Foreman)[22] (Pl. 25, fig. 18).

The radiolarian assemblage from the Famennian part of the Kowala section in central Poland (Vishnevskaya et al., 1997, 2002; Racki, 1999) is characterized by the absence of spiny forms and abundant spherical species, including *Radiobisphaera palimbola*[23] (Foreman).

Apparently, a new expansion of the geographic range of radiolarians with two porous spheres and one main spine began from the Polar Urals. Members of the species *Radiobisphaera palimbola* are recorded in the following beds (Fig. 34):

(1) flinty slates of the Lemvin Zone of the Polar Urals (Nazarov, 1988; Afanasieva, 2000a; this work);

(2) upper part of the section in a member of interbedding siliceous–clayey shale, siltstones, and limestones on the Unya River in the Evtropiny Noski locality of the Malaya Pechora allochthon on the western slope of the Northern Urals (Nazarov, 1988);

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[22] The species *Radiobisphaera palimbola* was originally described by Foreman and assigned to the genus *Entactinosphaera* (Foreman, 1963, pp. 277–278); however, judging from morphological features, it should be transferred to the genus *Radiobisphaera* Won (1997a, p. 351); see revision of the genus *Entactinosphaera* in Chapter 6.

[23] See Footnote 22.

(3) siliceous–aleurolitic beds on the Gryaznukha River, near Razdol'naya Hill of the Gornyi Altai (Obut and Iwata, 2005; Afanasieva et al., 2008, 2009);

(4) Rezh Structural–Facies Zone of the eastern slope of the Middle Urals (Amon and Korovko, 1992; Amon, 1995);

(5) ophiolitic formations of the Chara Zone of eastern Kazakhstan (Nazarov, 1988, 1989; Iwata et al., 1994, 1997);

(6) argillaceous clays, with interbeds of gray limestone and in marls of the Elets Formation of the Pripyat Depression of Belarus (Kruchek and Nazarov, 1977; Nazarov, 1988);

(7) carbonate strata with interbeds of cherts of the reference section of Kowala in the Holy Cross Mountains of central Poland (Vishnevskaya et al., 1997, 2002; Racki, 1999);

(8) flinty slates of Frankenwald in Germany (Schmidt-Effing, 1988);

(9) Ohio, North America, wherefrom the species *Radiobisphaera palimbola* was described for the first time by Foreman (1963) from carbonate nodules of the Huron Member;

(10) eastern Alaska, in the lower part of black layered siliceous shale of the Ford Lake Shale Formation, which outcrops on the northern bank of the Yukon River (Holdsworth et al., 1978);

(11) Chulitna Terrane in the southern central Alaska (Won et al., 1999).

SCENARIO OF EXPANSION OF RADIOLARIANS WITH TWO POROUS SPHERES AND ONE MAIN SPINE

Our studies allowed us to trace throughout the Devonian Period dynamics of appearance, flourishing, and extinction of the new radiolarian morphotype with two porous spheres and one main spine as a result of adaptation to new conditions of general climatic warming after global changes in environments at the Silurian–Devonian boundary (Afanasieva and Amon, 2009b, 2009c, 2009d, 2009e, 2010a).

Late Silurian glaciation, regression of the sea at the end of the Silurian, which reached a maximum in the Early Devonian, and a long geocratic epoch in the Late Silurian and Early Devonian resulted in almost complete disappearance of 88.9% of Early Paleozoic radiolarian species.

Therefore, it is possible to name the initial stage of almost simultaneous appearance in the Emsian Age in Japan, New South Wales of Australia, and the Southern Urals of the new morphotype of radiolarians as the time of coenophobes. Radiolarians of that time had a propensity for inhabiting relatively shallow and quiet waters of marginal continental areas.

Ascending tectonic movements were replaced in the Middle Devonian in many regions of the world by gradual immersion of continents; as a result, a new sea transgression on the platforms began. In connection with progressing transgressions on a background of an increase in mildness and humidity of the climate, species of the morphotype considered, which at the initial stage of existence were *coenophobes*, underwent gradual *coenophilization*.

In contrast to the Early Devonian epoch, the Frasnian Age of the Late Devonian was the time of wide development of marine transgressions and prevailing dominance of the sea over land. Frasnian radiolarians almost everywhere developed in marine conditions of equatorial and tropical paleobelts. In the Frasnian Age, the time of coenophiles began; it was marked by flourishing and explosive speciation and formation of new genera of the radiolarian morphotype considered in the Early Frasnian of western Australia and in the Middle Frasnian of the Timan–Pechora Basin and Rudny Altai.

The Famennian was marked by the beginning of a new transgression–regression cycle of sedimentation. In contrast to the Frasnian, the Famennian Age was characterized by uplifts of continents and, hence, regressions of the sea on a background of fall in temperature (Tikhii, 1975; Berner and Kothavala, 2001). In the Famennian Age, the time of coenophobes returned; it was accompanied, on the one hand, by a decrease in morphological diversity of radiolarians with two porous spheres and one main spine, which are represented in all localities by only one species, and, on the other hand, by the appearance of a new species, *Radiobisphaera palimbola*,[24] and wide expansion of its geographic range.

The analysis of Devonian distribution of the radiolarian morphotype considered shows that invasion of species into a new ecological system occurred according to the model of the formation of *solitary population waves* of Kovalev–Vechernin (Kovalev and Vechernin, 1986, 1989). It has been shown that, during invasion and adaptation of species to new conditions, struggle for existence between *coenophobic* and *coenophilic* species occurs. Four solitary population waves are established and the scenario of expansion of radiolarians with two porous spheres and one main spine is developed (Afanasieva and Amon, 2009b, 2009e, 2009f) (Fig. 34).

The First Population Wave

he first population wave arose in the Early Emsian of Japan, beginning from the appearance of the juvenile coenophobic species *Trilonche trifoliolata* and attenuating in the Famennian of southern China (Fig. 34).

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[24] See Footnote 22.

The Second Population Wave

The second, parallel, but somewhat delayed population wave began in the Middle Emsian in New South Wales of Australia with the appearance of a new juvenile coenophobic species, *Heliosoma echinatum*[25] and was accompanied by an abrupt increase in abundance, speciation and appearance of new genera in the Early Frasnian in western Australia (Fig. 34).

The Third Population Wave

The third most intense population wave arose in the Late Emsian of the Southern Urals, beginning from the appearance of the juvenile coenophobic species *Radiobisphaera rozanovi*. This wave is characterized by the radial distribution of the new morphotype in the Late Eifelian in the Prague Basin, in the Givetian of Northern Mugodzhary, and in the Middle Frasnian on the Rudny Altai, and in the Volga–Ural and Timan–Pechora basins (Fig. 34). In this case, the burst of speciation is marked in the Middle Frasnian of the Rudny Altai and, particularly, in the Domanik beds of the Timan–Pechora Basin. In the Late Frasnian of southern China and Rudny Altai, radiolarians with one spine are represented by two species; in central Poland, by three species; and in Northern Mugodzhary, one species of this morphotype.

In the Famennian Age, the third population wave attenuated: in the Famennian of southern China, only one species of this morphotype has been recorded (Wang et al., 2003); in the Early Famennian of the Timan–Pechora Basin, the last representatives of the species *Radiobisphaera domanicensis* and *R. rozanovi* occurred; the ancestors of the last species appeared in the Early Devonian of the Southern Urals.

The Fourth Population Wave

The fourth population wave arose in the Early Famennian of the Polar Urals, beginning from the appearance of a juvenile coenophobic species, *Radiobisphaera palimbola*.[26] This wave reflects profound changes in the taxonomic composition of radiolarians at the Frasnian–Famennian boundary in connection with the onset of a fall in temperature (Afanasieva et al., 2005d; Afanasieva and Amon, 2006a, 2006b). In transitional deposits of the Rudny Altai (Obut et al., 2007) and central Poland (Vishnevskaya et al., 1997, 2002), radiolarians of the third and fourth waves of distribution of the morphotype with two porous spheres and one main spine co-occur.

The fourth wave displayed radial expansion of the geographic range of this morphotype, directed to the northeast (eastern slope of the Middle Urals, Northern Urals, Polar Urals, Rudny Altai, and the Chara Zone of eastern Kazakhstan), south (Pripyat Depression of Belarus, Poland, and Germany), southwest (Ohio, United States), and northwest (central and eastern Alaska) (Fig. 34).

The features of appearance and distribution of radiolarians with two porous spheres and one main spine in the Devonian basins of the World Ocean provide a vivid example of the synchronous formation and effect of wave distribution of a new morphotype in conditions of a warm Devonian climate. This wave distribution of morphological novelties and dynamics of biological burst in the zone of invasion, which showed the hyperbolic growth of population, provide a perfect means for paleoecological reconstruction and improvement of local and regional stratigraphical schemes.

MIGRATION FLOWS OF EARLY FAMENNIAN RADIOLARIANS IN BASINS OF EURAMERICA

The Early Famennian phase in the developmental history of radiolarians of Euramerica requires closer consideration in more detail. The reconstruction of Early Famennian paleobiogeography of radiolarians allows us (1) to reveal the centers of origin of regional radiolarian faunas and direction of their migrations, (2) to reconstruct directions of the major migration pathways, and (3) to gain an understanding of causes of certain trends and patterns of distribution of morphotypes in space and time.

After a break in sedimentation at the Frasnian–Famennian boundary, the Ural Paleocean penetrated again into the Russian Platform, particularly, in its central and northern areas, marking the beginning of a new transgression–regression cycle of sedimentation. Famennian radiolarians still preferred relatively shallow waters not far from continental land, i.e., neighboring areas of Ancient Russian Continent and island arches.

Early Famennian radiolarians were described by Bykova (1955) in the Southern Urals and Volga–Ural Province; Chuvashov (1968) recorded them in the Kama Region and on the western Urals; Nazarov (Kruchek and Nazarov, 1977) investigated them in the Pripyat Depression; and Bykova (1955) and Nazarov (1988), in the Northern and Polar Urals; Amon (Amon and Korovko, 1992; Amon, 1995), on the eastern slope of the Middle Urals; and Afanasieva (2000a), on the Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin (Fig. 35). We investigated new assemblages of Early Famennian radiolarians in the Polar Urals and on the western slope of the Middle Urals (Vilva River) (Figs. 6, 35).

Beyond the Urals and Russian Platform, Early Famennian radiolarians of the peripheral and epicontinental seas of Euramerica are known in Poland (Vishnevskaya et al., 1997, 2002), Germany (Schmidt-Effing, 1988; Braun et al., 1992; Kiessling and Tragelehn, 1994), the United States in eastern

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[25] See Footnote 9.

[26] See Footnote 22.

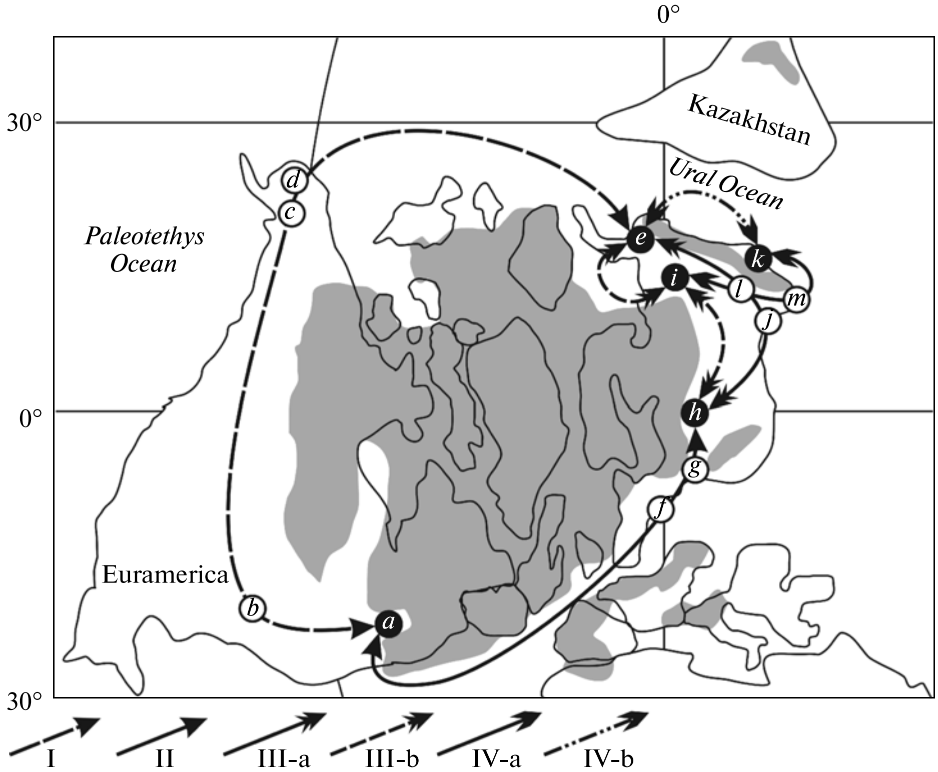

Fig. 35. Migration flows of radiolarians in the Early Famennian basins of Euramerica. (*a*) United States, Ohio, Lake Erie, (*b*) United States, Oklahoma, (*c*) central Alaska, (*d*) eastern Alaska, (*e*) Polar Urals, Lemvin Zone, (*f*) Germany, (*g*) Poland, (*h*) Belarus, Pripyat Depression, (*i*) Timan–Pechora Basin, Saremboi–Lekkeyaga Swell, (*j*) Kazakhstan, Caspian Depression, northern slope, (*k*) Middle Urals, western slope, Vilva River, (*l*) Volga–Ural Basin, and (*m*) Southern Urals. Designations: (I) northwestern flow; (II) southern flow; (III) eastern flow: (III-a) eastern stream, (III-b) western stream; (IV) northeastern flow: (IV-a) southern stream, and (IV-b) northern stream. Radiolarian localities are mapped in the global reconstruction of continents and oceans for the Late Devonian (after McKerrow and Scotese, 1990; Scotese, 1997).

(Holdsworth et. al., 1978; Holdsworth and Jones, 1980a, 1980b) and central Alaska (Won et al, 1999), Ohio (Foreman, 1959, 1963) and Oklahoma (Schwartzapfel and Holdsworth, 1996) (Fig. 35).

Early Famennian radiolarians of Euramerica are represented by 120 species of 41 genus (Table 7). The analysis of the taxonomic composition of five regional radiolarian associations of the Early Famennian has shown the following ratios of species and genera (Table 7; Fig. 36):

- United States, Ohio, Lake Erie (Fig. 35a): 58 species of 24 genera;
- Polar Urals, Palnik-Yu River (Fig. 35e): 53 species of 26 genera;
- Pripyat Depression (Fig. 35h): 43 species of 22 genera;
- Timan–Pechora Basin, Saremboi–Lekkeyaga Swell (Fig. 35i): 28 species of 16 genera;
- Middle Urals, Vilva River (Fig. 35k): six species of three genera.

The comparison on the species and generic compositions of these associations (Table 7) shows high relative frequency of the basic core of associations, about 39.0–63.4% of genera and 23.3–48.3% of species and regular migrations of taxa (Fig. 35) (Afanasieva and Amon, 2010c, 2010f, 2010g).

The migration patterns allowed us to establish four migration streams of radiolarians in the Early Famennian (Afanasieva and Amon, 2010g): Northwestern (North America, Lake Erie ⇄ Polar Urals), Southern (North America, Lake Erie ⇄ Pripyat Depression), Eastern (Pripyat Depression ⇄ Polar Urals) and Northeastern (Polar Urals ⇄ Middle Urals) (Fig. 35).

Northwestern migration stream (North America, Lake Erie ⇄ Polar Urals) brought from Lake Erie in Ohio through Oklahoma and Alaska to the basin of the Polar Urals (Fig. 35, I) and back 16 shared radiolarian species (Tables 7, 13).

Southern migration stream (North America, Lake Erie ⇄ Pripyat Depression) brought from Lake Erie of Ohio through Germany and Poland to the basin of the Pripyat Depression and back (Fig. 35, II) 20 common radiolarian species (Tables 7, 13).

Eastern migration stream (Pripyat Depression ⇄ Polar Urals), passing to the north from the Pripyat

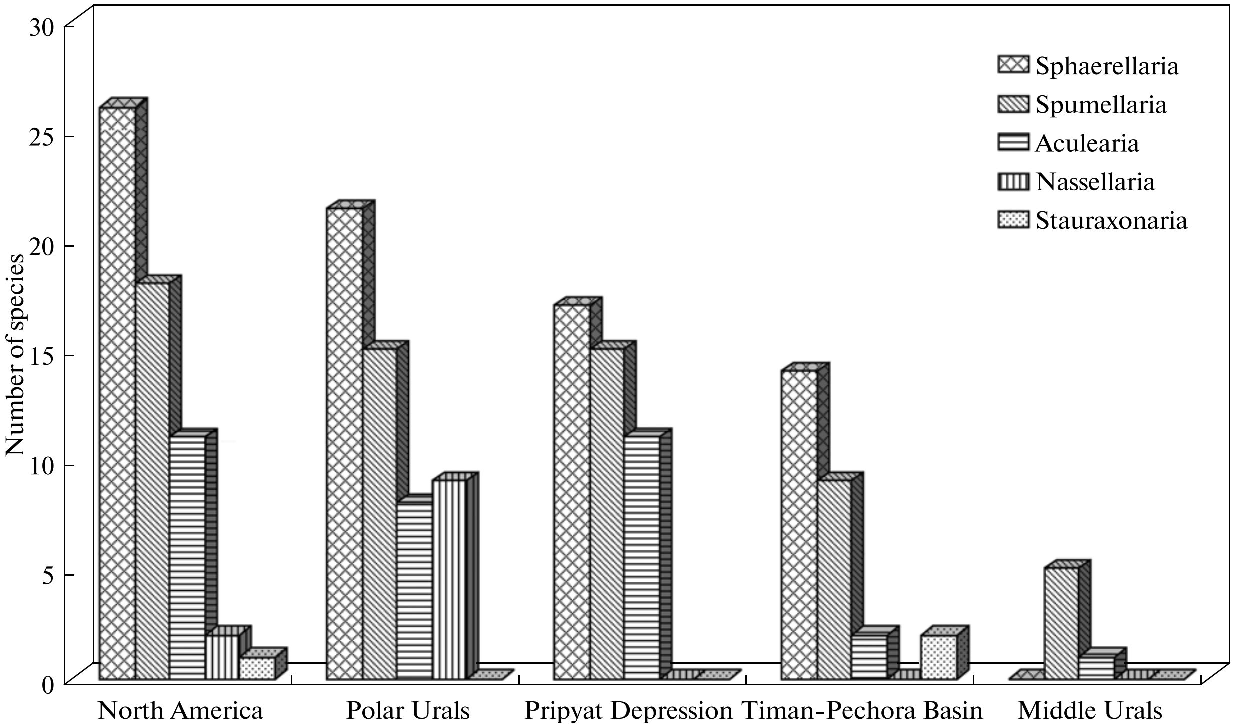

Fig. 36. Ratio of classes in Early Famennian radiolarian assemblages of North America, Pripyat Depression, Timan–Pechora Basin, Polar and Middle Urals.

Depression in the basin of the Polar Urals, was divided into two flows, eastern and western (Fig. 35, III-a, III-b).

Eastern flow (Fig. 35, III-a) brought from the Pripyat Depression through the Northern Caspian Region and Volga–Ural Basin to the basin of the Polar Urals and back 17 radiolarian species (Tables 7, 13).

Western flow (Fig. 35, III-b) brought from the Pripyat Depression to the Timan–Pechora Basin and back only nine radiolarian species; this was probably caused by the complexity of transit of species through relatively shallow water areas, with many low islands, in the central Russian Platform. At the same time, northerly, between the epicontinental Timan–Pechora Basin and a relatively deepwater area of the Polar Urals, exchange involved 16 radiolarian species (Tables 7, 13).

Northeastern migration stream (Polar Urals ⇄ Middle Urals) is divided into two flows: southern and northern (Fig. 35, IV-a, IV-b).

Southern flow (Fig. 35, IV-a) brought from the Timan–Pechora Basin through the Volga–Ural Basin and Southern Urals to the waters of the Middle Urals and back four Frasnian radiolarian species: *Haplentactinia alekseevi* Afanasieva, *Haplentactinia rhinophyusa* Foreman, *Polyentactinia circumretia* Nazarov et Ormiston, and *Palaeothalomnus arrhinia* (Foreman) (Tables 7, 13).

Northern flow (Fig. 35, IV-b) brought from the basin of the Polar Urals to western water areas of the Middle Urals and back only two tracery latticed species, *Haplentactinia rhinophyusa* Foreman and *H. kuzminae* Afanasieva et Amon, sp. nov. and one spiny species, *Palaeothalomnus arrhinia* (Foreman). The homogeneous taxonomic composition (six species of three genera) of radiolarians of the Middle Urals suggests that the association was probably formed in conditions of the open Ural Ocean (Tables 7, 13).

The analysis of the taxonomic composition of radiolarian assemblages of the Early Famennian of Euramerica and patterns of their migration has revealed three interesting laws.

First, all Early Famennian radiolarian associations are dominated by representatives of the class Spumellaria, which form about one-third of the total species number of assemblages, i.e.,

- 31% in the United States, Ohio, Lake Erie (Fig. 35a);
- 28.3% in the Polar Urals, Palnik-Yu River (Fig. 35e);
- 34.9% in the Pripyat Depression (Fig. 35h);
- 33.3% in the Timan–Pechora Basin, Saremboi–Lekkeyaga Swell (Fig. 35i);
- 83.3% in the Middle Urals, Vilva River (Fig. 35k).

Second, there is a distinct trend of increasing taxonomic diversity of Spumellaria in the ancient northeastern direction, from the marginal epicontinental paleo-

Table 13. Number of species shared in Early Famennian radiolarian assemblages of Euramerica

North America, USA, Ohio, Erie Lake 58 species ↓	20 species (46.5%)	6 species (22.2%)	16 species (30.2%)	1 species (16.7%)
20 species (34.5%)	↑ **Russian Platform, Pripyat Depression 43 species** ↓	9 species (33.3%)	17 species (32.1%)	1 species (16.7%)
6 species (10.3%)	9 species (20.9%)	↑ **Russian Platform, Timan-Pechora Basin, Saremboy-Lekkeyaga Swell 28 species** ↓	17 species (32.1%)	–
16 species (27.6 %)	17 species (39.6%)	17 species (60.7%)	↑ **Polar Urals, Lemvin Zone, Palnik-Yu River 53 species** ↓	3 species (50.0%)
1 species (1.7 %)	1 species (2.3%)	–	3 species (5.6%)	↑ **Middle Urals, west side Vilva River 6 species**

seas of Euramerica to the open water areas of the Ural Ocean (Fig. 35): 31% of species in North America (Lake Erie) ⟶ 34.9% in the Pripyat Depression ⟶ 33.3% in the Timan–Pechora Basin ⟶ 28.3% in the Polar Urals ⟶ 83.3% in the Middle Urals.

The introduction and dominant development of the mobile Frasnian coenophobic species *Haplentactinia alekseevi* Afanasieva from the Timan–Pechora Basin in the water area of the Middle Urals probably caused the appearance and flourishing of the juvenile endemic coenophilic species *Haplentactinia vilvaensis* Afanasieva et Amon, sp. nov. The biological burst in the zone of invasion of tracery latticed radiolarians (up to 83.3%) in the Early Famennian of the Middle Urals is another vivid example of the effect of wave distribution of a new morphotype in conditions of a warm climate of the Devonian.

Third, the distribution of radiolarians with pylome and pseudo-pylome shows the following trends:

(1) The Southern migration stream (Fig. 35, II) brought from North America to Germany (Fig. 35f) only one genus with pylome, *Archocyrtium*, and unusual spiny *Holoeciscus*, which is characterized by the formation of a pseudo-pylome. Further, in paleonorthern direction, in Poland, the Pripyat Depression, and Timan–Pechora Basin (Figs. 34g–34i), this morphotypes are absent.

(2) The Northwestern migration stream (Fig. 35, I) brought in the basin of the Polar Urals (Fig. 35e) nine species of six radiolarian genera with pylome (*Archocyrtium, Caspiaza, Cyrtisphaeractenium, Cyrtisphaeronemium, Pylentonema, Robotium*) and three unusual spiny *Holoeciscus*. Of them members of two genera (*Caspiaza* and *Holoeciscus*) passed further in the basin of the northern Caspian Region (Fig. 35j), following the Eastern flow of the eastern migration stream (Fig. 35, III-a). Later, in the Early Carboniferous, descendants of *Caspiaza* expanded their range and occurred in the northern Caspian Region and Tien Shan (Fig. 31) (Afanasieva, 1986, 1993, 2000a).

CHAPTER 6. CLASSIFICATION OF RADIOLARIANS AND ITS QUESTIONS

Two approaches to the classification of Paleozoic radiolarians at the generic and family levels are presently developed; they are named here *eastern* and *western* schools.

The eastern school is implemented in works of Japanese and Chinese researchers; its principles were applied for the first time in works of Aitchison, involving Australia material (Aitchison, 1988a, 1988b, 1993; Aitchison et al., 1999; Aitchison and Stratford, 1997; Stratford and Aitchison, 1997). In his works, the taxonomy of radiolarian genera and families follows the scheme of Hinde (1890, 1899a, 1899b) developed at the end of the 19th century. In turn, Hinde mostly followed the classification of radiolarians developed Haeckel (1862, 1887). Thus, the eastern school is based on an out-of-date and inexact system (Paverd, 1995; Baumgartner et al., 1995; De Wever et al., 2001; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a).

The western school originates from works of Deflandre (1952, 1953), Foreman (1963), and Holdsworth (1966). It was supported by studies of Ormiston and Lane (1973) and Nazarov (1973, 1974, 1975, 1981a, 1984, 1988, 1989) and, particularly, joint research of Nazarov and Ormiston (1983a, 1983b, 1984, 1985, 1986, 1993). This approach was rather productively used in works of Kozur and Mostler (1981, 1989), Won (1983, 1990, 1997a, 1997b, 1998), Afanasieva (1986, 1993, 1997b, 1999, 2000a, 2000b, 2002), Amon (1999b, 1999c), and Afanasieva and Amon (2003, 2006a) and many other researchers, who formed the basis of the systematics of Paleozoic radiolarians. The western school is characterized by complete abandonment of the conceptual and terminological foundation of the Haeckel's system and development of radiolarian classification on essentially new basis, attaching particular significance to the structure and evolution of radiolarian skeletons (Afanasieva et al., 2004a, 2004b).

Within the framework of the eastern school, Aitchison and Stratford (1997) proposed to take the genus *Entactinia* Foreman, 1963 for a junior synonym of the genus *Stigmosphaerostylus* Rüst, 1892 and the genus *Entactinosphaera* Foreman, 1963 for a junior synonym of *Trilonche* Hinde, 1899. However, the skeletal morphology of members of these genera suggests that they belong to different families and even different classes (Afanasieva and Amon, 2008a; Afanasieva, 2011).

An example of eclectic classification schemes is the study of Noble et al. (2008) devoted to Tournaisian radiolarians of Turkey, which combined the genera *Astroentactinia, Meschedea, Polyentactinia* according to the western school of radiolarian classification and *Trilonche* and *Stigmosphaerostylus*, according to the eastern school. In doing so, well known and well founded species were revised and referred to other genera; in particular, the species *Polyentactinia tortispina* Ormiston et Lane, 1976 was transferred to the genus *Stigmosphaerostylus*, the species *Entactinia vulgaris* Won, 1983 was transferred to the genus *Stigmosphaerostylus*, and the species *Entactinosphaera palimbola* Foreman, 1963 was referred to the genus *Trilonche*. This was stated virtually without comment.

Exercises of this kind are not harmless, as could have been thought at first glance. The redetermination of known genera and species in favor of certain theoretical views entail partial or complete changes in the generic and species composition of regional radiolarian faunas. This has undoubted negative effect on correlation potential of stratigraphically significant assemblages and on the reconstruction of paleobiogeographic links between water areas and particular provinces of the World Ocean. Ungrounded redetermination disturbs the picture of general biodiversity of radiolarians in particular epochs of historical development of the group, underestimating (rarely) or overestimating (more frequently) the number of taxa.

A rational question at this point is whether or not it is possible to bridge the gap between the two different schools? The answer seems negative, because "Oh, East is East, and West is West, and never the twain shall meet ..." (Rudyard Kipling).[27] Attempts at compilation, mechanical association, and mixing fragments of the classification schemes developed in traditions of eastern and western schools have recently been undertaken (Vishnevskaya, 2001; Vishnevskaya et al., 2002; Sennikov et al., 2002, 2007; Umeda et al., 2004; Obut and Iwata, 2005; Obut, 2006; Obut et al., 2005, 2007), although no good comes of it.

Each analytical work devoted to either paleobiogeography of radiolarians or estimation of diversity should include an initial stage based on the revision of faunas and removal of synonyms. This was clearly indicated by Kiessling (2002) in work devoted to biodiversity and radiolarian provinces of boundary epochs of the Jurassic and Cretaceous. He emphasized that, prior to the creation of an adequate species database, he had to balance between three concepts of species accepted in different schools: (1) North American (Pessagno et al., 1986, 1987, 1989); (2) Tethyan (Baumgartner et al., 1995; Dumitrica et al., 1997), and (3) Antarctic (Kiessling et al., 1999). As a result, after removal of synonyms from the initial list of 865 species, the group of 427 species was taken for data processing.

The analysis of diversity of Phanerozoic radiolarians based on the database compiled by Agarkov, taking into account synonyms, has shown the following dynamics of generic diversity: Cambrian, 22; Ordovician, 35; Silurian, 33; Devonian, 73; Carboniferous, 59; Permian, 46; Triassic, 227; Jurassic, 286; Cretaceous, 281; Paleogene, 280; Neogene, 199; Quaternary (without Holocene), 72 (Agarkov, 2000; Afanasieva et al., 2005a, 2005d; Afanasieva and Amon, 2006a, 2006b).

In September, 2009, at the final session of INTERRAD-12 in China, the Catalogue of Mesozoic radiolarian genera was presented, in which, as a result of revision, only 332 Jurassic–Cretaceous genera of 580 were regarded as valid (*Catalogue* ..., 2009).

The validity of the reconstructed dynamics of biodiversity of radiolarian faunas is largely derivative

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[27] Cited after Kipling (1895).

Table 14. Spatial and temporal distribution of Frasnian radiolarians of the Rudny Altai, Northern Mugodzhary, Southern and Middle Urals: (1–3) western Australia, Canning Basin: (1) Nazarov and Ormiston, 1983; (2) Aitchison, 1993; (3) Won, 1997; (4, 5, 11) Timan-Pechora Basin, Afanasieva, 1997, 2000a; (6) Southern Urals, Argagan Mountain, Afanasieva and Amon, 2008b, 2009a; (7, 8) Rudny Altai Mountains, Afanasieva et al., 2009; (9) Northern Mugodzhary Mountains, Aitpaika River, Nazarov, 1973, 1975, 1988; Nazarov and Ormiston, 1993; (10) Middle Ural Mountains, eastern slope, Rezh River, Afanasieva, Amon, this study; 12 - China, eastern and south-eastern Guangxi, Li et Wang, 1991

System	Devonian											
Series	Upper											
Stage	Frasnian											
Substage	Lower				Middle			Upper				
Formation, Regional Substage	Gogo			Ust'-Yarega	Domanik	Mukasov	Kamenev		Egindy	Askyn	Lyaiol	Liukiang
							Lower	Upper				
Radiolarians / Authors	1	2	3	4	5	6	7	8	9	10	11	12
Spongentactinella veles (Foreman, 1963)	▨		▨		▨		▨		▨	▨		
Spongentactinella corynacantha Nazarov et Ormiston, 1983	▨				▨		▨		▨			▨
Ceratoikiscum planistellare Foreman, 1963	▨				▨		▨		▨		▨	▨
Palaeoscenidium robustum Aitchison, 1993		▨			▨		▨					
Bientactinosphaera hystricosa (Foreman, 1963)		▨			▨		▨					
Haplentactinia labyrinthica (Aitchison, 1993)		▨			▨		▨		▨			
Palaeoscenidium delicatum Aitchison, 1993		▨			▨		▨		▨			
Palaeoscenidium tabernaculum Aitchison, 1993		▨			▨		▨				▨	
Bientactinosphaera pinica Afanasieva, 2000		▨			▨		▨	▨		▨	▨	
Bientactinosphaera egindyensis (Nazarov, 1975)		▨			▨		▨		▨	▨	▨	▨
Spongentactinia diplostraca (Foreman, 1963)			▨				▨	▨	▨			
Moskovistella allbororum Afanasieva, 2000			▨		▨		▨		▨			
Moskovistella victorialis Afanasieva, 2000			▨		▨		▨				▨	
Borisella bykovae Afanasieva, 2000				▨	▨		▨	▨			▨	
Ceratoikiscum simplum Cheng, 1986					▨		▨					
Entactinia bifida Afanasieva, 2000					▨		▨					
Moskovistella mira Afanasieva, 2000					▨		▨					
Nazarovites mikhailovae Afanasieva, 2000					▨		▨					
Haplentactinia barskovi Afanasieva, 2000					▨		▨					
Primaritripus patella (Hinde, 1899)					▨	▨	▨	▨				
Radiobisphaera domanicensis (Bykova, 1955)					▨	▨	▨	▨				
Astroentactinia tikhomirovi Afanasieva, 2000					▨		▨		▨			
Ceratoikiscum incomptum Nazarov, 1975					▨		▨		▨			
Ceratoikiscum spinosum Cheng, 1986					▨		▨		▨			
Radiobisphaera assidera (Nazarov, 1975)					▨		▨		▨			
Spongentactinella windjanensis Nazarov, 1982					▨		▨		▨			
Astroentactinia vishnevskayae Afanasieva, 2000					▨			▨				
Palaeodiscaleksus tumefactus Afanasieva et Amon, 2008					▨	▨				▨		
Palaeodiscaleksus punctus (Hinde, 1899)					▨	▨				▨	▨	
Palacantholithus stellatus Deflandre, 1973					▨	▨	▨				▨	
Ceratoikiscum ukhtensis Afanasieva, 2000					▨		▨		▨		▨	
Bientactinosphaera obtusa (Hinde, 1899)					▨		▨	▨			▨	
Bientactinosphaera pittmani (Hinde, 1899)					▨			▨	▨	▨	▨	
Astroentactinia biaciculata Nazarov, 1975					▨			▨	▨	▨	▨	

Table 14. (Contd.)

System	Devonian											
Series	Upper											
Stage	Frasnian											
Substage	Lower				Middle			Upper				
Formation, Regional Substage	Gogo			Ust'-Yarega	Dom-anik	Muka-sov	Kamenev		Egindy	Askyn	Lyaiol	Liu-kiang
							Lower	Upper				
Radiolarians / Authors	1	2	3	4	5	6	7	8	9	10	11	12
Astroentactinia tenuis (Furutani, 1990)						▨						
Trochodiscus planatus Hinde, 1899						▨						
Primaritripus buribayensis Afanasieva et Amon, 2008						▨	▨					
Primaritripus chuvashovi Afanasieva et Amon, 2008						▨	▨					
Palaeodiscaleksus cribrarius (Hinde, 1899)						▨	▨					
Primaritripus chuvashovi Afanasieva et Amon, 2008						▨	▨					
Primaritripus kariukmasensis Afanasieva et Amon, 2009						▨	▨					
Radiobisphaera rozanovi Afanasieva et Amon, 2009						▨	▨	▨		▨		
Entactinia sp. A							▨					
Spongentactinia fungosa Nazarov, 1975							▨	▨	▨	▨		
Entactinia herculea Foreman, 1963							▨	▨	▨			▨
Adamasirad cf. *cathedrarius* (Afanasieva, 2000)										▨		
Adamasirad sp.										▨		
Archocyrtium cf. *riedeli* Deflandre										▨		
Astroentactinia cf. *robusta* (Hinde, 1899)										▨		
Astroentactinia cf. *paronae* (Hinde, 1899)										▨		
Astroentactinia sp.										▨		
Bientactinosphaera cf. *grandis* (Nazarov, 1975)										▨		
Bientactinosphaera cf. *vetusta* (Hinde, 1899)										▨		
Bientactinosphaera sp.										▨		
Ceratoikiscum sp.										▨		
Entactinia cf. *bella* Afanasieva et Amon, sp. nov.										▨		
Entactinia cf. *diversita* Nazarov, 1973										▨		
Entactinia sp.										▨		
Haplentactinia sp.										▨		
Moskovistella cf. *khaini* Afanasieva, 2000										▨		
Moskovistella cf. *additiva* (Foreman, 1963)										▨		
Palaeodiscaleksus sp.										▨		
Palaeoscenidium sp.										▨		
Polyentactinia cf. *circumretia* Nazarov et Ormiston, 1993										▨		
Polyentactinia cf. *kossistekensis* Nazarov, 1975										▨		
Polyentactinia cf. *propinqua* Nazarov, 1975										▨		
Polyentactinia sp.										▨		
Radiobisphaera sp.										▨		
Russirad cf. *kazintsovae* Afanasieva, 2000										▨		

from the state of classification and taxonomy of this group. The removal of surplus subjective and objective synonyms and mistakes, which have accumulated during two centuries of studies, is an urgent task well understood by the modern international community of radiolarian paleontologists. During the first decade of the 21st century, a number of extensive pioneering revisions were published (Afanasieva, 2000a; De Wever et al., 2001; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a); however, this work is certainly far from complete.

TAXONOMIC SIGNIFICANCE OF MORPHOLOGICAL CHARACTERS OF RADIOLARIAN SKELETONS

Abrupt introduction in practical paleontology of computer data processing and creation of databanks provide a new insight into the problem of the diagnosis of taxa. At present, it is urgent to reconsider the taxonomic significance of skeletal morphological characters, i.e., turn to a number of tasks of the age-old problem of comparison of paleontological objects: (1) classification, (2) diagnostics, and (3) minimization of the number of characters determining a taxon (Vanchurov, 1973, 1975, 1979, 2000; Chediya, 1978; Negadaev-Nikonov et al., 1983; Petrushevskaya, 1986; Petrushevskaya and Menshutkin, 1990; Amon, 1995b, 1996; Afanasieva, 1997b, 1997c, 2000a).

Problem of the Diagnosis of Taxa

In paleontological practice, the identification of an object is connected with significant difficulties and doubts. This is mostly caused by the fact that almost each new specimen provides new information, which frequently changes the previous point of view on the diagnosis of taxa and, hence, on classification, rather than by the diagnostics itself. However, as Petrushevskaya (1986, p. 178) remarked, "if a radiolariologist thinks that it is possible to set available data into a computer and it "by itself" will provide understanding of the matter, he is mistaken. These computers are not cleverer than researchers, so that they are unable to resolve correctly an incorrectly posed problem."

Classification (differentiation of objects by a certain character into taxa) and diagnostics (assignment of an object to one of previously established taxa) may be realized by different formalized approaches. In so doing, the concepts of *reliable* and *forbidden* relationships are introduced. When classifying, a reliable relationship fixes the assignment of objects to one taxon. In diagnostics, it determines the primary relationship between two objects, in contrast of interrelations of one object with all others. Alternative conclusion corresponds to a forbidden relationship (Vanchurov, 1973, 1975, 1979, 2000; Negadaev-Nikonov et al., 1983).

Vagueness of ideas about taxonomic significance of characters and taxonomic ranks results in ambiguous, sometimes contradictory solutions concerning the same questions. From the new standpoint of computer logic, the establishment of similarity and distinctions between taxa requires unequivocal treatment of properties of various morphological characters, free of ambiguous understanding of the diagnoses of taxa at all levels. It should be based on the minimum set of characters, allowing no ambiguous understanding of the diagnosis of taxa of all levels (Amon, 1996; Vanchurov, 1973, 1975, 1979, 2000; Negadaev-Nikonov et al., 1983; *Paleontologiya i paleoekologiya* ..., 1995; Afanasieva, 2000a; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a):

- *property* is what is characteristic of any object or phenomenon, making similar or distinguishing them from each other;
- *character* is any fixed property of an object, allowing the recognition of the object, i.e., its similarity to some objects and differences from others;
- *diagnosis* is the minimum set of characters of a taxonomic unit in question, separating one taxon from all other taxa of the same taxonomic rank;
- *description* is a simplified model of an object in the form of a "sketch," performed in a strictly unified terminology and consisting of a list of characters.

Descriptions of species are a key element of classification. In so doing, some characters change with growth of the organism and others characterize variability of the group investigated. Based on morphological analysis of taxa, it is possible to construct a maximum similarity tree, which does not contradict a priori data on phylogenetic relationships of taxa. To compare various taxonomic groups of organisms, it is necessary to determine the stability of each character, i.e., its variability and variation range of the entire set of characters (Vanchurov, 1973, 1975, 1979, 2000; Chediya, 1978; Negadaev-Nikonov et al., 1983; Petrushevskaya, 1986; Petrushevskaya and Menshutkin, 1990; Amon, 1995b, 1996; Afanasieva, 2000a; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a).

Nevertheless, one should keep in mind the well-known saying of Linnaeus (1735):[28] that characters do not determine the genus, but the genus determines characters. Properties of any taxon are objective, i.e., exist independently of our will and desire. Moreover, neither absolute identity nor absolute distinctions exist in the nature. Consequently, hypotheses and conclusions concerning similarity or distinctions of paleontological taxa are always more or less subjective. A negative aspect of any description is the absence of exact information on the number of characters required for comparison of taxa of different levels.

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[28] Cited after Petrushevskaya (1986, p. 99).

Table 15. Main morphological characters of radiolarian skeletons

1. Geometry of skeleton	Geometrical shape		Construction		
	1 – spherical, 2 – conical, 3 – square, 4 – triangular, 5 – pyramidal, 6 – discoidal, 7 – spindle-shaped, 8 – oviform, 9 – raylike, 10 – intersecting spines, 11 – other		1 – skeleton proportions, 2 – number of rays, 3 – spines intersecting in one center, 4 – three spines merged to form triangular frame		
2. Symmetry of skeleton	1 – homaxal type (endless number of similar axes), 2 – monaxal type (one axis), 3 – heteropolar type (poles of the only axis are not equal), 4 – bilateral type				
3. Internal framework	Type		Construction		
			Spicule	Microsphere	
	1 – hollow sphere, 2 – hemisphere, 3 – polyhedron, 4 – spicule, 5 – subtriangular framework, 6 – microsphere		4-rayed, 6-rayed, 8-rayed, 12-rayed, multi-rayed	spherical or multifaceted (4–6-faceted)	
4. Primary skeleton sphere	Structural type	Microstructure	Relative dimensions (*D*/*Ds*)		
	1 – porous, 2 – latticed	1 – finely porous, 2 – microporous, 3 – variously porous	1 – very large (1.50–2.0), 2 – large (2.01–2.3), 3 – small (2.31–3.0), 4 – very small (3.1–4.5)		
5. Number of skeleton spheres	1, 2, 3, ... many				
6. Internal skeletal spheres	Structural type	Number of skeleton spheres	Microstructure		
	1 – latticed, 2 – cellular, 3 – spongy, 4 – porous	1, 2, 3, ... many	1 – thick-walled, 2 – thin-walled	1 – macroporous, 2 – finely porous, 3 – microporous, 4 – heteroporous	
7. External skeletal spheres	Structural type	Structural variety	Microstructure	Relative wall thickness (*D*/*tw*)	
	1 – latticed, cellular or spongy, 2 – porous, 3 – lamellar	1 – latticed, 2 – cellular, 3 – spongy, 4 – porous, 5 – lamellar	1 – macroporous, 2 – finely porous, 3 – microporous, 4 – heteroporous	1 – very thick (1.0–20.0), 2 – thick (20.1–30.0), 3 – thin (30.1–100.0), 4 – very thin (100.1–150.0)	
8. Pores and structure of intervening bars	Pores			Intervening bars	
	Form	Relative pore dimensions			
		Ratio of pore diameter and skeletal wall thickness (*dp*/*tw*)	Ratio of skeleton diameter and pore diameter (*D*/*dp*)	Shape of surface	Relative width (*dp*/*wp*)
	1 – circular, 2 – oval, 3 – angular-oval, 4 – rounded-polygonal, 5 – sub-triangular, 6 – angular-polygonal	1 – very narrow (0.1–0.8), 2 – narrow (0.9–1.0), 3 – wide (1.1–4.4), 4 – very wide (4.5–9.5)	1 – very large (4.0–10.0), 2 – large, (10.01–18.5), 3 – small, (18.6–63.0), 4 – very small (63.1–105.0)	1 – flattened, 2 – circular, 3 – rounded-pointed	1 – very narrow (9.5–6.1), 2 – narrow (6.0–4.1), 3 – wide (4.0–1.6), 4 – very wide (1.5–0.1)

Table 15. (Contd.)

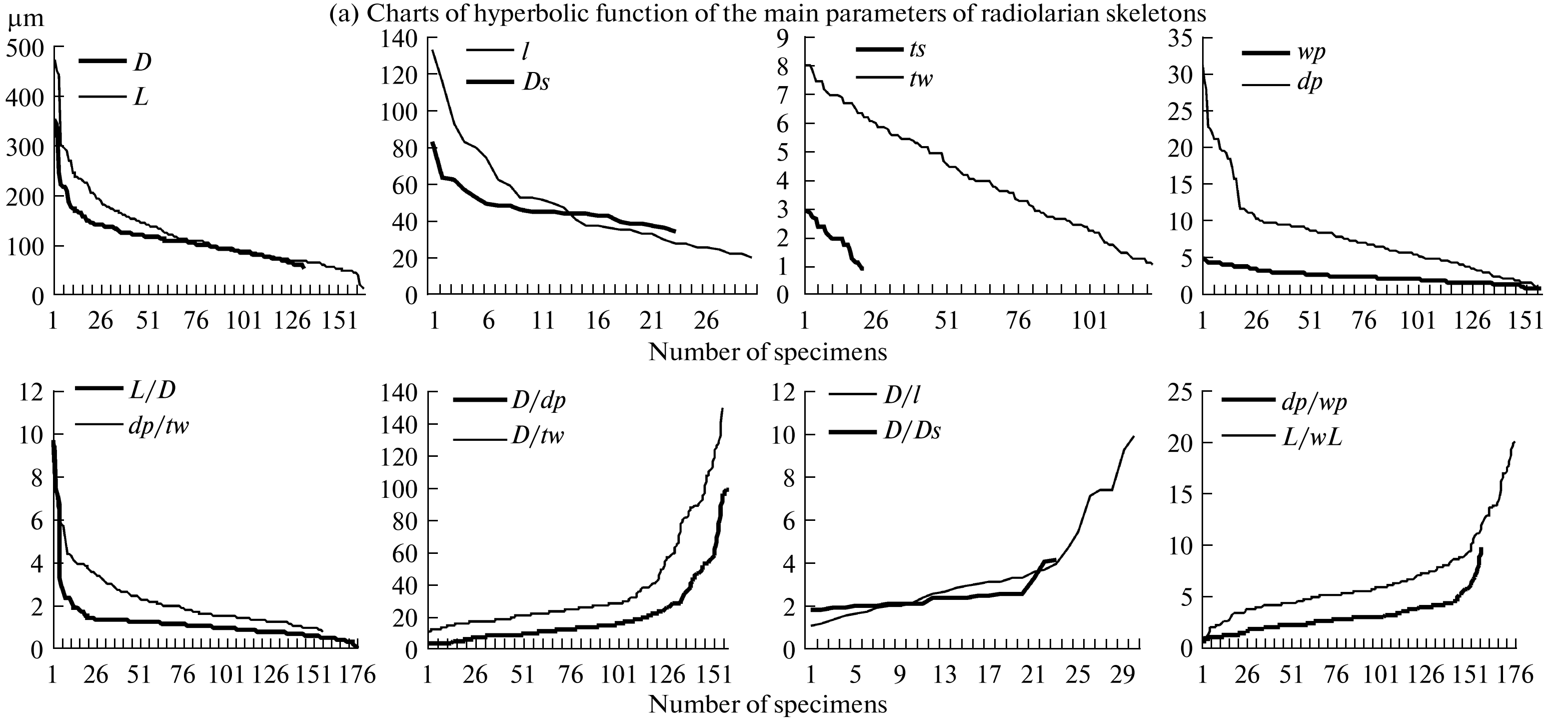
9. Mouth and Pylome	Availability		Construction					
	1 – absence, 2 – presence		1 – simple, 2 – framed		1 – ridge, 2 – collar, 3 – spines, 4 – peristome		1 – open, 2 – partly open, 3 – slitlike, 4 – closed	
10. Main spines	Num-bers	Shape of spines	Section of spines	Shape of facet	Section of facet	Spine structure	Relative length (L/D)	Relative thickness (L/wL)
	1, 2, 3, ... many	1 – tubular, 2 – conical, 3 – bladed, 4 – rodlike	✣ – shaped, Y – shaped, ✖ – shaped, ● – circular, ■ – subsquare	1 – blade-shaped, 2 – petaloid, 3 – sub-triangular	1 – blade-shaped, 2 – sub-rectangular	1 – hollow, 2 – solid, 3 – depression in basal part, 4 – straight, 5 – curved, 6 – double, 7 – helical, 8 – with apophyses	1 – very long (10.0–3.6), 2 – long (3.5–0.6), 3 – short (0.5–0.4), 4 – very short (0.3–0.1)	1 – massive (0.5–4.0), 2 –thick (4.1–6.0), 3 – thin (6.1–13.0), 4 – slender (13.1–25.0)
11. By-spines	Shape of by-spines		Section of spines		Relative length (D/l)		Relative thickness (l/wl)	
	1 – conical, 2 – rodlike, 3 – pyramidal		▲ triangular, ● – circular		1 – very long (1.0–2.0), 2 –long (2.1–3.0), 3 – short (3.1–8.0), 4 – very short (8.1–15.0)		1 – very thick, (3.0–4.5), 2 – thick, (4.6–8.0), 3 – thin, (8.1–11.0), 4 – slender (11.1–15.0)	
12. Sculptural elements	Type of sculpture		Shape of sculpture	Shape of apex	Shape of cells	Relative height (D/ht)		Frequency
	1 – thorns, 2 – bars, 3 – ridges		1 – rodlike, 2 – conical, 3 – platelike, 4 – cellular	1 – rounded, 2 – rounded-pointed, 3 – tapering, 4 – pointed	1 – circular, 2 – oval, 3 – rounded-polygonal, 4 – polygonal	1 – very height (8.0–20.0), 2 – height (20.1–36.0), 3 – low (36.1–60.0), 4 – very low (60.1–80.0)		1 – very frequent, 2 – frequent, 3 – rare, 4 – very rare
13. Ranked sizes of skeleton and its parts (Table 17)	Absolute							Relative
	Spherical and discoid skeletons					Spiny skeletons		
	D – diameter of the external sphere or disc, H – disc height, tw –wall thickness of external sphere, dp – pore diameter of external sphere, wp – width of intervening bars of external sphere, Ds – diameter of the primary sphere, ts – wall thickness of the primary sphere, ds – pore diameter of primary sphere, ws – width of intervening bars of primary sphere			L – length of the main spines, wL – width of the main spines base, l – length of by-spines, wl – width of by-spines base, ht – height of thorns and thorn-tubercles, ld – diameter of cell, formatted by costae, lw – width of costa, A – length of apophyses, dA – width of apophyses		a, b, i - main spines: a – a-rod, b – b-rod, i – intersector, at, bt, it – triangular frame sides, c – cavea rib, p – patagium, aL, bL, iL – length of main spines, al, bl, il – length of by-spines, d – pore diameter of spongy meshwork, w – width of intervening bars, r – arc radius		D/Ds D/H D/tw D/dp D/l D/ht dp/tw dp/wp L/D L/wL l/wl

Table 16. Taxonomic significance of morphological characters of radiolarian skeletons

Author \ Taxa	Legion/Order	Suborder	Superfamily	Family	Subfamily	Genus
Ehrenberg, 1846, 1847, 1875	1. Axis of symmetry 2. Main shape of skeleton		–	Shape of skeleton	–	Number of chambers
Haeckel, 1887	1. Type of symmetry 2. Structure of central capsule 3. Position of nucleus in central capsule 4. Chemical composition of skeleton	Morphotypes of skeletons, defined by the type of symmetry	–	1. Number of chambers 2. Shape of chambers 3. Open or closed last chamber 4. Structure of spherical shells 5. Spine shape 6. Number of chambers in Nassellaria, their shape and subdivision 7. Degree of closure of the last chamber of Nassellaria 8. Presence or absence of main spines 9. Number and arrangement of main spines		8. Number and arrangement of shells 9. Proportions of lengths of different spines 10. Presence of main spines in Nassellaria
Hollande and Enjumet, 1960	1. External morphological characters of skeleton 2. Nucleus structure 3. Structure of nucleoaxopodial apparatus		1. Arrangement of siliceous elements of skeleton 2. Structure of cytological body	–	–	–
Lipman, 1979	Type of skeleton		–	1. Number and shape of chambers 2. Open or closed last chambers 3. Presence or absence of spines 4. Number and arrangement of spines	5. Number of shells	6. Arrangement of shells 7. Structure of the rings (cameral rings) 8. Bars connecting cameral rings 9. Presence, shape, and arrangement of lobes and/or processes 10. Structure and size of lateral and wing-shaped spines 11. Structure and size of apertural spines 12. Structure of spines on the last chamber 13. Shape and arrangement of thorns and tubercles 14. Shape of the aperture 15. Structure of interchamber septa 16. Structure of facets and ridges separating them in pyramidal skeletons
Nazarov, 1984, 1988	Prevailing geometrical shape of skeleton		–	1. Structure of internal framework 2. Symmetry of skeletal outline	1. Number of rays of internal sphere or spicule 2. Number of external radial spines	1. Number of skeletal spheres: spherical or other shape 2. Structure of skeletal wall

Table 16. (Contd.)

<table>
<tr><th>Author \ Taxa</th><th colspan="2">Order</th><th>Superfamily</th><th>Family</th><th>Subfamily</th><th>Genus</th></tr>
<tr><td>Nazarov and Petrushevskaya, 1995</td><td colspan="2">1. Arrangement of central capsule, nucleus, axoplast (or axoplasts), axonemes, and skeleton
2. Arrangement of microtubules in axoneme
3. Symmetry of the cell, prevailing geometrical shape of the skeleton
4. Structure of central capsule and its wall</td><td colspan="3">1. Type of internal framework and approximate number of spines radiating from it
2. Approximate number of spherical shells or chambers (with spiral or linear arrangement) and ratio of their sizes and mode of their internal division
3. Types of skeletal structure of initial joints (spongy, lattice-like, porous, etc.)
4. Approximate number of external skeletal spheres</td><td>1. Number of spherical, spiral, or linear spheres, shells, chambers, joints, and ratios of their measurements
2. Number and measurements of internal septa between these parts of skeleton
3. Structure of wall
4. Arrangement, measurements, and number of pores, rods, costae, tubercles, etc.
5. Arrangement of main spine ramifications (verticils)6. Number and shape of external shell apophyses</td></tr>
<tr><td>Afanasieva, 1997, 2000, 2002</td><td colspan="2">1. Dominant symmetry of skeleton
2. Dominant geometrical shape of skeleton
3. Dominant types of inner framework
4. Presence or absence of pylome</td><td>1. Symmetry of skeleton
2. Geometrical shape of skeleton
3. Structural type of outer shell
4. Type of inner framework</td><td>1. Structure of skeleton
2. Number (from/to) of rays of inner framework
3. Type of additional skeletal tissue of patagium</td><td>1. Number of skeletal shells
2. Ratios of main spines</td><td>1. Structure of inner framework
2. Structure of pylome
3. Structural type of inner shells and skeletal tissue of patagium
4. Number of main spines
5. Shape of main spines
6. Construction of tangential elements of skeletal surface</td></tr>
<tr><td>Amon, 1999, 2000</td><td colspan="2">1. Dominant general skeletal geometry, its subdivision
2. Presence of radial and tangential structures, predominant shape of the latter
3. Type of inner framework
4. External structures5. Structure of segments of skeleton</td><td>1. Type of inner framework
2. Number and shape of radial structures
3. Number, shape, and type of tangential structures
4. Predominant type of skeletal tissue structure
5. Topography of segments
6. Pylome
7. External apophyses</td><td>1. Characterization of inner framework
2. Characterization of skeletal tissue
3. Structure of segments and of walls between segments
4. Patagium</td><td>–</td><td>1. Outline of skeleton, total size
2. External surface, ornamentation
3. Patterns in arrangement of pores or external structures
4. Structure of pylome and patagium
5. Structure of external apophyses</td></tr>
<tr><td rowspan="2">Afanasieva and Amon, 2005, 2006</td><td>1. Dominant geometrical shape of skeleton
2. Dominant symmetry of skeleton
3. Structural type of outer shell
4. Presence of mouth or pylome</td><td>1. Geometrical shape of skeleton
2. Structural variety of outer shell of skeleton
3. Type of inner framework</td><td rowspan="2">1. Shape of skeleton
2. Symmetry of skeleton
3. Type of inner framework</td><td rowspan="2">1. Structure of skeleton
2. Structural variety of outer shell of skeleton
3. Number of rays of inner framework
4. Type of additional skeletal tissue of patagium</td><td rowspan="2">Number of skeletal shells</td><td rowspan="2">1. Structure of inner framework
2. Structure of pylome
3. Structural variety of inner shells and skeletal tissue of patagium
4. Number of main spines
5. Shape of main spines
6. Shape of by-spines
7. Presence of sculptural elements</td></tr>
<tr><td>Class</td><td>Order</td></tr>
</table>


(a) Charts of hyperbolic function of the main parameters of radiolarian skeletons

(b) Main absolute and relative measurements of radiolarian skeletons

Measurements, μm	Absolute											Relative										
	D	*dp*	*wp*	*tw*	*Ds*	*ts*	*L*	*wL*	*l*	*wl*	*ht*	*D/Ds*	*D/H*	*D/tw*	*D/dp*	*D/l*	*D/ht*	*L/D*	*L/wL*	*l/wl*	*dp/tw*	*dp/wp*
Very large, very long, etc.	360.0–180.1	35.0–25.1	10.0–4.1	8.0–7.1	100.0–60.1	5.0–3.1	470.0–350.1	60.0–50.1	135.0–90.1	>9.6	15.1–20.0	1.5–2.5	1.0–1.3	1.0–20.0	4.0–10.0	1.0–2.0	8.0–20.0	10.0–3.6	0.50–4.0	3.0–4.5	9.5–4.5	0.1–1.5
Large, long, etc.	180.0–130.1	25.0–15.1	4.0–3.1	7.0–4.1	60.0–46.1	3.0–2.1	350.0–153.1	50.0–25.1	90.0–70.1	9.5–7.6	10.1–15.0	2.6–3.5	1.4–1.6	20.1–30.0	10.1–18.5	2.1–3.0	20.1–36.0	3.5–0.6	4.1–6.0	4.6–8.0	4.4–1.1	1.6–4.0
Small, short, etc.	130.0–88.1	15.0–6.1	3.0–2.1	4.0–2.1	46.0–40.1	2.0–1.0	153.0–52.1	25.0–15.1	70.0–29.1	7.5–4.6	5.1–10.0	3.6–4.0	1.7–2.0	30.1–100.0	18.6–63.0	3.1–8.0	36.1–60.0	0.5–0.4	6.1–13.0	8.1–11.0	1.0–0.9	4.1–6.0
Very small, very short, etc.	88.0–20.0	6.0–1.0	2.0–1.0	2.0–1.0	40.0–35.0	–	52.0–15.0	15.0–4.5	29.0–20.0	4.5–3.0	0.9–5.0	4.1–4.5	2.1–3.0	100.1–150.0	63.1–105.0	8.1–15.0	60.1–80.0	0.3–0.1	13.1–25.0	11.1–15.0	0.8–0.1	6.1–9.5

Table 17. Main skeleton parameters of spherical and discoidal Paleozoic radiolarians (Afanasieva, 2000a; Afanasieva et al., 2005d; Afanasieva and Amon, 2006): (*D*) diameter of external sphere or disc, (*dp*) pore diameter of external sphere, (*wp*) width of intervening bars of external sphere, (*tw*) wall thickness of external sphere, (*H*) height of disc, (*Ds*) diameter of primary skeleton sphere, (*ts*) wall thickness of primary sphere, (*L*) length of the main spines, (*wL*) width of the main spines base, (*l*) length of by-spines, (*wl*) width of by-spines base, and (*ht*) height of thorns and thorn-tubercle

Significance of Morphological Characters of the Radiolarian Skeleton for Classification

Classification is construction of a system of similarities and distinctions between objects based on a certain minimum set of characters, down to one. As a system of extinct organisms is developed, the classification levels in its different parts are nonequivalent. This induces search for the opportunity of using formal methods of computer data processing for classification of objects described by a large set of characters. In doing so, the diagnosis of a taxon of any level requires the knowledge of the minimum number of characters (sometimes only one character), which distinguish it from other taxa. In addition, the diagnosis of a high-rank taxon should not contain characters of taxa of lower ranks and, on the contrary, lower-rank taxa should not repeat characters of a higher-rank taxon.

A character may be a measurement or data on the presence, absence, or extent of manifestation of certain features. A diagnostic character should (1) meet one of three requirements: "and," "or," "not and should not be"; (2) follow three principles: obligatory, desirable, sufficient; and (3) be subject to the law of feedback. The frequently used terms *large, small*, etc. and other quantitative diagnostic characteristics (length, width, height, and their ratios) should be reduced to ranked absolute and relative parameters of the skeleton and its parts. In addition, the algorithm of computer data processing prevents the use of pseudoquantitative parameters, such as *more, less, greater, lesser.*

The analysis of morphological characters of Paleozoic radiolarians (Table 15) has revealed their repeatability and confinement to certain hierarchical levels (Table 16). Statistical analysis of absolute and relative skeletal parameters of new radiolarian species from the Domanik Formation of the Middle Frasnian of the Timan–Pechora Province has shown a stable pattern of changes in quantitative characteristics (Table 17) (Afanasieva, 2000a). The first five diagrams are close in general appearance to the hyperbolic function, i.e., described by the equation $y = 1/x$, and three others are their mirror reflection (Table 17a); this allows the probabilistic characteristics of distributions to be determined (Rodionov, 1981; Aivazyan et al., 1985).

The presence of such stable dependencies allows the formalization of classification of the data and the use in descriptions of species the terms *very large, large, small*, and *very small*, which correspond to certain quantitative values (Table 17b).

Statistical analysis of absolute and relative parameters of Paleozoic radiolarian skeletons was most efficient in the study of fine distinctions in skeletal structure between *Bientactinosphaera variacanthina* (Foreman)[29] and *Bientactinosphaera grandis* (Nazarov)[30] (Fig. 37). The initial diagnoses and descriptions of these species do not give a clear understanding of distinctions between them; therefore, in many paleontological works, this taxa are identified mistakenly. The analysis of absolute (Fig. 37a) and relative (Figs. 37a, 37b) values of the length of the main spines (L), skeleton diameter (D), and their ratio (L/D) in 26 skeletons of *Bientactinosphaera grandis* and 28 skeletons of *Bientactinosphaera variacanthina* and comparison with the holotypes have shown distinct patterns in the ratio of the lengths of the main spines and skeleton diameter. The two species clearly differ at $L/D = 1.2$. This pattern is distinctly visible both in the diagram, which displays changes in each skeletal parameter considered and their ratios (Fig. 37a), and in the scatter diagram, which allow the variation ranges of the parameters of these species (Fig. 37b).

Based on the above assumptions and analysis of taxonomic significance of morphological characters of radiolarian skeletons, which takes into account the data on modern and ancient radiolarians (Table 16), the system of a fixed set of morphological characters has been developed to obtain diagnoses and descriptions of radiolarians of various taxonomic levels:

class: (1) prevailing symmetry of the skeleton, (2) prevailing geometrical shape of the skeleton, (3) structural type of the outer shell of the skeleton, and (4) the presence or absence of pylome;

order: (1) geometrical shape of the skeleton, (2) structural variant of the outer shell of the skeleton, and (3) type of the internal framework;

superfamily: (1) symmetry of the skeleton, (2) skeleton shape, and (3) type of the internal framework;

family: (1) skeleton structure, (2) structural variant of the outer shell of the skeleton, (3) number of rays of the internal framework, and (4) type of additional skeletal tissue of the patagium;

subfamily: number of shells in the skeleton;

genus: (1) structure of the internal framework, (2) pylome structure, (3) structural variant of the internal shells and skeletal tissue of the patagium, (4) number of the main spines, (5) shape of the main spines, (6) shape of the by-spines, and (7) the presence or absence of sculptural elements;

species: (1) microstructure and thickness of the outer shell of the skeleton and skeletal tissue of the patagium, (2) microstructure and thickness of the internal shells of the skeleton, (3) structure of the main spines, (4) structure of the by-spines, (5) shape

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[29] *Entactinosphaera variacanthina* described by Foreman (1963, p. 278, pl. 3, fig. 8; pl. IV, figs. 3a, 3b) as having "One or two spherical lattice-shells with six three-bladed main spines of variable width and length, and long, needle-like by-spines..."

[30] *Entactinosphaera grandis* described by Nazarov (1975, p. 65, pl. V, figs. 11–12; pl. VII, figs. 1–4) as having "a shell with six large, approximately equal in size main spines ..."

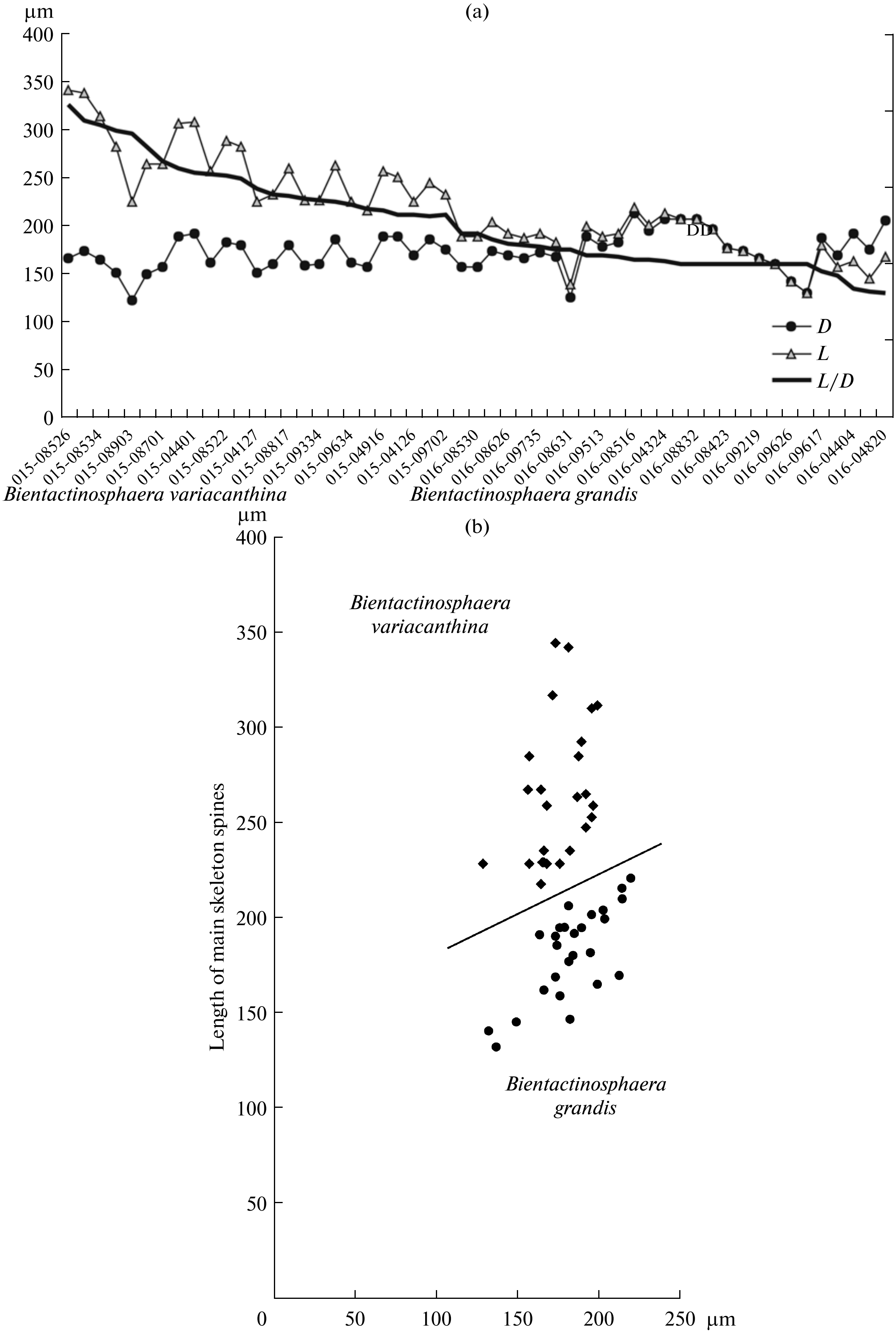

Fig. 37. Graph of (a) absolute and (b) relative lengths of the main spines (*L*), diameter of the external sphere of skeleton (*D*), and their ratio (*L*/*D*) in *Bientactinosphaera grandis* (Nazarov) and *Bientactinosphaera variacanthina* (Foreman).

and structure of sculptural elements, (6) shape and structure of pores, pore canals, and interpore bars, (7) ranked absolute and relative dimensions of the skeleton and its parts.

The number of characters for different taxa is formally greater than the number of characters which are used by different authors as the basis of classifications (Table 16). In other words, it seems that the diagnostics was considerably complicated. However, this is not the case. In the previously proposed systems of morphological characters (Table 16), first, there is discordance between particular skeletal features and certain taxonomic ranks of radiolarians, in particular, as obviously species-level characters (measurements) fall in characteristics of genera or even families; second, morphological characters of spiny radiolarians and radiolarians with a pylome are not taken into account; third, these systems of characters do not correspond to rigid requirements of the computer logic.

Our approach, implying thorough analysis of taxonomic significance of morphological skeletal characters for the diagnosis of radiolarians of various taxonomic levels, provides classification schemes more accurately describing the taxonomic position of certain morphotypes.

The system proposed of morphological characters opens an opportunity to take into account almost any data on fossil organisms and allows simple determination of the taxonomic rank of any newly considered object.

In doing so, various skeletal elements are considered to be systems of interconnected and interdependent morphological designs, interaction of which determines certain body plan at different evolutionary stages. Previously, this was impossible based only on general geometry and symmetry of skeletons, which prevailed in classifications of Haeckel and his followers. Geometry alone, without the analysis of the time of appearance and development of various skeletal tissues, spines, and other morphological elements, allow the recognition of only simple geometrical structures, such as spheres, ellipsoids, disks, cones, etc. These skeletal designs are repeated in many taxonomic groups of radiolarians during the Phanerozoic, although they are frequently unrelated. This causes “simple” classification schemes, inevitable confusion in the nomenclature, and excessively expanded stratigraphic ranges of some species and genera, occasionally, from the Cambrian–Silurian up to the Recent.

Expansion of the knowledge of radiolarian morphology and improvement of the methodology of determination of taxonomic significance of morphological characters of the skeleton have shown practical use of the new approaches to classification and recognition of separate taxa (Afanasieva, 2000a, 2011; Afanasieva and Amon, 2003, 2006a; Afanasieva et al., 2005d).

RADIOLARIANS WITH ONE POROUS SPHERE

Paleozoic radiolarians with one porous sphere and internal framework in the shape of a six-rayed spicule belong to the subfamily Entactiniinae Riedel, 1967, which presently comprises six genera: *Altaiesphaera* Obut et Iwata, 2000 ($Є_{1-2}$), *Apophysisphaera* Won, 1997 (D_2–D_3fr_1), *Archaeocenosphaera* Obut et Iwata, 2000 ($Є_{1-2}$), *Borisella* Afanasieva, 2000 (O–?–D), *Entactinia* Foreman, 1963 (O_2–S–D_1–P–T_{2-3}), and *Futobari* Furutani, 1990 (S_1w–D_1).

Since 1963, after the study of Foreman (1963) devoted to Famennian radiolarians of Ohio, United States, all Paleozoic radiolarians with one porous sphere, six-rayed internal spicule with a medial bar, and six three-bladed main spines have been assigned to the genus *Entactinia* Foreman, 1963. However, Aitchison and Stratford (1997) proposed to regard the genus *Entactinia* as a junior subjective synonym of the genus *Stigmosphaerostylus* Rüst, 1892.

Genus *Entactinia*

The genus *Entactinia* was described by Foreman (1963) from Upper Devonian (Famennian) carbonate nodules of the Huron Member of the shale strata of Ohio, United States (Foreman, 1963). A very rich and diverse radiolarian assemblage from this locality consists of 57 species of 20 genera. Spherical radiolarian forms are characterized by the presence of the internal spicule, “... three or more rays originating from each end of a short median bar or of four rays originating from a point” (Foreman, 1963, p. 267).

The diagnosis of the genus *Entactinia*, with the type species *E. herculea* (Figs. 38a, 38b), marks that it has “a single well-developed latticed or spongy shell (sometimes with external spongy material) and an internal six-rayed double spicule more delicate than the main spines” (Figs. 38b, 38c) (Foreman, 1963, p. 271).

Foreman was the first to propose that “the internal spicules of these species and some others previously described from the Paleozoic are believed to differ fundamentally from the internal spicular structures (which may represent reduced medullary shells) described for a few Recent genera, and may provide a justifiable basis for their segregation as a separate family or suborder” (Foreman, 1963, p. 267).

Further, Foreman (1963, p. 267) wrote that “Popofsky (1912, p. 89) described the two Recent genera *Centrolonche* and *Centracontium*, each based on a single specimen, as having six internal radial rays joined at a central point. He regarded this point of union as perhaps representing a reduced medullary shell, and, whether or not this interpretation is correct, it seems advisable not to use these names for Paleozoic forms in which the internal rays arise eccentrically from a median bar or a point.”

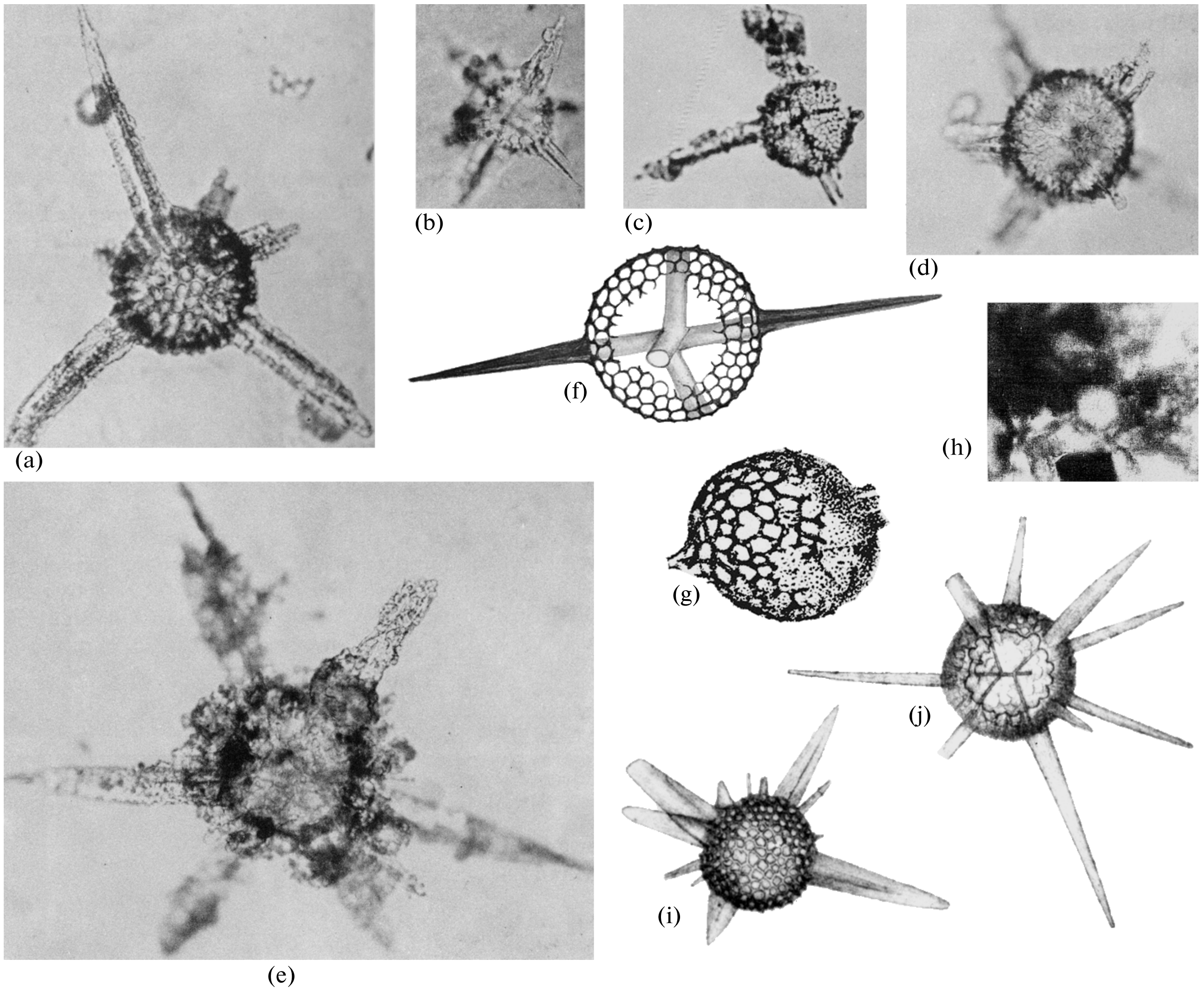

Fig. 38. Original figures of radiolarians of the genera *Entactinia* (a–e), *Stigmosphaerostylus* (f–h), *Heliosphaera* (i), and *Acanthosphaera* (j): (a, b) *Entactinia herculea* Foreman, 1963, after (a) Foreman, 1963, pl. 1, fig. 3b, ×160; (b) Foreman, 1963, pl. 1, fig. 3c, ×160; (c) *Entactinia paula* Foreman, 1963, after Foreman, 1963, pl. 2, fig. 11, ×160; (d, e) *Entactinia crustescens* Foreman, 1963, after (d) Foreman, 1963, pl. 1, fig. 9b, ×128, (e) Foreman, 1963, pl. 1, fig. 9f, ×128; (f) *Stigmosphaerostylus notabilis* Rüst, 1892, after Rüst, 1892, pl. 10, fig. 2, ×85; (g) *Stigmosphaerostylus inaequalis* Hinde, 1899, after Hinde, 1899b, pl. 16, fig. 3, ×200; (h) *Stigmosphaerostylus etheridgei* (Hinde, 1899), after Aitchison and Stratford, 1997, figs. 1–7, ×60; (i) *Heliosphaera clavata* Hinde, 1899, after Hinde, 1899a, pl. 8, fig. 28, ×200; (j) *Acanthosphaera etheridgei* Hinde, 1899, after Hinde, 1899a, pl. 8, fig. 24, ×200.

Then, Foreman (1963, p. 268) emphasized that "Paleozoic species with internal spicules which may be homologous with those of the Ohio Devonian forms, rather than with those of Recent genera, include *Stigmosphaera rothpletzii* Rüst, 1892, *Stigmosphaera mira* Rüst, 1892, *Stigmosphaera echinata* Hinde, 1899, *Stigmosphaera suspecta* Rüst, 1892, *Stigmosphaerostylus notabilis* Rüst, 1892, *Stigmosphaerostylus inaequalis* Hinde, 1899, *Staurosphaera pusilla* Hinde, 1899a, *Centrolonche obscura* Deflandre, 1953, *Acanthosphaera etheridgei* Hinde 1899, *Acanthosphaera australis* Hinde, 1899, *Acanthosphaera entactinia* Rüst, 1892, *Heliosphaera robusta* Hinde, 1899, and *Ellipsostigma australe* Hinde, 1899" (Rüst, 1892; Hinde, 1899a, 1899b; Deflandre, 1953).

In addition, Foreman (1963, p. 269) remarked that "sphaerellarians with internal spicules appear to be rather common in Carboniferous assemblages described by Rüst (1892) from the Harz Mountains, in the Devonian of New South Wales (Hinde, 1899a), and in the Visean of the Montagne Noire (Deflandre, 1960). They may indeed be more common than indicated in the literature, but may not be recognized because of poor preservation."

The generic name *Entactinia* has become widely accepted in descriptions of Paleozoic radiolarians. Beginning from the first publication of the genus in

1963 and up to the present time, 48 authors in 49 scientific works described the genus *Entactinia* and its species or indicated its taxonomic position in the publications devoted to classification of radiolarians (see synonymy of the genus *Entactinia*), based on materials from the Ordovician–Permian of 11 countries (Australia, Belgium, Germany, China, Korea, Mongolia, Russia, United States, Thailand, France, and Japan). Three fundamental monographs (De Wever et al., 2001; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a) indicate global distribution of the genus *Entactinia* during almost the whole of the Paleozoic from the Middle Ordovician to the terminal Permian. In the Triassic, the last members of the genus *Entactinia* have been described (Bragin, 1999, 2002). In addition, De Wever et al. (2001, pp. 180–181) regarded the genus *Entactinia* as the type genus of the family Entactiniidae Riedel, 1967 and included the genus *Stigmosphaerostylus* in the list of valid genera of this family.

Entactinia is the type genus of the family Entactiniidae, which was established by Riedel in 1967. The family included eight genera (Riedel, 1967a, p. 148): *Stigmosphaerostylus* Rüst, 1892, *Ellipsostigma* Hinde, 1899, *Haplentactinia* Foreman, 1963, *Entactinia* Foreman, 1963, *Entactiniosphaera* Foreman, 1963, *Polyentactinia* Foreman, 1963, *Tetrentactinia* Foreman, 1963, and *Cyrtentactinia* Foreman, 1963. The family Entactiniidae (Riedel, 1967a, 1967b, 1971) is presently used in all classification schemes of Paleozoic radiolarians (Nazarov, 1975, 1988; Nazarov and Ormiston, 1984; Afanasieva, 1999, 2000a, 2002; Amon, 1999a, 1999b, 1999c; De Wever et al., 2001; Afanasieva and Amon, 2003, 2006a; Afanasieva et al., 2005d).

Genus *Stigmosphaerostylus*

The genus *Stigmosphaerostylus* Rüst, 1892, with the type species *S. notabilis* Rüst, 1892 (Fig. 38f), was described for the first time by Rüst from thin sections of Lower Carboniferous siliceous shales of the Harz Mountains (without exact indication of locality) in Germany (Rüst, 1892). In the diagnosis of the genus, it is marked that these radiolarians are characterized by one spherical latticed shell with two identical polar spines and radial bars at the center of the skeleton. From the description of the only type species *S. notabilis,* it is evident that these radiolarians are rare and, inside the spherical skeleton with very thin, tracery latticed shell (0.296 mm in diameter) and two narrow polar spines (0.299 mm long), there are six thick (0.034 mm in diameter) cylindrical skeletal bars originating from one center.

In 1899, as the new species *Stigmosphaerostylus inaequalis* (Fig. 38g) from presumably Ordovician siliceous shale of Mallion Island near the Cornwall Peninsula in southwestern Great Britain was described, Hinde (1899b, p. 216) repeated the diagnosis of the genus *Stigmosphaerostylus* presented by Rüst: "the test is a simple latticed sphere, with radial rods in the interior and two opposite radial spines."

The generic name *Stigmosphaerostylus* Rüst, 1892 was used by Hinde (1899b) and, then, was not used for 55 years until Campbell (1954) published the Chapter *Radiolaria* in the American *Treatise on Invertebrate Paleontology.* The classification of radiolarians proposed by Campbell (1954) was not accepted in the Russian *Fundamentals of Paleontology* (Khabakov et al., 1959) and this was probably connected with the fact that the genus *Stigmosphaerostylus* Rüst, 1892 was not mentioned there. In *Review of the Systematics of Radiolarians*, Chediya (1959) presented the diagnosis of the genus *Stigmosphaerostylus* according to Rüst (1892) and remarked that "this genus requires special consideration" (Chediya, 1959, p. 80).

Only 27 years after the publication of *Treatise on Invertebrate Paleontology* (Campbell, 1954), Kozur and Mostler (1981, 1989) used the name *Stigmosphaerostylus* in the description of Early Permian radiolarians of the Southern Urals.

Finally, Aitchison and Stratford (1997; Stratford and Aitchison, 1997) proposed to return to the generic name *Stigmosphaerostylus* without morphological arguments for the use of this genus instead of the genus *Entactinia* in the description of Paleozoic radiolarians.

In addition, Aitchison and Stratford (1997) proposed to regard the genus *Entactinia* as a junior subjective synonym of the genus *Stigmosphaerostylus* Rüst, 1892, because "this name has priority and it is appropriate that *Entactinia* is placed in synonymy" (Aitchison and Stratford, 1997, p. 372).

In doing so, Aitchison and Stratford believed that the diagnosis of the genus *Entactinia* reported by Foreman (1963) based on radiolarian skeletons extracted from enclosing matter was more precise than the diagnosis of the genus *Stigmosphaerostylus* established by Rüst (1892) based on thin sections, and accepted it "as an appropriate emendment" (Aitchison and Stratford, 1997, p. 380): the genus *Stigmosphaerostylus* Rüst, 1892, emend. Foreman, 1963.

At the same time, Foreman (1963) did not regard the genus *Stigmosphaerostylus* described by Rüst (1892) based on thin sections as a synonym of the genus *Entactinia*, which she established based on radiolarian skeletons extracted from enclosing matter.

During the last 12 years (1999–2010), the generic name *Stigmosphaerostylus* was used by 23 authors in seven works devoted to radiolarians from the Silurian–Early Carboniferous of five countries (Australia, Greece, Thailand, China, and Poland). At the same time, in the study of Late Devonian radiolarians of Poland, Vishnevskaya et al. (2002) indicated that, following Aitchison and Stratford (1997; Stratford and Aitchison, 1997) the genus *Entactinia* is treated as a junior synonym of the genus *Stigmosphaerostylus*. However, Vishnevskaya et al. (2002, p. 215) proposed that "this problem requires further consideration, because the genera *Entactinia* and *Stigmosphaerostylus* differ in the number of the main spines of the skeleton, i.e., a morphological character of the generic level."

Taxonomic Position of the Genera *Entactinia* Foreman, 1963 and *Stigmosphaerostylus* Rüst, 1892

A revision of the genera *Entactinia* Foreman and *Stigmosphaerostylus* Rüst shows that the main difference of *Entactinia* from *Stigmosphaerostylus* is the structure of the outer shell of the skeleton, internal spicule, and the number of the main spines.

The analysis of morphological characters of radiolarian skeletons displays taxonomic significance of (1) the wall structure of the skeleton, as the assignment of a taxon to certain class is determined; (2) internal spicule, as the order and family are determined; (3) the number of the main spines of the skeleton, as the subfamily and genus are determined (Foreman, 1963; Nazarov, 1975, 1988; Petrushevskaya, 1986; Nazarov and Petrushevskaya, 1995; Afanasieva, 1997b, 2000a, 2002, 2007; Amon, 1999b, 1999c; Afanasieva and Amon, 2003, 2006a, 2008a; Afanasieva et al., 2005d).

Consequently, according to the modern concept of the taxonomic rank of particular morphological characters, the genera *Entactinia* and *Stigmosphaerostylus* are not synonyms; moreover, they belong to different families, orders, and even classes (Afanasieva and Amon, 2003, 2006a, 2008a; Afanasieva et al., 2005d):

- the genus *Entactinia* Foreman, 1963 is distinguished by the porous skeletal wall, the narrow double spicule with the median bar and six main spines; therefore, this genus is assigned to the subfamily Entactiniinae Riedel, 1967, family Entactiniidae Riedel, 1967, order Entactiniata Riedel, 1967, class Sphaerellaria Haeckel, 1881;
- the genus *Stigmosphaerostylus* Rüst, 1892 has a thin tracery latticed shell of the skeleton, thick spicule, the rays of which originate from one center, and two polar main spines and should be regarded as a separate genus of the subfamily Haplentactiniinae Nazarov, 1980, family Haplentactiniidae Nazarov, 1980, order Cancelliata Afanasieva et Amon, 2003, class Spumellaria Ehrenberg, 1875.

At the same time, Aitchison and Stratford (1997) did not provide morphological arguments for synonymy of the genera *Entactinia* and *Stigmosphaerostylus*, and the figure of the species *Stigmosphaerostylus etheridgei* (Hinde) does not stand up to criticism (Fig. 38h). Moreover, they marked poor preservation of specimens of Hinde and included *Acanthosphaera etheridgei* Hinde (1899a, p. 49, pl. 8, fig. 24) (Fig. 38j); *Heliosphaera clavata* Hinde (1899a, p. 50, pl. 8, fig. 28) (Fig. 38i); and *Entactinia crustescens* Foreman (1963, p. 272, pl. 1, figs. 9a, 9b) (Figs. 38d, 38e) in synonyms of *Stigmosphaerostylus etheridgei.*

As the figure of *Stigmosphaerostylus etheridgei* provided by Aitchison and Stratford (1997) (Fig. 38h) is compared with the description and figure of the species *Acanthosphaera etheridgei* provided by Hinde (1899a, p. 49, pl. 8, fig. 24) (Fig. 38j), it is evident that they belong to different taxa.

The diagnosis of the species *Acanthosphaera etheridgei* reads "test small, with delicate lattice-frame and circular pores; the spines are slender and elongate: nine are shown in the specimen. In the interior of the test there are six rods, three radiating from each end of a small central bar; they extend to the surface of the test, and apparently connect with the radial spines" (Hinde, 1899a, p. 49). The description of species is accompanied by a clear figure (Hinde, 1899a, pl. 8, fig. 24) (Fig. 38j). Judging from the description and figure, this species should be removed from the genus *Acanthosphaera* Ehrenberg, 1858, described from the Recent beds of the Arctic Ocean near Greenland and lacking an internal spicule (Ehrenberg, 1858), and referred to the genus *Astroentactinia* Foreman, 1963.

Aitchison and Stratford (1997) regarded the species *Heliosphaera clavata* Hinde, 1899 as a synonym of *Stigmosphaerostylus etheridgei*, with the note *nomen dubium* because of insufficient preservation of the specimen. However, the description and figure of the genus and species provided by Hinde show the opposite. In the description of the genus, Hinde (1899a, p. 50) indicated that "the test is a simple latticed sphere, with large radial and intermediate smaller secondary spines."

The species described by Hinde should be removed from the genus *Heliosphaera* described by Haeckel (1862) from the Recent beds of the Mediterranean Sea, in the Messina Gulf of Sicily and lacking an internal spicule. However, it should not be referred to the genus *Stigmosphaerostylus* Rüst, 1892, which has two polar main spines and a six-rayed spicule, the rays of which originate from one point. The figure of *Heliosphaera clavata* with six massive main spines and many by-spines (Fig. 38i) closely resembles the species *Entactinia crustescens* Foreman, 1963 (Figs. 38d, 38e), suggesting that it belongs to the genus *Entactinia* Foreman, 1963.

Thus, according to the ICZN (*International Code ...*, 1999), article 23.3.6, it is incorrect to regard the genus *Entactinia* Foreman, 1963 as a junior synonym of the genus *Stigmosphaerostylus* Rüst, 1892 and redetermine on this basis all members of *Entactinia* described by Foreman and other researchers.

Following a number of researchers (Rüst, 1892; Hinde, 1899b; Campbell, 1954; Foreman, 1963; Riedel, 1967a, 1967b; De Wever et al., 2001), we regard *Stigmosphaerostylus* Rüst, 1892 as a separate genus, which was originally described from the Upper Carboniferous beds based on thin sections. However, many Paleozoic species described during the last years and assigned to the genus *Stigmosphaerostylus* (Kozur and Mostler, 1981, 1989; Aitchison and Stratford, 1997; Stratford and Aitchison, 1997; Aitchison et al., 1999; Wang et al., 2000, 2003; Luo et al., 2002; Sashida et al., 2002; Vishnevskaya et al., 2002; Larchi et al., 2005), should be transferred to the genus *Entactinia* based on morphological characters.

RADIOLARIANS WITH TWO AND THREE POROUS SPHERES

Paleozoic radiolarians with two porous spheres and the internal framework in the shape of a six-rayed spicule belong to the subfamily Bientactinosphaerinae Afanasieva, 1999, which presently comprises members of the following 11 genera: *Bientactinosphaera* Afanasieva, 2000 (O_{2-3}–?–D–C_1–P–T_2), *Hindeosphaera* Kozur et Mostler 1979 (T_{2-3}), *Muelleritortis* Kozur 1988 (T_{2-3}), *Mulderella* Kozur et Mostler 1981 (T_{2-3}), *Ornatoentactinia* Afanasieva, 2000 (D_{2-3}), *Palaeoactinosphaera* Noble, 1994 (S_1w–S_2), *Parasepsagon* Dumitrica, Kozur et Mostler 1980 (T_{2-3}), *Pseudostylosphaera* Kozur et Mostler 1981 (T_{2-3}), *Radiobisphaera* Won, 1997 (D–C–P_1), *Sepsagon* Dumitrica, Kozur et Mostler 1980 (T_{2-3}), and *Tritortis* Kozur 1988 (T_{2-3}).

Paleozoic radiolarians with three porous spheres and the internal framework in the shape of a six-rayed spicule belong to the subfamily Entactinosphaerinae Afanasieva, 2011, which presently comprises members of four genera: *Belowea* Won, 1983 (C_1), *Cyclocarpus* Li et Wang, 1991 (D_3), *Duplexia* Won, 1983 (D_3–C_1–P_1), and *Entactinosphaera* Foreman, 1963 (S_1–D_3–C_1).

In the study devoted to revision of Devonian radiolarians of eastern Australia, Aitchison and Stratford (1997) proposed to return to the generic names which were used by Hinde (1890, 1899a, 1899b). In particular, the genus *Entactinosphaera* Foreman, 1963 was regarded as a junior synonym of the genus *Trilonche* Hinde, 1899, which has a different diagnosis and type species.

Genus *Entactinosphaera*

Among spherical Paleozoic radiolarians, the genus *Entactinosphaera* Foreman, 1963 is widely known. The diagnosis of the genus reads "Two or more well-developed, spherical or subspherical shells, and an internal, six-rayed double spicule. When secondary spines are present, the six spines developed from the ray of the internal spicule are generally differentiated and recognizable as main spines" (Foreman, 1963, p. 274).

However, in the volume established by Foreman (1963, p. 274), this genus is composite (Fig. 39), including species with two and three spheres, with porous, latticed, and even spongy shell of the external sphere, which actually belong to different genera. The majority of species described by Foreman in this genus have only two shells.

The type species *Entactinosphaera esostrongyla* Foreman has three spheres (Fig. 39a). The diagnosis includes the following: "Three spherical lattice-shells and six, approximately equal, three-bladed main spines. The intermediate shell is the most robust. It has small subcircular pores somewhat variable in size. By-spines arise from this surface, branch horizontally and form a delicate, irregular, outer lattice-shell. The by-spines on some specimens continue beyond this outer shell, and branch and rejoin, but have never been observed to form a complete fourth shell. The inner shell is large, about half the diameter of the intermediate shell, and has delicate angular pores of very variable size. A well-developed, internal, six-rayed double spicule extends to form sturdy, three-bladed, radial rays between the inner and intermediate shells, and three-bladed main spines of approximately equal width beyond. Secondary radial beams between the inner and intermediate shells have been observed in some specimens" (Foreman, 1963, pp. 274–275).

In 1975, Nazarov indicated in the diagnosis of the genus *Entactinosphaera* the presence of "two spherical shells connected to the internal framework by rays formed at the ends of the six-rayed spicule." In the section *Remarks*, he proposed that a new type species should be designated (Nazarov, 1975, pp. 59–60). Moreover, in the same year, Nazarov established and described two new genera, *Spongentactinia* and *Tecentactinia.*

The genus *Spongentactinia* Nazarov, 1975 is distinguished by the presence of the external spongy shell and internal porous shell. The type species of the genus is *S. fungosa* Nazarov, 1975. Nazarov (1975) transferred the species *Entactinosphaera? diplostraca* Foreman (Foreman, 1963, pl. 6, fig. 3) (Fig. 39d) to this genus. In addition, in the section *Remarks*, Nazarov proposed that the genus *Spongentactinia* includes the species *Entactinia spongites* Foreman and *E. somphorhips* Foreman (Foreman, 1963, pl. 1, fig. 7; pl. 2, fig. 10), which have a spongy layer varying in thickness and located on a thin latticed base (Nazarov, 1975, p. 75) (Figs. 39e, 39f).

The genus *Thecentactinia* Nazarov, 1975 has three spherical shells: the internal and external shells are porous and the intermediate shell is reticulate. Nazarov (1975) transferred to this genus the following Foreman's species: *Entactinosphaera esostrongyla* Foreman (type species of the genus *Entactinosphaera*), *E.? erebenna* Foreman, and *E. riedeli* Foreman (Figs. 39a–39c). Nazarov (1975) designated *Entactinosphaera riedeli* as the type species of the genus *Thecentactinia.*

These taxonomic conclusions were repeated in later works of Nazarov (Nazarov, 1981, 1988; Nazarov et al., 1982; Nazarov and Ormiston, 1983a, 1983b, 1984, 1985, 1986, 1990, 1993; Nazarov and Petrushevskaya, 1995). However, direct indication of changes in the diagnosis of the genus *Entactinosphaera* and replacement of its type species are absent; this contradicts the ICZN (*International Code* ..., 1999, article 61.1.3.), which reads "... the name-bearing type of any nominal taxon, once fixed in conformity with the provisions of the Code, is not subject to change ...."

It is evident that the genus *Thecentactinia* Nazarov, 1975 is a junior synonym of the genus *Entactinosphaera* Foreman, 1963, the diagnosis of which is

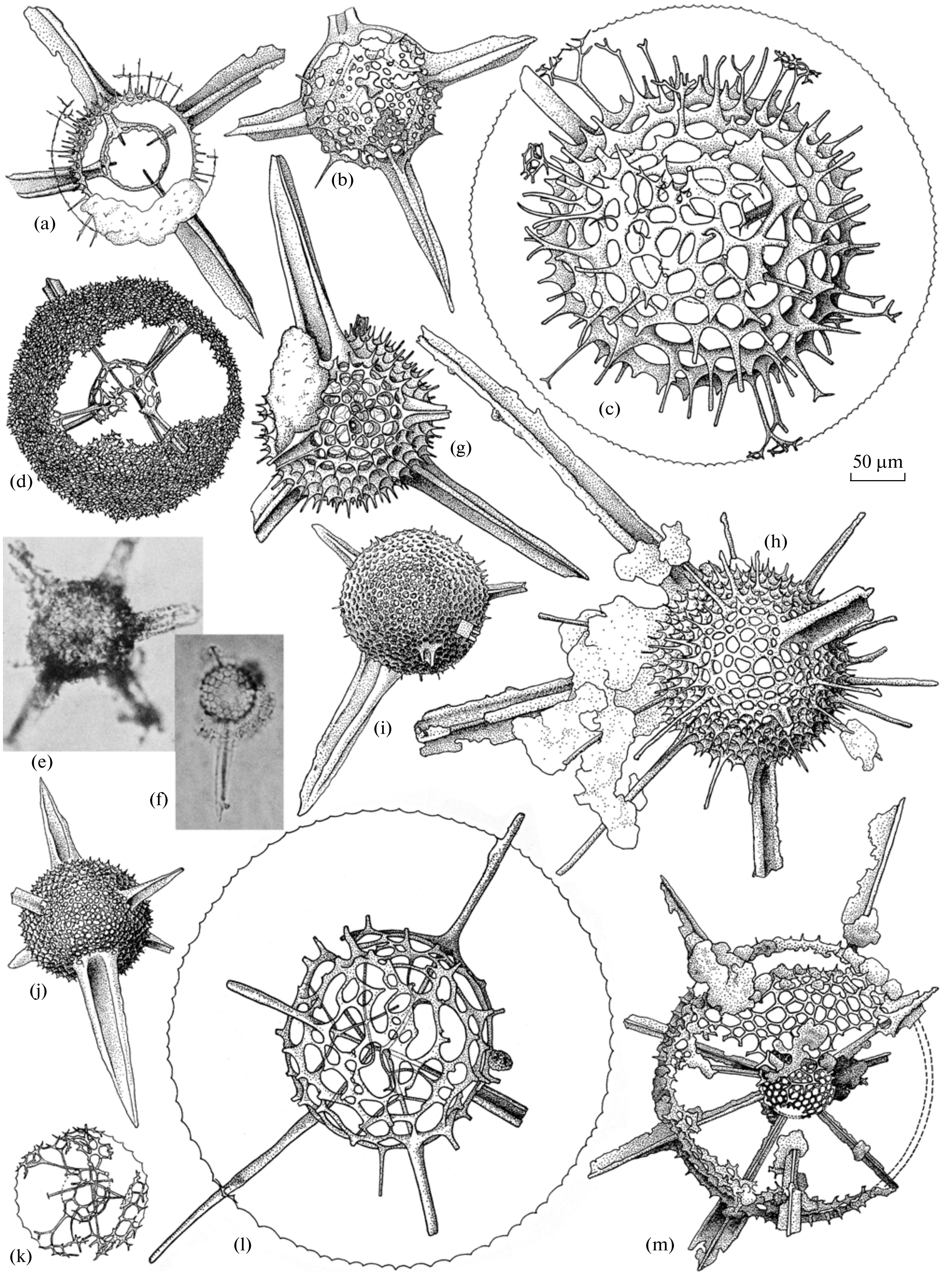
(a)
(b)
(c)
(d)
(g)
50 μm
(h)
(e)
(f)
(i)
(j)
(k)
(l)
(m)

Fig. 39. Original figures of radiolarians described by Foreman in the genus *Entactinosphaera:* (a, b) *Entactinosphaera*: (a) *E. esostrongyla* (Foreman, 1963, pl. 6, fig. 1a), (b) *E. erebena* (Foreman, 1963, pl. 6, fig. 6), (c) *E. riedeli* (Foreman, 1963, pl. 6, fig. 9); (d–f) *Spongentactinia*: (d) *S. diplostraca* (Foreman, 1963, pl. 6, fig. 3), (e) *S. spongites* (Foreman, 1963, pl. 1, fig. 7), (f) *S. somphorhips* (Foreman, 1963, pl. 2, fig. 10); (g, h) *Bientactinosphaera*: (g) *B. variacanthina* (Foreman, 1963, pl. 3, fig. 8), (h) *B. echinata* (Hinde, 1899) (Foreman, 1963, pl. 3, fig. 10); (i, j) *Radiobisphaera*: (i) *R. assidera* (Nazarov, 1975) (Foreman, 1963, pl. 3, fig. 3b); (j) *R. palimbola* (Foreman, 1963, pl. 3, fig. 3c); (k) *Magnisphaera dystactotata* (Foreman, 1963, pl. 6, fig. 5); (l) *Retientactinosphaera fredericki* (Foreman, 1963, pl. 6, fig. 8); and (m) *Helioentactinia polyacanthina* (Foreman, 1963, pl. 6, fig. 11). Scale bar, 43 μm.

amended according to the diagnosis of the type species *Entactinosphaera esostrongyla* Foreman, 1963, i.e., the shell with three spherical shells, six-rayed spicule, and six main spines (Afanasieva, 2011).

Won (1997a) attempted to stabilize the generic composition of radiolarians with two porous spherical shells; in so doing, two new genera were established, *Bisphaera* Won, 1997 (two spheres, six- or eight-rayed spicule, six or eight main spines[31] and *Radiobisphaera* Won, 1997 (two spheres, six-rayed spicule, many spines, one or six of which are larger than others.[32]

Unfortunately, the generic name *Bisphaera* Won, 1997 is preoccupied. The senior homonyms is the genus *Bisphaera* Birina, 1948 (Birina, 1948, p. 129) of foraminifers from the Devonian–Carboniferous boundary beds of the Russian Platform; therefore, the generic name *Bisphaera* Won, 1997 is invalid and, according to the ICZN (*International Code* ..., 1999, article 52.1), this name should be replaced.

At the same time, we follow the principle of minimization of objectively necessary and sufficient number of characters, which distinguish taxa of the same hierarchical level and do not allow ambiguous treatment of the diagnosis. Therefore, the analysis of taxonomic significance of morphological skeletal characters of the genus *Bisphaera* has shown that its species in fact belong to four genera of the order Entactiniata Riedel, 1967 (Afanasieva, 2011):

- skeletons with two porous spheres, six-rayed spicule, and six main spines belong to the genus *Bientactinosphaera* Afanasieva, 2000: *B. beniguna* (Won, 1997a, pl. 2, figs. 9–11), *B. cribrisimilis cribrisimilis* (Won, 1997a, pl. 3, figs. 1, 3, 7), *B. cribrisimilis crassa* (Won, 1997a, pl. 3, fig. 4) [=*B. variacanthina* (Foreman, 1965)], and *B. solidispinosa* (Won, 1997a, pl. 3, figs. 9–11);
- skeletons with two porous spheres, six-rayed spicule, and one main spine belong to the genus *Radiobisphaera* Won, 1997: *R. cribrisimilis crassa* (Won, 1997a, pl. 3, fig. 8) and *R. uniprocera* (Won, 1997a, pl. 3, figs. 12, 13);
- skeletons with two porous spheres (external sphere is complicated by a system of tangential structures, which divide the skeleton surface into particular cells), six-rayed spicule, and six main spines belong to the genus *Ornatoentactinia* Afanasieva, 2000: *O. cribrisimilis cribrisimilis* (Won, 1997a, pl. 3, figs. 2, 5, 6) [=*O. solita* Afanasieva, 2000];
- skeletons with two porous spheres, eight-rayed spicule, and eight main spines belong to the genus *Helioentactinia* Nazarov, 1975: *H. dissimilicortex* (Won, 1997a, pl. 2, figs. 13–20).

The morphologically prominent genus *Radiobisphaera* Won, 1997 we accept with some reservation: dominant development of only one main spine, which distinguishes this genus from other genera of the subfamily Bientactinosphaerinae Afanasieva, 1999 (family Entactiniidae Riedel, 1967, order Entactiniata Riedel, 1967). Hence, we removed species *R. nazaroviana* (Won, 1997a, pl. 3, figs. 14–16) with six main spines from the genus *Radiobisphaera.* Based on this character, we transfer this species to the genus *Bientactinosphaera* Afanasieva, 2000.

Afanasieva (2000a) established a new genus, *Bientactinosphaera* Afanasieva, 2000 for radiolarians with two spherical porous shells and six three-bladed main spines. The type species is *Entactinosphaera variacanthina* Foreman, 1963 (Fig. 39g), previously described by Foreman (1963, pl. 3, fig. 8). Judging from morphological features, the genus *Bientactinosphaera* is presently considered to include the following species established by Foreman (1963): *Entactinosphaera cancellicula* Foreman, *E. echinata* (Hinde) (Fig. 39h), *E. euthlasta* Foreman, *E. hapala* Foreman, *E. hystricosa* Foreman, *E. inusitata* Foreman, *E. symphypora* Foreman, *E. tretactinia* Foreman, and *E. variacanthina* Foreman.

Characteristic morphological features of other species described by Foreman (1963) within the genus *Entactinosphaera* allow the following revision of their taxonomic positions (Afanasieva, 2011):

- the species *Entactinosphaera palimbola* Foreman, with two porous spheres and one main spine is transferred to the genus *Radiobisphaera* Won, 1997 and divided into two separate species (Figs. 39i, 39j), *Radiobisphaera palimbola* (Foreman, 1963) (Foreman, 1963, pl. 2, figs. 7a–7c; pl. 3, figs. 3a, 3c) and *Radiobisphaera assidera* (Nazarov, 1975) (Foreman, 1963, pl. 2, figs. 7d, 7e; pl. 3, figs. 3b, 3d);
- the species *Entactinosphaera? polyacanthina* Foreman (Foreman, 1963, pl. 4, fig. 6; pl. 6, fig. 11)

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[31] "Two spherical latticed shells with six to eight inner spines as well as a six- to eight-rays of an internal spicule with a medial bar. No radial beam between the shells" (Won, 1997a, p. 344).

[32] "Two latticed shells, an outer and inner shell; generally numerous outer spines, one or six of these commonly are much or slightly stronger than the others; with six inner spines which are the continuations of the six rays of an internal spicule with a median bar; radial beams arising from the surface of the inner shell and commonly protruding out of the outer shell; no apophyses present" (Won, 1997a, p. 350).

with two porous shells and 10–15 three-bladed main spines is transferred to the genus *Helioentactinia* Nazarov, 1975 (Fig. 39m);

- the species *Entactinosphaera dystactotata* Foreman (Foreman, 1963, pl. 9, fig. 6; pl. 6, fig. 5) with two thin latticed shells with very large cells is transferred to the genus *Magnisphaera* Won, 1997 (Fig. 39k);
- the species *Entactinosphaera fredericki* Foreman (Foreman, 1963, pl. 5, figs. 5a–5c; pl. 6, fig. 8) with two reticulate spheres and one main spine (Fig. 39l) is transferred to the genus *Retientactinosphaera* Afanasieva, 2011, which comprises four species: *Retientactinosphaera fredericki* (Foreman, 1963), *R. magnifica* Afanasieva, 2011, *R. unimana* (Nazarov, 1977), and *R. clavata* Afanasieva, 2011.

The analysis of morphological features of the above considered radiolarians with two and three spheres, one and six main spines allowed to assign the previously established species of the genus *Entactinosphaera* Foreman, 1963 to seven genera, which are presently considered to belong to three orders of two radiolarian classes (Afanasieva and Amon, 2003, 2006a; Afanasieva et al., 2005d; Afanasieva, 2011):

Class Sphaerellaria Haeckel, 1881
Order Entactiniata Riedel, 1967
Family Entactiniidae Riedel, 1967
Subfamily Bientactinosphaerinae Afanasieva, 1999
Genus *Bientactinosphaera* Afanasieva, 2000
Genus *Radiobisphaera* Won, 1997
Subfamily Entactinosphaerinae Afanasieva, 2011
Genus *Entactinosphaera* Foreman, 1963
Family Astroentactiniidae Nazarov et Ormiston, 1985
Subfamily Helioentactiniinae Afanasieva, 1999
Genus *Helioentactinia* Nazarov, 1975
Class Spumellaria Ehrenberg, 1875
Order Cancelliata Afanasieva et Amon, 2003
Family Haplentactiniidae Nazarov, 1980
Subfamily Pseudorotasphaerinae Noble, 1994
Genus *Retientactinosphaera* Afanasieva, 2011
Family Polyentactiniidae Nazarov, 1975
Subfamily Magnisphaerinae Afanasieva, 1999
Genus *Magnisphaera* Won, 1997
Order Spongiata Afanasieva et Amon, 2003
Family Spongentactiniidae Nazarov, 1975
Subfamily Spongentactiniinae Nazarov, 1975
Genus *Spongentactinia* Nazarov, 1975.

Genus *Trilonche*

When studying Devonian radiolarians, many researchers of the eastern school widely use the genus *Trilonche*, with many species, particularly, *Trilonche echinata* and *T. palimbola*. The wide use of the genus *Trilonche* started after the publication of Aitchison and Stratford (1997) devoted to the revision of Devonian radiolarians of New South Wales of Australia, originally described by Hinde (1890, 1899a, 1899b).

Certainly, the methods for studying radiolarians develop with time and, hence, inevitably are improved, the time of taxonomic revisions comes. Nevertheless, original descriptions of taxa should attentively and carefully be involved in generalizations.

The genus *Trilonche* was established by Hinde (1899a, p. 47) with the following diagnosis: "The test consists of two concentric latticed spheres, with three radial spines at equal or unequal distances apart. Secondary surface-spines are also sometimes present. The forms included in this genus are very numerous in the Tamworth radiolarian rocks." In the generic name, Hinde marked the main morphological features of the skeleton, the Greek τρεϊζ λόγχαι means three spears [three spines] (Figs. 40b–40f).

At the same time, in opinion of Aitchison and Stratford (1997), the diagnosis of the genus *Trilonche* presented by Hinde (1899a) has a limited character, restricting the morphotype of the genus to only three main spines.

Foreman (1963) established a new genus, *Entactinosphaera,* which, as marked above, actually combines seven essentially different genera: *Bientactinosphaera* Afanasieva, 2000, *Entactinosphaera* Foreman, 1963, *Helioentactinia* Nazarov, 1975, *Magnisphaera* Won, 1997, *Radiobisphaera* Won, 1997, *Retientactinosphaera* Afanasieva, 2011, and *Spongentactinia* Nazarov, 1975.

Foreman (1963, p. 274) noted the following: "Hinde (1899a) describes several species, *Stylosphaera vetusta, Staurolonche davidi, S. tenella, S. scitula, Staurolonchidium obliquum, Trilonche vetusta, T. vetusta* var. *A, T. pittmani* and *T. elegans*, which also are characterized by an inner lattice-shell similar to that found in the species listed above. Bykova (1955) also notes some specimens with this characteristic inner lattice-shell and assigns them to *Trilonche vetusta* Hinde and *Staurolonche davidi* Hinde. The species described by Hinde and Bykova are distributed among a number of the genera based mainly on the number of spines observed. It is possible that, as these studies were made with thin sections, the complete number of spines could not always be accurately counted and that fewer genera are actually represented, some of which may be identical with species of *Entactinosphaera* listed above."

Based on this, Aitchison and Stratford (1997) regarded the genus *Entactinosphaera* Forman, 1963 as a junior synonym of the genus *Trilonche* Hinde, 1899 and, therefore, the wider and better substantiated diagnosis of the genus *Entactinosphaera* was taken for amended diagnosis of the genus *Trilonche.*

The basic argument of Aitchison and Stratford (1997) for the association of the genera *Entactinosphaera* and *Trilonche* is poor preservation of skeletons

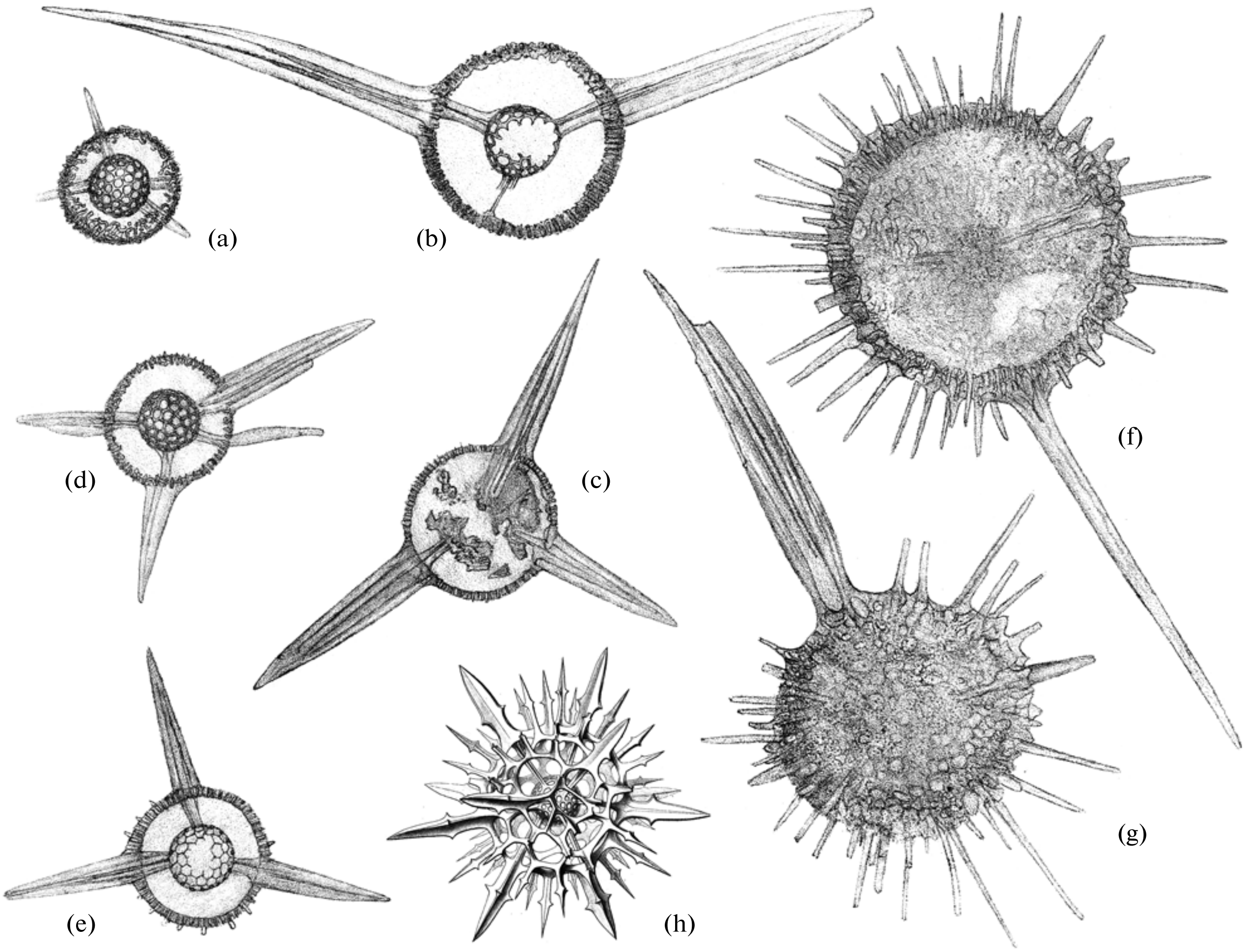

Fig. 40. Original figures of radiolarians of the genera *Trilonche* (a–e) and *Heliosoma* (f–h): (a) *Trilonche elegans* Hinde, 1899, ×200, pl. 8, fig. 22; (b, c) *Trilonche pittmani* Hinde, 1899, ×200: (b) pl. 8, fig. 20; (c) pl. 8, fig. 21; (d, e) *Trilonche vetusta* Hinde, 1899, ×200: (d) pl. 8, fig. 19; (e) pl. 8, fig. 18; (f, g) *Heliosoma echinatum* Hinde, 1899, ×200: (f) pl. 9, fig. 1; (g) pl. 9, fig. 2; (h) *Heliosoma hastatum* Haeckel, 1881, pl. 28, fig. 4, ×400.

and the fact that Hinde (1899a) studied radiolarians in thin sections. However, this is an improper argument for joining different taxa with different skeletal morphology into one genus and destabilization of classification.

In addition, Aitchison and Stratford (1997) regard the genus *Staurodruppa* Hinde, 1899 as a synonym of *Trilonche*. However, the morphotype of the genus *Staurodruppa* is distinguished by the formation of two ellipsoidal shells of the skeleton. Hinde (1899a, p. 51) assigned this genus to the order Prunoidea. According to the modern approaches to classification of radiolarians, this genus belongs to the family Staurodruppidae Afanasieva, 2000 (order Oviformata Afanasieva et Amon, 2005, class Stauraxonaria Afanasieva et Amon, 2005) (Afanasieva, 2000a; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a).

Aitchison and Stratford (1997) referred spherical porous radiolarians with predominant development of one main spine to the species *Trilonche echinata* (Hinde, 1899). At present, this species is understood very widely and, in our opinion, unites several essentially different species. It remains uncertain why radiolarians with the well-pronounced generic character (primary development of one main spine) were referred by Aitchison and Stratford (1997) to the genus *Trilonche*, which initial diagnosis includes three main spines, and amended diagnosis, six main spines.

We assign species with two porous spheres and primary development of one main spine to the genus *Radiobisphaera* Won, 1997, which includes more than 20 species and subspecies, including *R. acuta* Won, 1997, *R. assidera* (Nazarov, 1975), *R. cribrisimilis crassa* (Won, 1997), *R. domanicensis* (Bykova, 1955), *R. flamans* Won, 1997, *R. magnifenestra* Won, 1997, *R. menneri* Afanasieva, 2000, *R. multa* Won, 1997, *R. multiaculeata* Won, 1997, *R. multiaculeata multiaculeata* Won, 1997, *R. multiaculeata stellaepolus* Won, 1997, *R. palimbola* (Foreman, 1963), *R. rozanovi* Afanasieva et Amon, 2009, *R. trifoliata* (Umeda, 1998), *R. variantia* Won, 1997, *R. variantia inaequalis* Won, 1997, *R. variantia variantia* Won, 1997, and *R. uniprocera* (Won, 1997).

Aitchison and Stratford (1997) included the species *Heliosoma echinatum* in synonyms of *Trilonche echinata.*

At the same time, the initial diagnosis of the species *Heliosoma echinatum* reads (Hinde, 1899a, p. 50): “The cortical test has small lattice-pores; the medullary test is small, with very slender lattice-framework and polygonal pores; the larger radial spines are robust and gradually tapering, the smaller are very numerous, slender needle-shaped, and unequal in length. Only sections of this form are as yet known, and in the specimens figured one alone of the radial spines in each case is preserved, but there are indications of the broken-off bases of others. The radial spine of fig. 1 probably represents merely the central portion of the spine; it may originally have been equally as stout as that in fig. 2. The medullary test is faintly shown in fig. 1” (Figs. 40f, 40g).

Moreover, in the description of the species *Entactinosphaera echinata?* (Hinde), Foreman (1963, p. 279) noted “Two spherical lattice-shells with six three-bladed main spines. The outer shell has pores of very variable size and shape, twenty to thirty per half a circumference, with generally heavy intervening bars.... The six main spines, which extend from the radial rays, are three-bladed, heavy, and somewhat variable in width and length on the same specimen” (Fig. 40h).

Thus, two authors (Hinde, 1899a, p. 50; Foreman, 1963, p. 279) indicated and we supported that the main morphological character of the species *echinata* is six three-bladed main spines, with a **Y**-shaped section and saber-shaped blade.

In addition, the genus *Heliosoma*, with the type species *H. hastatum* Haeckel (Fig. 40h) was established by Haeckel (1881) from Recent beds of the Pacific Ocean. The description of the species *H. hastatum* reads: “Cortical shell very thin walled, with large, irregular, polygonal meshes, three to six times as broad as the bars; four to six on the radius. Medullary shell one-third as large, with small, regular, circular pores. The two shells connected by twelve regularly disposed radial beams, which are prolonged outside into twelve very stout three-sided pyramidal main spines, somewhat longer than the radius, spear-shaped; each of the three wings in the middle part with one tooth. Scattered on the surface numerous by-spines of the same form, half as long and only one-fourth as broad” (Haeckel, 1881, p. 241).

Consequently, based on morphological characters, the species *Heliosoma echinatum* Hinde, 1899 (with six main spines) should be removed from the genus *Heliosoma* Haeckel, 1881, which is characterized by the formation of twelve main spines.

Thus, on the one hand, we take the species *Heliosoma echinatum* in the sense of Foreman (1963, p. 279), but assign it to the genus *Bientactinosphaera* Afanasieva, 2000, which differs in the development of six main spines, *Bientactinosphaera echinata* (Hinde, 1899) (Fig. 39h).

However, on the other hand, incompletely certain interpretation of Hinde (1899a, p. 50, pl. IX, figs. 1–3) of figures of *Heliosoma echinatum* allows us to assign these morphotypes (Figs. 40f, 40g) to the genus *Radiobisphaera* Won, 1997, which is distinguished by the predominant development of one main spine, *Radiobisphaera echinata* (Hinde, 1899).

Based on the analysis of morphological features of the genus *Trilonche* Hinde, 1899, we propose to assign to it two species, *T. vetusta* and *T. pittmani* (Figs. 40b–40e).

Other species assigned to the genus *Trilonche* in works of Hinde (1899a, 1899b), Aitchison and Stratford (1997), and other researchers (Vishnevskaya et al., 2002; Wonganan and Caridroit, 2005; Obut et al., 2007; Noble et al., 2008) require careful taxonomic revision. For example, we refer *Trilonche elegans* Hinde, 1899 (Fig. 40a) to the genus *Bientactinosphaera.* When describing the species *Trilonche palimbola* (Foreman, 1963), Noble et al. (2008) indicated the presence of six bladed spines.[33] Therefore, it is impossible to refer this Tournaisian form to the species *Radiobisphaera palimbola* (Foreman, 1963), which is distinguished by the predominant development of one massive main spine (Fig. 40j), or to the genus *Trilonche* Hinde, 1899, which is characterized by the formation of only three main spines (Figs. 40b–40e).

Taxonomic Position of Genera with Two and Three Porous Spheres

The analysis of morphological features of the above described radiolarians with two and three spheres and establishment of separate genera have displayed actual improvement of modern methods for studying radiolarians and application of new approaches in classification of taxa (Afanasieva and Amon, 2003, 2006a; Afanasieva et al., 2005d).

Works of Hinde (1890, 1899a, 1899b) devoted to Devonian radiolarians of Scotland, England, and New South Wales of Australia are the first studies applying the treatment of the rock surface with hydrochloric acid. Ancient radiolarians were for the first time investigated not only in traditional thin sections, but also in three-dimensional state. In this case, in partially disrupted specimens, the internal structure is visible.

Hinde (1890, 1899a, 1899b) described for the first time several most important Paleozoic taxa and recognized the presence of several spherical shells in the

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[33] *Trilonche palimbola* (Foreman, 1963)—“Two shells enveloping eccentric six-rayed bar-centered spicule. Six bladed spines of unequal size; one spine considerably larger and remaining five equal to each other in size. Cortical shell exhibits latticed pore frames that are finely spinose” (Noble et al., 2008, p. 53).

skeleton of ancient radiolarians, which he assigned to different genera:

- one sphere—*Acanthosphaera* Ehrenberg, 1858, *Cenosphaera* Ehrenberg, 1854, *Dorysphaera* Hinde, 1890, *Heliosphaera* Haeckel, 1862, *Spongoplegma* Haeckel, 1881, *Staurosphaera* Haeckel, 1881, and *Xiphosphaera* Haeckel, 1881;
- two spheres—*Heliosoma* Haeckel, 1881, *Liosphaera* Haeckel, 1881, *Staurolonche* Haeckel, 1881, *Staurolonchidium* Haeckel, 1887, *Stylosphaera* Ehrenberg, 1847, and *Trilonche* Hinde, 1899;
- three spheres—*Rhodosphaera* Haeckel, 1881.

The overwhelming majority of the genera described by Hinde followed the classification schemes of Haeckel (1862, 1881, 1887) and Ehrenberg (1847, 1854b, 1858), which were based on the study of radiolarians from the Recent beds of the World Ocean. It is highly improbable that Recent forms existed throughout the range of 300–400 m.y. Therefore, it is expedient to replace these genera by Paleozoic taxa.

The study of Foreman (1963) was a new step in the understanding of Paleozoic radiolarians, which attracted attention to the high taxonomic significance of internal structural elements of the skeleton. The study of complete skeletons, extracted from enclosing matter, with the aid of electron microscopy were developed somewhat later and provided a mighty means for the reconstruction of natural phylogenetic relationships between radiolarian groups.

The species established by Foreman (1963) in the genus *Entactinosphaera* are presently assigned based on morphological features to seven genera, which belong to three orders of two radiolarian classes, the class Sphaerellaria, order Entactiniata (*Bientactinosphaera* Afanasieva, 2000, *Entactinosphaera* Foreman, 1963, *Helioentactinia* Nazarov, 1975, and *Radiobisphaera* Won, 1997) and the class Spumellaria, the order Cancelliata (*Retientactinosphaera* Afanasieva, 2011 and *Magnisphaera* Won, 1997) and the order Spongiata (*Spongentactinia* Nazarov, 1975).

A revision of the genus *Bisphaera* Won, 1997 shows that, on the one hand, it is a junior homonym of the genus *Bisphaera* Birina, 1945 and, on the other hand, its species should be referred based on morphology to four genera of the order Entactiniata: *Bientactinosphaera* Afanasieva, 2000, *Helioentactinia* Nazarov, 1975, *Ornatoentactinia* Afanasieva, 2000, and *Radiobisphaera* Won, 1997.

The description and figure of the species *Heliosoma echinatum* Hinde, 1899 give evidence that, on the one hand, it should be accepted in the sense of Foreman (1963, p. 279), but assigned to the genus *Bientactinosphaera* Afanasieva, 2000, which is distinguished by the development of six main spines, *Bientactinosphaera echinata* (Hinde, 1899) (Fig. 39h); and, on the other hand, the initial figures of this species (Figs. 40f, 40g), which are incompletely certain in interpretation of Hinde (1899a, p. 50, pl. IX, figs. 1–3) suggest that these particular morphotypes to the species *Radiobisphaera echinata* (Hinde, 1899) of the genus *Radiobisphaera* Won, 1997, which is distinguished by the predominant development of one main spine.

The genus *Trilonche* as it is treated by Aitchison and Stratford (1997) introduces uncertainty and destabilization in the classification of Paleozoic radiolarians. Therefore, *Trilonche* sensu Aitchison and Stratford should be regarded as nomen dubium.

The genera established by Hinde (1890, 1899a, 1899b) remain valid. However, the genus *Trilonche* should be treated within the framework of the initial diagnosis of Hinde (1899a), who recognized the morphotype with two porous spheres and three main spines.

CHAPTER 7. SYSTEMATIC PALEONTOLOGY

Phylum Radiolaria Müller, 1858

Class Sphaerellaria HaeckeL, 1881

Order Entactiniata Riedel, 1967

Family Entactiniidae Riedel, 1967

Subfamily Entactiniinae Riedel, 1967

Genus *Entactinia* Foreman, 1963

Entactinia: Foreman, 1963, p. 271; Riedel, 1967a, p. 148; Riedel, 1967b, p. 291; Riedel, 1971, p. 650; Nazarov, 1973, p. 697; Nazarov, 1974, p. 39; Nazarov, 1975, p. 46; Nazarov and Popov, 1980, p. 25; Nazarov et al., 1981, p. 82; Nazarov et al., 1982, p. 164; Nazarov and Ormiston, 1983, p. 457; Won, 1983, p. 142; Nazarov and Ormiston, 1984, p. 71; Nazarov and Ormiston, 1985, p. 18; Sashida and Tonishi, 1985, p. 9; Isakova and Nazarov, 1986, p. 62; Nazarov, 1988, p. 58; Schmidt-Effing, 1988, p. 34; Braun, 1989a, p. 87; Braun, 1989b, p. 103; Giese and Schmidt-Effing, 1989, p. 72; Amon et al., 1990, p. 120; Braun, 1990b, p. 108; Renz, 1990, p. 370; Won, 1990, p. 135; Li and Wang, 1991, p. 398; Wang, 1991, p. 249; Noble, 1992, p. 146; Aitchison, 1993, p. 112; Li and Bian, 1993, p. 413; Nazarov and Ormiston, 1993, p. 30; Wang and Kuang, 1993, p. 284; Nazarov and Petrushevskaya, 1995, p. 143; Wang, 1997, p. 151; Wang and Fan, 1997, p. 66; Won, 1997a, p. 347; Kuwahara and Yao, 1998, p. 37; Won, 1998, p. 236; Amon, 1999b, p. 60; Amon, 1999c, p. 190; Afanasieva, 1999, p. 253; Bragin, 1999, p. 40; Afanasieva, 2000a, p. 41; Afanasieva, 2000b, p. 11; Sashida et al., 2000, p. 797; De Wever et al., 2001, p. 180; Afanasieva, 2002, p. 20; Feng et al., 2004, p. 384; Afanasieva et al., 2005d, p. S271; Afanasieva and Amon, 2006a, p. 107.

Tlecerina: Furutani, 1983, p. 110; Kurihara and Sashida, 2000, p. 62.

Stigmosphaerostylus: Kozur and Mostler, 1981, p. 10; Kozur and Mostler, 1989, p. 188; Aitchison and Stratford, 1997, p. 380; Stratford and Aitchison, 1997, p. 247; Aitchison et al., 1999, p. 148; Wang et al., 2000, p. 245; Luo et al., 2002, p. 116; Sashida et al., 2002, p. 135; Vishnevskaya et al., 2002, p. 215; Wang et al., 2003, p. 132; Larchi et al., 2005, p. 128; non Rüst, 1892, p. 142; non Hinde, 1899b, p. 216; non Campbell, 1954, p. D54.

Type species. *Entactinia herculea* Foreman, 1963 (p. 271, pl. 1, figs. 3a–3d); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States (Figs. 38a, 38b).

Diagnosis. Test spherical, with one porous shell. Internal framework represented by double spicule, six rays of which narrower than main spines, originating from median bar. Rays of spicule continued by main three-bladed spines.

Species composition. More than 50 species from the Middle Ordovician–Permian, including *Entactinia austrouralica* Nazarov, 1986 from the Upper Carboniferous of Russia (Southern Urals); *E. bella* Afanasieva et Amon, sp. nov. from the Upper Devonian of Russia (Timan–Pechora Basin, Middle and Polar Urals); *E. bifida* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin and Rudny Altai); *E. bogdanovi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals); *E. cometes* Foreman, 1963 from the Upper Devonian of the United States (Ohio) and Belarus (Pripyat Depression); *E. consociata* Nazarov, 1975 from the Upper Devonian of Kazakhstan (Northern Mugodzhary); *E. crustescens* Foreman, 1963 from the Middle Devonian of Czechia (Prague Basin); from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals) and United States (Ohio); *E. dagmarae* (Suleimanov, 1945) var. *crassitheca* (Antropov, 1950) from the Middle and Upper Devonian of Russia (Volga–Ural Basin); *E. densissima* Nazarov et Ormiston, 1985 from the Lower Permian of Russia (Southern Urals); *E. dimidiata* Nazarov, 1975 from the Upper Devonian of Kazakhstan (Northern Mugodzhary) and Southern China; *E. dissora* Nazarov, 1975 from the Upper Devonian of western Australia, Kazakhstan (Northern Mugodzhary), and southern China; *E. diversita* Nazarov, 1973 from the Upper Devonian of Russia (Timan–Pechora Basin and Middle Urals), Kazakhstan (Northern Mugodzhary), and Poland; *E. dolichoacus* Nazarov, 1986 and *E. dolichoacus dolichoacus* Nazarov, 1986 from the Upper Carboniferous of Russia (Southern Urals); *E. dolichoacus praematura* Nazarov, 1986 from the Upper Carboniferous and Lower Permian of Russia (Southern Urals); *E. duksundiensis* Nazarov, 1981 from the Upper Devonian of Russia (Kolyma Uplift); *E. echinata* (Hinde, 1899) from the Middle Devonian of Australia (New South Wales) and Czechia (Prague Basin); *E. faceta* Amon et Braun, 1990 from the Lower Permian of Russia (Southern Urals); *E. faveolata* Nazarov, 1975 from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of Russia (Volga–Ural Basin) and Kazakhstan (Northern Mugodzhary); *E. herculea* Foreman, 1963 from the Upper Devonian of the United States (Ohio), Russia (Polar Urals and Rudny Altai), Kazakhstan (Northern Mugodzhary), Germany (Bavaria), and southern China; *E. hexagonalis* (Aberdeen, 1940) from the Upper Silurian of Japan; *E. horrida* (Furutani, 1983) from the Lower–Middle Devonian of Russia (Southern Urals) and Japan; *E. inaequoporosa* Won, 1983 from the Upper Devonian of Russia (Polar Urals) and Lower Carboniferous of Russia (Orenburg Fore-Urals) and Germany (Rhine Shale Mountains); *E. itsukaichiensis* Sashida et Tonishi, 1985 from the Upper Permian of Japan, Malaysia, the United States (western Texas), southern China, and Thailand; *E. isensis* (Kurihara et Sashida, 2000) from the Lower Devonian of Russia (Southern Urals) and Lower–Middle Devonian of Japan; *E. micra* (Renz, 1990) from the Upper Ordovician of the United States (Nevada); *E. micula* Foreman, 1963 of the Upper Devonian of the United States (Ohio), Russia (Timan–Pechora Basin), and Poland; *E. modesta* Sashida et Tonishi, 1995 from the Upper Permian of the United States (western Texas) and Japan; *E. monalloea* Foreman, 1963 from the Middle Devonian of western Australia, from the Upper Devonian of the United States (Ohio) and Belarus (Pripyat Depression); *E. ormistoni* Won, 1983 and from the Lower Carboniferous of Germany (Rhine Shale Mountains) and Russia (Orenburg Fore-Urals); *E. oumonhaoensis* Wang, 1997 from the Upper Devonian of Russia (Polar Urals) and southern China; *E. parapycnoclada* Nazarov et Ormiston, 1985 from the Upper Permian of the United States (western Texas) and Japan; *E. parva* Won, 1983 from the Middle Devonian of Czechia (Prague Basin), Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals), and Lower Carboniferous of Germany (Rhine Shale Mountains); *E. patorovaria* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals) and Belarus (Pripyat Depression); *E. paula* Foreman, 1963 from the Middle Devonian of Czechia (Prague Basin), Upper Devonian of the United States (Ohio), Russia (Timan–Pechora Basin), and Belarus (Pripyat Depression); *E. paulis* (Bykova, 1955) from the Middle and Upper Devonian of Russia (Volga–Ural Basin); *E. postadditiva* Nazarov et Ormiston, 1993 and *E. praepycnoclada* Nazarov et Ormiston, 1993 from the Middle Carboniferous of Russia (Kolyma Uplift);

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Explanation of Plate 36

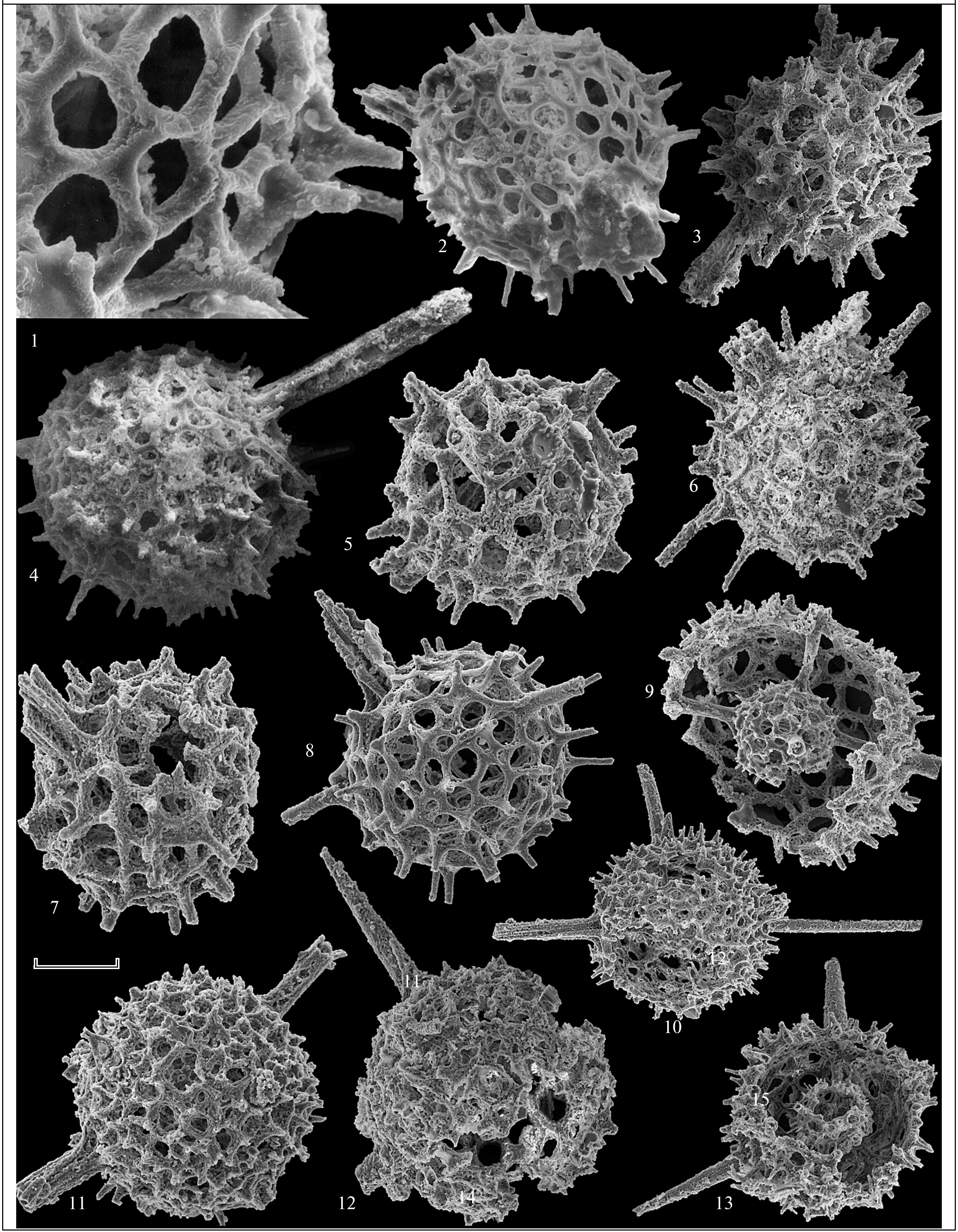
Entactinia bella Afanasieva et Amon (1–8) and *Bientactinosphaera zuraevi* Afanasieva et Amon (9–13).

Figs. 1–8. *Entactinia bella* Afanasieva et Amon, sp. nov.: (1, 2) specimen PIN, no. 5311/12801: (1) fragment, scale bar, 21 μm; (2) scale bar, 55 μm); (3) specimen PIN, no. 5312/15915; scale bar, 74 μm); (4) specimen PIN, no. 5311/12934; scale bar, 68 μm); (5) specimen PIN, no. 5312/15760; scale bar, 50 μm); (6) specimen PIN, no. 5312/15913; scale bar, 72 μm); (7) specimen PIN, no. 5312/15735; scale bar, 61 μm); (8) holotype PIN, no. 5312/15731; scale bar, 62 μm.

Figs. 9–13. *Bientactinosphaera zuraevi* Afanasieva et Amon, sp. nov.: (9) specimen PIN, no. 5312/15732; scale bar, 68 μm; (10) holotype PIN, no. 5312/15718; scale bar, 108 μm; (11) specimen PIN, no. 5312/15774; scale bar, 64 μm; (12) specimen PIN, no. 5312/15956; scale bar, 68 μm; (13) specimen PIN, no. 5312/15958; scale bar, 85 μm.

Upper Devonian, Lower Famennian Substage; (1, 2, 4) Timan–Pechora Basin, Saremboi–Lekkeyaga Swell, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth), sample 86g; Polar Urals, Lemvin Zone, Palnik-Yu River: (5, 7–11) sample 101/594, (3, 6) sample 101/593; and (12, 13) sample 101/599.

Plate 36



E. praenuntia Nazarov et Ormiston, 1993 from the Upper Devonian of Belarus (Pripyat Depression); *E. proceraspina* Aitchison, 1993 from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of western Australia; *E. prodigialis* Nazarov, 1975 from the Upper Devonian of Kazakhstan (Northern Mugodzhary); *E. pycnoclada* Nazarov et Ormiston, 1985 from the Lower Permian of Russia (Southern Urals) and Upper Permian of the United States (western Texas); *E. quantilla* Foreman, 1963 from the Upper Devonian of the United States (Ohio) and Kazakhstan (Northern Mugodzhary); *E. reticulata* Sashida et Tonishi, 1995 from the Upper Permian of the United States (western Texas) and Japan; *E. rostriformis* Afanasieva et Amon, 2008 from the Lower Devonian of Russia (Southern Urals) and Lower Carboniferous of Russia (Orenburg Fore-Urals); *E. spinifera* Amon et Braun, 1990 from the Lower Permian of Russia (Southern Urals); *E. subvasta* (Bykova, 1955) from the Upper Devonian of Russia (Volga–Ural Basin); *E.? sychnacanthina* Foreman, 1963 from the Upper Devonian of the United States (Ohio); *E. tuberculata* (Lipina, 1950) from the Middle and Upper Devonian of Russia (Volga–Ural Basin); *E. variospinas* (Won, 1983) from the Lower Carboniferous of Russia (Orenburg Fore-Urals) and Germany (Rhine Shale Mountains), from the Upper Devonian of southern China and the United States (Alaska); *E. vulgaris* Won, 1983 from the Lower Carboniferous of Russia (Orenburg Fore-Urals) and Germany (Rhine Shale Mountains); and *E. wildei* (Noble et Jin, 2010) from the Upper Permian of the United States (western Texas) and Japan.

Comparison. The genus *Entactinia* differs (1) from the genus *Apophysisphaera* Won, 1997 in the absence of apophyses on the main three-bladed spines; (2) from the genus *Borisella* Afanasieva, 2000 in the formation of three-bladed rather than rod-shaped main spines; (3) from the genus *Altaiesphaera* Obut and Iwata, 2000 in the development of three-bladed rather than conical main spines.

Remarks. See Chapter 6.

Entactinia bella **Afanasieva et Amon, sp. nov.**

Plate 36, figs. 1–8

Etymology. From the Latin *bella* (charming).

Holotype. PIN, no. 5312/15731; Polar Urals, Lemvin Zone, Palnik-Yu River; Upper Devonian, Lower Famennian Substage.

Description.[34] The test is very large, with one relatively thick-walled porous shell and six main spines. The pores are circular, very large, mostly equal in size. The pore canals are wide. The interpore bars are rounded, wide, complicated by sculptural elements in the shape of very long pointed thorns. One main spine is long (even if broken off, the main spine is only slightly shorter than the test diameter: L/D = 0.6–0.9), massive, tetrahedral, with a ✖-shaped section of the spine base and lobate section of lateral blades. Other main spines are very short, conical, equal in size to by-spines. By-spines are mostly long; in some specimens, short, very thick, rod-shaped or conical.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*L*	*wL*	*l*	*wl*	*ht*	*tw*	*dp*	*wp*
15731	175.9	107.3	25.7	64.4	12.9	32.2	8.6	25.7	6.4
12801	191.8	–	33.4	–	12.5	33.4	8.3	25.1	6.3
12934	211.6	191.1	31.9	36.4	9.1	22.8	9.1	27.3	6.8
15913	197.5	–	42.5	72.5	16.5	47.5	7.5	32.5	8.5

Specimen PIN, no. Holotype	*D/tw*	*D/dp*	*D/l*	*D/ht*	*L/D*	*L/wL*	*l/wl*	*dp/tw*	*dp/wp*
15731	20.5	6.8	2.7	5.5	0.6	4.2	4.9	3.0	4.0
12801	23.1	7.6	–	5.7	–	–	–	3.0	4.0
12934	23.3	7.8	5.8	9.3	0.9	5.6	4.0	3.0	4.0
15913	26.3	6.1	2.7	4.2	–	–	4.4	4.3	3.8

Comparison. The new species differs from *Entactinia rostriformis* Afanasieva et Amon, 2008 (with one short, thick, three-bladed, beaked main spine) in the development of one straight tetrahedral main spine; from the species *E. cometes* Foreman, 1963 in the skeleton with only one tetrahedral main spine and the larger pores; in *E. cometes*, the pore diameter ranges from 6 to 15 μm, mostly 10–12 μm (Foreman, 1963, p. 271), whereas, in the new species *E. bella*, the pore diameter (*dp*) is more stable, ranging within 25.1–32.7 μm.

Occurrence. Upper Devonian, Upper Frasnian Substage, Rezh Structural–Formational Zone on the eastern slope of the Middle Urals; Lower Famennian Substage, Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin and Lemvin Zone of the Polar Urals.

Material. Twelve specimens from the type locality (Fig. 6b, IX); borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth) of the Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin (Fig. 6b, XI); from the "Sokharevo" section on the Rezh River and boreholes P-21, P-31 on the Boroukhino Tectonic Plate of the eastern slope of the Middle Urals (Fig. 1c).

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[34] Statistical analysis of absolute and relative skeletal parameters of radiolarians has shown stable patterns of changes in measurements of the skeleton, its parts, and their ratios (Afanasieva, 2000a; Afanasieva et al., 2005d; Afanasieva and Amon, 2006a). The presence of these patterns allows the formalization of classification of the data and use in the description of species the terms *very large, large, small*, and *very small*, which correspond to certain ranked quantitative values (Table 17).

Subfamily Entactinosphaeriinae Afanasieva, 2011

Genus *Entactinosphaera* Foreman, 1963

Entactinosphaera: Foreman, 1963, p. 274; Afanasieva, 2011, p. 7 (123).

Thecentactinia: Nazarov, 1975, p. 71.

Thecoentactinia: Nazarov, 1988, p. 60; Amon, 1999b, p. 57.

Type species. *Entactinosphaera esostrongyla* Foreman, 1963 (pp. 274–275, pl. 2, fig. 1; pl. 6, figs. 1a, 1b); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States (Fig. 39a).

Diagnosis. Test spherical with three shells: external shell porous, fine-pored, less often, reticulate; intermediate shell reticulate, less often, porous; internal shell porous. Internal framework in central position, represented by narrow six-rayed spicule, rays of which continued by three-bladed main spines.

Species composition. Four species from the Lower Silurian–Lower Carboniferous: *Entactinosphaera indeterminata* (Nazarov, 1975) from the Lower Silurian of Russia (Southern Urals); *E. esostrongyla* Foreman, 1963 from the Upper Devonian of the United States (Ohio) and Lower Carboniferous of Thailand; *E.? erebenna* Foreman, 1963 from the Upper Devonian of the United States (Ohio); and *E. riedeli* Foreman, 1963 from the Upper Devonian of the United States (Ohio) and Belarus (Pripyat Depression).

Comparison. The genus *Entactinosphaera* differs from *Bientactinosphaera* Afanasieva, 2000 in the development of three porous shells and from *Radiobisphaera* Won, 1997 in the development of three porous shells and six main spines.

Remarks. See Chapter 6.

Subfamily Bientactinosphaeriinae Afanasieva, 1999

Genus *Radiobisphaera* Won, 1997

Radiobisphaera: Won, 1997a, p. 351; Afanasieva, 2000a, p. 60; 2011, p. 9 (125).

Type species. *Radiobisphaera variantia* Won, 1997 (p. 356, pl. 5, figs. 1–7, 9–11); Upper Devonian, Frasnian Stage, Gogo Formation; Canning Basin, Western Australia.

Diagnosis. Test spherical with two porous shells. Internal framework represented by narrow spicule, six rays of which originating from median bar. Rays of spicule continued by main three-bladed spines, one of which larger than others. Internal sphere complicated by many conical spines, continued by by-spines of external sphere.

Species composition. More than 20 species and subspecies from the Lower Devonian–Lower Permian, including *Radiobisphaera acuta* Won, 1997, *R. cribrisimilis crassa* (Won, 1997), *R. flamans* Won, 1997, *R. magnifenestra* Won, 1997, *R. multa* Won, 1997, *R. multiaculeata* Won, 1997, *R. multiaculeata multiaculeata* Won, 1997, *R. multiaculeata stellaepolus* Won, 1997, *R. variantia* Won, 1997, *R. variantia inaequalis* Won, 1997, *R. variantia variantia* Won, 1997, and *R. uniprocera* (Won, 1997) from the Upper Devonian of western Australia; *R. assidera* (Nazarov, 1975) from the Middle Devonian of Russia (Southern Urals) and western Australia, from the Upper Devonian of western Australia, Belarus (Pripyat Depression), southern China, Poland, Russia (Timan–Pechora Basin, Northern Mugodzhary, Polar Urals, and Rudny Altai), and the United States (Alaska, Ohio), from the Lower Carboniferous of United States (Oklahoma) and from the Upper Carboniferous–Lower Permian of Russia (Southern Urals); *R. domanicensis* (Bykova, 1955) from the Upper Devonian of Russia (Volga–Ural and Timan–Pechora Basins, Rudny Altai, Polar and Southern Urals), Kazakhstan (Caspian Depression, Karachaganak Mountain Range), and the United States (Alaska, Ohio); *R. echinata* (Hinde, 1899) from the Middle Devonian of Australia (New South Wales), southern China and southwestern Japan, from the Upper Devonian of southwestern Japan, Poland, and Russia (Rudny Altai); *R. menneri* Afanasieva, 2000 from the Upper Devonian of Russia (Polar Urals, Volga–Ural and Timan–Pechora basins), Germany (Bavaria) and Poland; *R. palimbola* (Foreman, 1963) from the Upper Devonian of Russia (Polar and Middle Urals), Germany (Bavaria), and the United States (Alaska, Ohio), from the Lower Carboniferous of France and Germany (Rhine Shale Mountains); *R. rozanovi* Afanasieva et Amon, 2009 from the Lower Devonian of Russia (Southern Urals), from the Middle Devonian of Russia (Southern Urals) and Czechia (Prague Basin), from the Upper Devonian of Russia (Timan–Pechora Basin, Rudny Altai, Southern, Middle, and Polar Urals); and *R. trifoliolata* (Umeda, 1998) from the Lower Devonian of southwestern Japan.

Comparison. The genus *Radiobisphaera* differs from *Entactinosphaera* Foreman, 1963 in the development of two porous shells and one main spine and from *Bientactinosphaera* Afanasieva, 2000 in the predominant development of one main spine.

Remarks. See Chapter 6.

Genus *Bientactinosphaera* Afanasieva, 2000

Entactinosphaera: Nazarov, 1975, pp. 59–60; 1988, p. 60; Amon, 1999b, p. 64.

Bientactinosphaera: Afanasieva, 2000a, pp. 13–14; 2000b, pp. 47–48; 2011, p. 8 (124).

Type species. *Entactinosphaera variacanthina* Foreman, 1963 (pp. 278–279, pl. 3, fig. 8; pl. 4, figs. 3a, 3b); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States (Fig. 39g).

Diagnosis. Test spherical with two porous shells. Internal framework in central position, represented by narrow six-rayed spicule, rays of which continued by three-bladed main spines.

Species composition. More than 60 species from the Middle Ordovician–Lower Permian, including *Bientactinosphaera aculeastissima* (Aitchison, 1993) from the Upper Devonian of western Australia and Poland; *B. aculeata* (Nazarov, 1975) and *B. inpercepta* (Nazarov, 1975) from the Upper Ordovician of central Kazakhstan; *B. aenigma* (Nazarov, 1986) from the Lower Permian of Russia (Southern Urals); *B. aitpaiensis* (Nazarov, 1973) from the Upper Devonian of Russia (Timan–Pechora Basin), Kazakhstan (Northern Mugodzhary), and southern China; *B. aksakensis* (Nazarov, 1975), *B. explicata* (Nazarov, 1975), and *B. inconstans* (Nazarov, 1975) from the Middle–Upper Ordovician of central and eastern Kazakhstan; *B. altasulcata* (Won, 1983) from the Upper Devonian of western Australia, Lower Carboniferous of Germany (Rhine Shale Mountains) and Russia (Orenburg Fore-Urals); *B. australis* (Aitchison, 1993) from the Upper Devonian of western Australia, Poland, and Russia (Timan–Pechora Basin); *B. baragensis* Nazarov, 1981 from the Upper Devonian of Russia (Kolyma Uplift); *B. beniguna* (Won, 1997), *B. cribrisimilis cribrisimilis* (Won, 1997), *B. cribrisimilis crassa* (Won, 1997), *B. nazaroviana* (Won, 1997), and *B. solidispinosa* (Won, 1997) from the Upper Devonian of western Australia; *B. bellula* (Wang, 1997) from the Upper Devonian of southern China; *B. cancellicula* (Foreman, 1963) from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of western Australia, Russia (Timan–Pechora Basin and Southern Urals), and the United States (Ohio); *B. clavata* (Hinde, 1899) from the Middle Devonian of Australia (western Australia and New South Wales) and Czechia (Prague Basin); *B. conglobata* (Nazarov, 1975) from the Upper Devonian of Russia (Timan–Pechora Basin) and Kazakhstan (Northern Mugodzhary); *B. echinata* (Hinde, 1899) from the Lower Devonian of Russia (Western Siberia) and southern China, Middle Devonian of Australia (New South Wales), southern China, and Czechia (Prague Basin), and Upper Devonian of Belarus (Pripyat Depression), Poland, Kazakhstan (Northern Mugodzhary), and the United States (Ohio); *B. egindyensis* (Nazarov, 1975) from the Upper Devonian of western Australia, Russia (Timan–Pechora Basin, Rudny Altai, Southern and Middle Urals), Kazakhstan (Northern Mugodzhary), and southern China; *B. elegans* (Hinde, 1899) from the Lower Devonian of Russia (Southern Urals) and Middle Devonian of Australia (Western Australia and New South Wales), southern China, and Czechia (Prague Basin); *B. euthlasta* (Foreman, 1963) from the Upper Devonian of Belarus (Pripyat Depression) and the United States (Ohio); *B. foremanae* (Ormiston et Lane, 1976) from the Lower Carboniferous of the United States (Oklahoma); *B. grandis* (Nazarov, 1975) from the Middle Devonian of western Australia, Upper Devonian of western Australia, Russia (Middle Urals, Timan–Pechora and Volga–Ural Basins), Kazakhstan (Northern Mugodzhary), and southern China; *B. guangxiensis* (Li et Wang, 1991) from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals) and southern China; *B. hapala* (Foreman, 1963) from the Upper Devonian of the United States (Ohio); *B. hindea* (Aitchison et Stratford, 1997) from the Lower Devonian of Australia (New South Wales); *B. hystricosa* (Foreman, 1963) from the Upper Devonian of western Australia, Russia (Timan–Pechora Basin and Rudny Altai), and the United States (Ohio); *B. inusitata* (Foreman, 1963) from the Middle Devonian of western Australia and Upper Devonian of western Australia, Russia (Timan–Pechora Basin), Kazakhstan (Northern Mugodzhary), southern China, and the United States (Ohio); *B. limpida* (Lipnitskaja, 2002) and *B.* (?) *tortilispina* (Lipnitskaja, 2002) from the Lower Devonian of Russia (Western Siberia); *B. linquidambarfructa* (Ormiston et Lane, 1976) from the Lower Carboniferous of Russia (Orenburg Fore-Urals) and the United States (Oklahoma); *B. maslakovae* Afanasieva, 2000 from the Upper Devonian of western Australia and Russia (Timan–Pechora Basin); *B. miletenkoi* Afanasieva, 2000 and *B. morozovi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin); *B. nanningensis* (Luo, Aitchison et Wang, 2002) from the Middle Devonian of southern China; *B. nigra* (Hinde, 1899) from the Middle Devonian of Australia (New South Wales) and Russia (Southern Urals); *B. octaparvispina* (Won, 1983) from the Lower Carboniferous of Germany (Rhine Shale Mountains); *B. obtusa* (Hinde, 1899) from the Middle Devonian of Australia (New South Wales) and Russia (Southern Urals) and from the Upper Devonian of Russia (Timan–Pechora Basin, Polar Urals, and Rudny Altai); *B. parapalimbola* (Wang, 2003) from the Upper Devonian of southern China; *B. pinica* Afanasieva, 2000 from the Upper Devonian of western Australia and Russia (Timan–Pechora Basin, Middle Urals, and Rudny Altai); *B. pittmani* (Hinde, 1899) from the Lower Devonian of Russia (Southern Urals), Middle Devonian of Australia (New South Wales), Czechia (Prague Basin), and Russia (Southern Urals), and from the Upper Devonian of Russia (Timan–Pechora Basin, Rudny Altai, Middle and Southern Urals); *B. pseudocimelia* (Sashida et Tonishi, 1988) from the Middle Triassic of Thailand; *B. pulcherima* (Nazarov et Ormiston, 1993) from the Upper Devonian of Belarus (Pripyat Depression) and Russia (Middle Urals); *B. robusta* (Aitchison, 1993) from the Upper Devonian of western Australia; *B. spinofoliacea* Nazarov et Afanasieva, 2000 from the Upper Devonian of Belarus (Pripyat Depression) and Russia (Timan–Pechora Basin); *B. strangulata* (Nazarov et Ormiston, 1985) from the Lower Permian of Russia (Southern Urals); *B. symphypora* (Foreman, 1963) from the Middle Devonian of Russia (Southern Urals) and Upper Devonian of Belarus (Pripyat Depression), Russia (Timan–Pechora Basin), and the United States (Ohio); *B. tanheensis* (Luo, Aitchison et Wang, 2002) from the Middle Devonian of southern China; *B. tretactinia* (Foreman, 1963) from the Upper Devonian of the United States (Ohio); *B. variacanthina* (Foreman, 1963) from the Middle Devonian of Australia (New South Wales) and southern China, Upper Devonian of western Australia, Belarus (Pripyat Depression), Russia (Polar Urals, Timan–Pechora and Volga–Ural Basins), Kazakhstan (Northern Mugodzhary), southern China, and the United States (Ohio); *B. vetusta* (Hinde, 1899) from the Lower Devonian of Russia (Southern Urals) and southern China, Middle Devonian of Australia (western Australia and New South Wales), Kazakhstan (Northern Mugodzhary), southern China, and Russia (Southern Urals), and from the Upper Devonian of Russia (Middle Urals); *B. xinpoensis* (Luo, Aitchison et Wang, 2002) from the Middle Devonian of southern China; and *B. zuraevi* Afanasieva et Amon, sp. nov. from the Upper Devonian of Russia (Polar Urals).

Comparison. The genus *Bientactinosphaera* differs from *Entactinosphaera* Foreman, 1963 in the development of two porous shells; from *Ornatoentactinia* Afanasieva, 2000 in the absence of meshed sculpturing on the skeleton surface; and from *Radiobisphaera* Won, 1997 in the development of six main spines.

Remarks. See Chapter 6.

Bientactinosphaera zuraevi Afanasieva et Amon, sp. nov.

Plate 36, figs. 9–13

Etymology. The species is named in honor of O.A. Zuraev.

Holotype. PIN, no. 5312/15718; Polar Urals, Lemvin Zone, Palnik-Yu River; Upper Devonian, Lower Famennian Substage.

Description. The test is very large, with two porous shells and six main spines. The external sphere is thin-walled. The pores of the outer shell are circular, large, approximately equal in size. The pore canals are wide. The interpore bars are wide, sharpened, complicated by sculptural elements in the shape of very high pointed thorns. The internal sphere is very large, thick-walled. The pores of the internal sphere are circular, large, approximately equal in size. The main spines are long (the spine is slightly shorter than the shell diameter: $L/D = 0.7–0.9$) and narrow. Five main spines are rod-shaped, with circular section of the spine base. One main spine is three-bladed, with ⅄-shaped section of the spine base and lobate section of each side. By-spines are absent.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*L*	*wL*	*tw*	*dp*	*wp*	*ht*	*Ds*	*ts*
15718	246.1	211.5	23.1	7.7	15.4	9.6	23.1	96.1	3.8
15732	221.8	–	18.5	6.9	16.2	6.9	16.2	87.8	4.6
15774	203.3	–	25.4	6.9	13.9	6.9	13.9	–	–
15956	212.5	155.0	25.4	6.9	18.5	9.2	11.6	73.9	–
15958	194.1	129.4	20.6	6.7	14.7	7.4	17.6	76.4	4.4

Specimen PIN, no. Holotype	*D/tw*	*D/dp*	*D/ht*	*D/Ds*	*Ds/ts*	*L/D*	*L/wL*	*dp/tw*	*dp/wp*
15718	32.0	15.9	10.7	2.6	25.3	0.9	9.2	2.0	1.6
15732	32.1	13.7	13.7	2.5	19.1	–	–	2.4	2.4
15774	29.5	14.6	14.6	–	–	–	–	2.0	2.0
15956	30.8	11.5	18.3	2.9	–	0.7	6.1	2.7	2.0
15958	29.0	13.2	11.3	2.5	17.4	0.7	6.3	2.2	2.0

Comparison. The new species differs from *Bientactinosphaera cancellicula* (Foreman, 1963), with six three-bladed main spines, in the presence of five rod-shaped main spines and one three-bladed spine.

Occurrence. Upper Devonian, Lower Famennian Substage; Lemvin Zone of the Polar Urals, Palnik-Yu River.

Material. Five specimens from the type locality (Fig. 6b, IX).

Family Astroentactiniidae Nazarov et Ormiston, 1985

Subfamily Helioentactiniinae Afanasieva, 1999

Genus *Helioentactinia* Nazarov, 1975

Helioentactinia: Nazarov, 1975, p. 88; 1988, p. 62; Amon et al., 1990, p. 119; Amon, 1999b, p. 74; Afanasieva, 2000a, pp. 72–73; 2011, p. 9 (126).

Type species. *Entactinosphaera? polyacanthina* Foreman, 1963 (p. 280, pl. 4, fig. 6; pl. 6, fig. 11); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States (Fig. 39m).

Diagnosis. Test spherical, with two porous shells. Internal framework represented by narrow spicule, eight rays of which originating from median bar. External main spines numerous (from eight to twelve, less often, more), rod-shaped, conical or, mostly, three-bladed.

Species composition. More than 15 species from the Upper Cambrian (?)–Lower Ordovician–Lower Permian, including *Helioentactinia aster* Aitchison, 1993 from the Upper Devonian of western Australia, southern China, and Russia (Timan–Pechora Basin); *H. asymmetrica* Nazarov, 1975 from the Lower–Middle Ordovician of central and eastern Kazakhstan; *H. bakanasensis* Nazarov, 1975 from the Upper Cambrian (?)–Upper Ordovician of central and eastern Kazakhstan; *H. biexosphaera* Nazarov, 1986 and *H. ikka* Nazarov et Ormiston, 1993 from the Lower Permian of Russia (Southern Urals); *H. circumtexta* Nazarov, 1975 and *H. secutrix* Nazarov, 1975 from the Upper Devonian of Russia (Northern Mugodzhary); *H. dissimilicortex* (Won, 1997) from the Upper Devonian of western Australia; *H. gudymovae* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin); *H. perjucunda* Nazarov et Ormiston, 1983 from the Upper Devonian of western Australia, Belarus (Pripyat Depression), Kazakhstan (Northern Mugodzhary), and Russia (Timan–

Pechora Basin); *H. polyacanthina* (Foreman, 1963) from the Middle Devonian of Russia (Southern Urals) and Upper Devonian of western Australia, United States (Ohio), China (northern Xinjiang), and Russia (Timan–Pechora Basin); *H. stellaepolus* Aitchison, 1993 from the Upper Devonian of western Australia and Russia (Timan–Pechora Basin); *H. valavica* Nazarov et Ormiston, 1993 from the Upper Devonian of Belarus (Pripyat Depression) and Russia (Timan–Pechora Basin and Polar Urals); and *H. yunnanensis* Wang from the Middle Devonian of southern China.

Comparison. The genus *Helioentactiniinae* differs from *Astroentactinia* Nazarov, 1975 and *Multisphaera* Nazarov et Afanasieva, 2000 in the development of two porous shells and from *Moskovistella* Afanasieva, 2000 in the development of two porous shells and the absence of apophyses on numerous main spines.

Class Spumellaria Ehrenberg, 1875

Order Cancelliata Afanasieva et Amon, 2003

Family Haplentactiniidae Nazarov, 1980

Subfamily Haplentactiniinae Nazarov, 1980

Genus *Haplentactinia* Foreman, 1963

Haplentactinia: Foreman, 1963, p. 270; Nazarov, 1975, p. 58; 1988, pp. 64–65; Nazarov and Popov, 1980, pp. 52–53; Amon, 1999b, p. 87; Afanasieva, 2000a, pp. 30–31.

Type species. *Haplentactinia rhinophyusa* Foreman, 1963 (p. 270, pl. 1, fig. 2; pl. 3, fig. 7); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States.

Diagnosis. Test spherical, with one completely or partially developed latticed shell formed of nonuniformly developed apophyses at two levels of rays of spicule. Internal framework represented by massive six-rayed spicule, rays of which originating from one center. Rays of spicule continued by rod-shaped main spines.

Species composition. Fifteen species are known from the Lower Ordovician–Upper Devonian, although the number of species may be greater; they include *Haplentactinia alekseevi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin and Middle Urals); *H. aperticuva* (Aitchison, 1993) from the Middle and Upper Devonian of Australia (western Australia and New South Wales) and Upper Devonian of Russia (Timan–Pechora Basin); *H. armillata* Nazarov, 1980 from the Lower Ordovician of central Kazakhstan; *H. baltica* Nazarov, 1980 from the Upper Ordovician of Estonia and central Kazakhstan; *H. barskovi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin, Rudny Altai); *H. bornazi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin); *H. flagellifera* Nazarov et Ormiston, 1993 from the Upper Devonian of Belarus (Pripyat Depression) and Russia (Middle Urals); *H. inaudita* Nazarov, 1984 from the Upper Devonian of Kazakhstan (Northern Mugodzhary); *H. infida* Nazarov, 1975 and *H. juncta* Nazarov, 1975 from the Middle Ordovician of eastern Kazakhstan; *H. kuzminae* Afanasieva et Amon, sp. nov. from the Upper Devonian of Russia (Timan–Pechora Basin, Polar and Middle Urals); *H. labyrinthica* (Aitchison, 1993) from the Upper Devonian of Russia (Timan–Pechora Basin, Rudny Altai, and Southern Urals) and western Australia; *H. rhinophyusa* Foreman, 1963 from the Upper Devonian of Russia (Timan–Pechora Basin, Polar and Middle Urals) and the United States (Ohio); *H. silurica* Nazarov et Ormiston, 1990 from the Lower Silurian of Russia (Southern Urals); and *H. vilvaensis* sp. nov. from the Upper Devonian of Russia (Middle Urals).

Remarks. In works of Nazarov (1988) and Amon (1999b), the diagnosis of the genus *Haplentactinia* is supplemented by the statement that "the inner cavity of the shell is filled by chaotic interlacing spongy tissue," which is absent in the original diagnosis of Foreman: "Six-rays double spicule with branches arising at two levels along each ray and sometimes forming an irregular lattice-shell" (Foreman, 1963, p. 270).

Haplentactinia vilvaensis Afanasieva et Amon, sp. nov.

Plate 37, figs. 1–8

Etymology. From the Vilva River in the eastern Perm Region of the Middle Urals.

→

Explanation of Plate 37

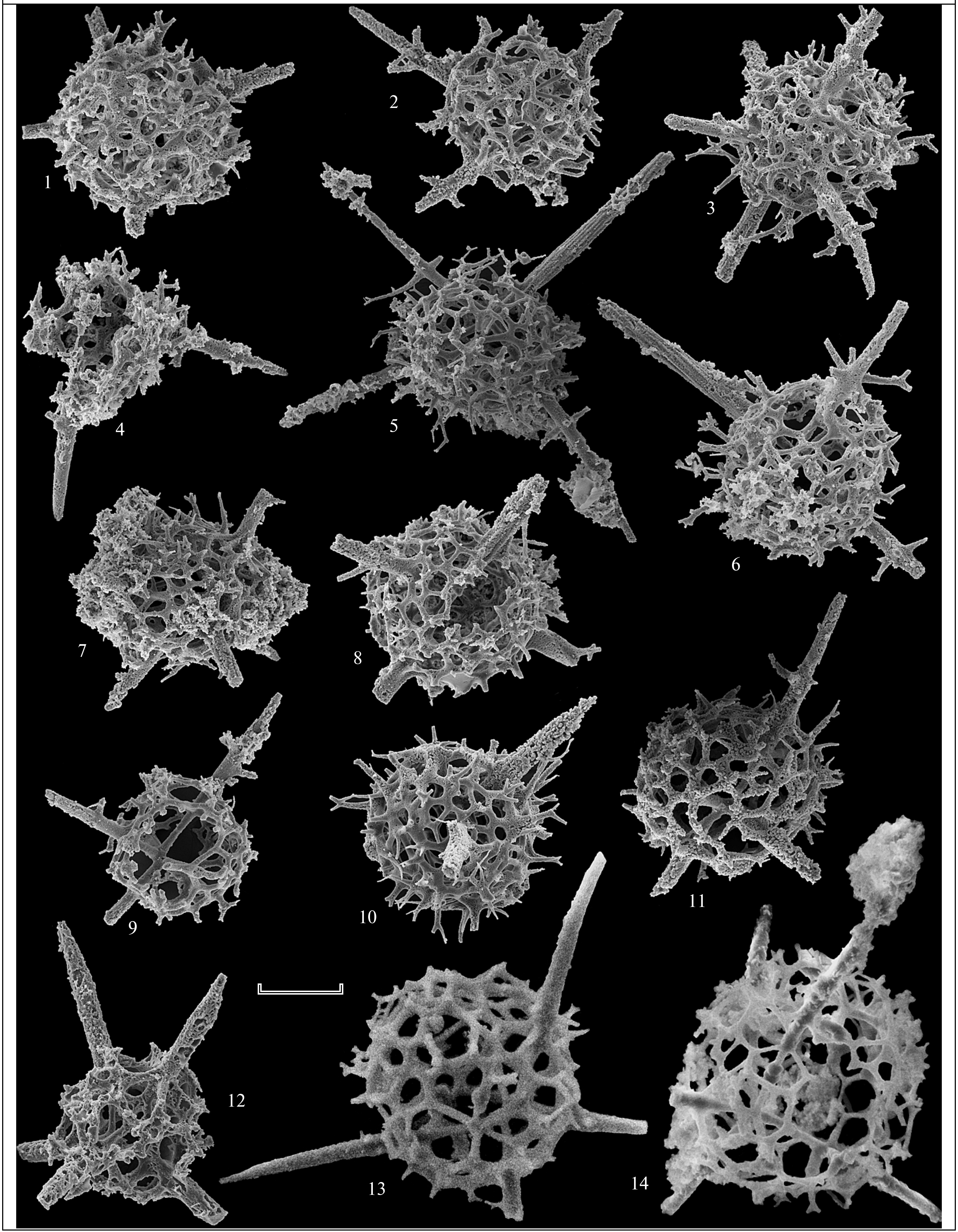
Haplentactinia vilvaensis Afanasieva et Amon (1–8) and *Haplentactinia kuzminae* Afanasieva et Amon (9–14).

Figs. 1–8. *Haplentactinia vilvaensis* Afanasieva et Amon, sp. nov.: (1) specimen PIN, no. 5369/15623; scale bar, 79 μm; (2) specimen PIN, no. 5369/15617; scale bar, 85 μm; (3) holotype PIN, no. 5369/15616; scale bar, 89 μm; (4) specimen PIN, no. 5369/15634; scale bar, 72 μm; (5) specimen PIN, no. 5369/15641; scale bar, 64 μm; (6) specimen PIN, no. 5369/15629; scale bar, 69 μm; (7) specimen PIN, no. 5369/15624; scale bar, 89 μm; (8) specimen PIN, no. 5369/15627; scale bar, 69 μm.

Figs. 9–14. *Haplentactinia kuzminae* Afanasieva et Amon, sp. nov.: (9) specimen PIN, no. 5369/15648; scale bar, 86 μm; (10) specimen PIN, no. 5369/15639; scale bar, 74 μm; (11) specimen PIN, no. 5369/15625; scale bar, 72 μm; (12) specimen PIN, no. 5312/15957; scale bar, 72 μm; (13) holotype PIN, no. 5311/11313; scale bar, 33 μm; (14) specimen PIN, no. 5311/05019; scale bar, 33 μm.

Upper Devonian: (1–11) Lower Famennian Substage; (13, 14) Middle Frasnian Substage, Domanik Formation. Middle Urals, Perm Region, Vilva River, southeast of the town of Gremyachinsk: (1–8, 10, 11) sample k-25, (9) sample k-07/1; (12) Polar Urals, Lemvin Zone, Palnik-Yu River, sample 101/594; Timan–Pechora Basin: (13) borehole Shuda-Yag-1003 (68.4–69.3 m of depth), sample 78; (14) Ukhta River, station 4, sample B-29.

Plate 37



Holotype. PIN, no. 5369/15616; Middle Urals, Perm Region, Vilva River, southeast of the town of Gremyachinsk; Upper Devonian, Lower Famennian Substage.

Description. The test is large, with one latticed shell formed by thick, relatively regular, interlacing rods. The pores are very large, rounded polygonal, approximately equal in size. The pore canals are wide. The interpore bars are wide, complicated by sculptural elements in the shape of numerous very high pointed thorns. The internal framework is located at the center of the skeleton. The main spines are long, narrow, rod-shaped, complicated by apophyses.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*L*	*wL*	*tw*	*dp*	*wp*	*ht*
15616	175.0	125.5	17.5	6.9	20.0	6.9	31.3
15617	155.8	129.4	20.6	5.9	23.5	5.9	20.6
15629	150.0	170.0	15.0	7.5	25.0	7.5	25.0
15641	159.3	212.4	18.6	6.6	24.3	6.6	35.4

Specimen PIN, no. Holotype	*D/tw*	*D/dp*	*D/ht*	*L/D*	*L/wL*	*dp/tw*	*dp/wp*
15616	25.4	8.8	5.6	0.7	7.2	2.9	2.9
15617	26.4	6.6	7.6	0.8	7.6	4.0	4.0
15629	20.0	6.0	6.0	1.1	11.3	3.3	3.3
15641	24.1	6.6	4.5	1.3	11.4	3.7	3.7

Comparison. The new species differs from *Haplentactinia alekseevi* Afanasieva, 2000 in the larger skeleton with many very high thorns and the main spines complicated by apophyses.

Occurrence. Upper Devonian, Lower Famennian Substage; Vilva River of the Perm Region, Middle Urals.

Material. Nine specimens from the type locality (Fig. 1b).

Haplentactinia kuzminae Afanasieva et Amon, sp. nov.

Plate 37, figs. 9–14

Haplentactinia alekseevi: Afanasieva, 2000a, pl. 24, figs. 6 and 9.

Etymology. The species is named in honor of Ya.M. Kuz'mina.

Holotype. PIN, no. 5311/11313; Timan–Pechora Basin, Ukhtinskii District, Ukhta River, station 4; Upper Devonian, Middle Frasnian Substage, Domanik Formation.

Description. The test is small, with one latticed shell formed of relatively regular interlacing thick rods. The pores are very large, rounded polygonal, varying in size. The pore canals are wide and very wide. The interpore bars are narrow, complicated by numerous sculptural elements in the shape of very high, pointed thorns. The main spines are long, narrow, rod-shaped. The internal framework is displaced relative to the center of the skeleton.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*L*	*wL*	*tw*	*dp*	*wp*	*ht*
11313	98.8	74.1	9.9	3.7	19.8	3.7	4.9
05019	111.2	86.5	7.4	3.7	17.3	3.7	9.9
15625	150.0	110.0	16.0	7.0	22.5	7.0	15.0
15639	145.0	120.0	20.0	6.0	20.0	6.0	15.0
15957	125.0	135.0	17.5	6.0	35.0	6.0	7.5

Specimen PIN, no. Holotype	*D/tw*	*D/dp*	*D/ht*	*L/D*	*L/wL*	*dp/tw*	*dp/wp*
11313	26.7	5.0	20.2	0.8	7.5	5.4	5.4
05019	30.1	6.4	11.2	0.8	11.7	4.7	4.7
15625	21.4	6.7	10.0	0.7	6.9	3.2	3.2
15639	24.2	7.3	9.7	0.8	6.0	3.3	3.3
15957	20.8	3.6	16.7	1.1	7.7	5.8	5.8

Comparison. The new species differs from *Haplentactinia alekseevi* Afanasieva, 2000 and *H. vilvaensis* Afanasieva et Amon sp. nov. in the internal framework displaced relative to the skeleton center and in the relatively shorter main spines without apophyses.

Occurrence. Upper Devonian, Middle Frasnian Substage, Domanik Formation of the Ukhtinskii District of the Timan–Pechora Basin; Lower Famennian Substage of the Lemvin Zone of the Polar Urals and Perm Region of the Middle Urals.

Material. Six specimens from the type locality (Fig. 6c), from borehole Shuda-Yag-1003 (68.4–69.3 m of depth) in the Ukhtinskii District of the Timan–Pechora Basin (Fig. 6c), from an outcrop on the Vilva River in the Perm Region of the Middle Urals (Fig. 6b, IX) and from an outcrop on the Palnik-Yu River in the Lemvin Zone of the Polar Urals (Fig. 1b).

Subfamily Pseudorotasphaerinae Noble, 1994

Genus *Retientactinosphaera* Afanasieva, 2011

Type species. *Retientactinosphaera magnifica* Afanasieva, 2011 (pp. 11–12, pl. 1, figs. 1–5); Timan–Pechora Basin, Saremboi–Lekkeyaga Swell, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth), sample 86g; Upper Devonian, Lower Famennian Substage, Zadonskaya Horizon.

Diagnosis. Test spherical, with two reticulate shells and one three-bladed main spine with ☢-shaped section of base. Internal framework represented by narrow spicule, six rays of which originating from median bar. Internal sphere very large, from half to three-fourths of shell diameter. Internal sphere complicated by many conical spines, connecting inner and outer shells of skeleton and terminating on shell surface into by-spines or thorns.

Species composition. Four species from the Upper Devonian: *Retientactinosphaera clavata* Afanasieva, 2011 from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals); *R. fredericki* (Foreman, 1963) from the Upper Devonian of the United States (Ohio); *R. magnifica* Afanasieva, 2011 from the Upper Devonian of Russia (Timan–Pechora Basin); and *R. unimana* (Nazarov, 1977) from the Upper Devonian of Belarus (Pripyat Depression).

Comparison. The genus *Retientactinosphaera* differs from *Cancellosphaera* Afanasieva, 2000 and *Russirad* Afanasieva, 2000 in the formation of two reticulate shells and only one main spine.

Family Polyentactiniidae Nazarov, 1975

Subfamily Magnisphaerinae Afanasieva, 1999

Genus *Magnisphaera* Won, 1997

Magnisphaera: Won, 1997, p. 366; Afanasieva, 2000a, p. 38; 2011, p. 10 (127).

Type species. *Magnisphaera gigantea* Won, 1997 (p. 368, pl. 6, figs. 3–5); Upper Devonian, Frasnian Stage, Gogo Formation; Canning Basin, western Australia.

Diagnosis. Test large spherical, with two latticed shells. Internal framework represented by narrow spicule, eight rays of which originating from median bar.

Species composition. Four species from the Upper Devonian: *Magnisphaera dystactotata* (Foreman, 1963) from the Upper Devonian of the United States (Ohio); *M. aitchisoniana* Won, 1997, *M. gigantea* Won, 1997, and *M. imperfecta* Won, 1997 from the Upper Devonian of western Australia.

Comparison. The genus *Magnisphaera* differs from *Polyentactinia* Foreman, 1963 in the presence of the internal latticed shell.

Order Spongiata Afanasieva et Amon, 2003

Family Spongentactiniidae Nazarov, 1975

Subfamily Spongentactiniinae Nazarov, 1975

Genus *Spongentactinia* Nazarov, 1975

Spongentactinia: Nazarov, 1975, p. 75; Nazarov, 1988, p. 60; Amon, 1999b, pp. 67–68; Afanasieva, 2000a, pp. 79–80; 2011, p. 10 (127).

Type species. *Spongentactinia fungosa* Nazarov, 1975 (pp. 75–76, pl. XI, fig. 6; pl. XII, fig. 6); Upper Devonian, Frasnian Stage, Egindy Formation; Southern Urals, Northern Mugodzhary, Aitpaika River.

Diagnosis. Test with two shells; outer shell spongy and internal shell latticed. Internal framework represented by spicule, six rays of which originating from very short median bar. Rays of spicule continued by three-bladed or, less often, rod-shaped main spines.

Species composition. About 15 species from the Lower Silurian–Lower Permian, including *S. concinna* Aitchison, 1993 and *S. exquisita* Aitchison, 1993 from the Upper Devonian of western Australia; *S. diplostraca* (Foreman, 1963) from the Middle Devonian of Czechia (Prague Basin) and from the Upper Devonian of Russia (Timan–Pechora Basin, Polar and Southern Urals, Rudny Altai), Belarus (Pripyat Depression), western Australia, and the United States (Ohio); *S. fungosa* Nazarov, 1975 from the Lower Devonian of Russia (Southern Urals), Middle Devonian of Czechia (Prague Basin), and Russia (Southern Urals), Upper Devonian of Russia (Rudny Altai, Southern and Middle Urals) and Kazakhstan (Northern Mugodzhary), and from the Lower Carboniferous and Lower Permian of Kazakhstan (Caspian Depression, Karachaganak Mountain Range); *S. indesserta* Nazarov, 1975 from the Upper Devonian of Kazakhstan (Northern Mugodzhary) and western Australia; *S. marina* Afanasieva et Amon, sp. nov. from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals); *S. nupera* Nazarov, 1981 from the Upper Devonian of Russia (Middle Urals and Kolyma Uplift); *S. polaris* Afanasieva et Amon, sp. nov. from the Upper Devonian of Russia (Timan–Pechora Basin and Polar Urals); *S. shaijingpoensis* Wang, 2000 from the Middle Devonian of southern China; *S. somphorhips* (Foreman, 1963) from the Upper Devonian of the United States (Ohio) and Poland; *S. spongites* (Foreman, 1963) from the Middle Devonian of Russia (Southern Urals) and Upper Devonian of Belarus (Pripyat Depression) and the United States (Ohio); and *S. subtiradiata* Nazarov, 1975 from the Lower Silurian of Russia (Southern Urals).

Comparison. The genus *Spongentactinia* differs from *Tetrentactinia* Foreman, 1963 and *Spongentactinella* Nazarov, 1975 in the presence of the internal latticed shell and from *Retisphaera* Won, 1997 in the thinner spongy external shell.

Spongentactinia polaris Afanasieva et Amon, sp. nov.

Plate 38, figs. 1–3

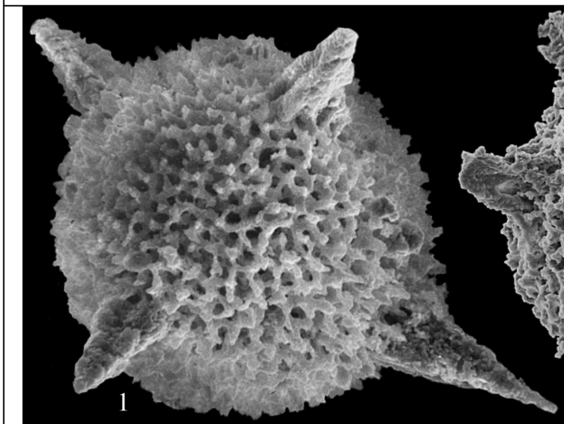
Spongentactinia crustescens (Foreman): Afanasieva, 2000a, p. 80, pl. 85, fig. 1.

Etymology. From the Greek πολοζ (pole) and the Latin *polaris* (polar).

Holotype. PIN, no. 5311/088-12836; Timan–Pechora Basin, Saremboi–Lekkeyaga Swell, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth); Upper Devonian, Lower Famennian Substage, Zadonsk Formation.

Description. The test is large, with two shells and six main spines. The outer shell is spongy, relatively thin-walled. The pores are small, circular, mostly equal in size. The pore canals are very wide ($dp/tw = 1.5$). The interpore bars are very wide, sharpened. The internal sphere is very small, porous, thick-

Plate 38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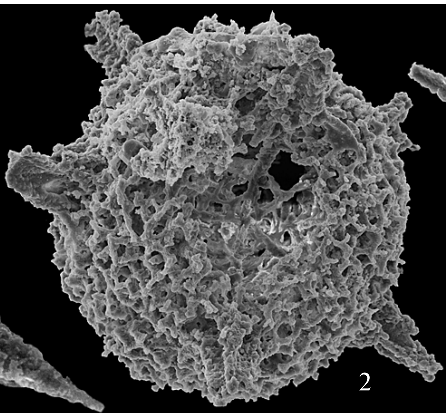
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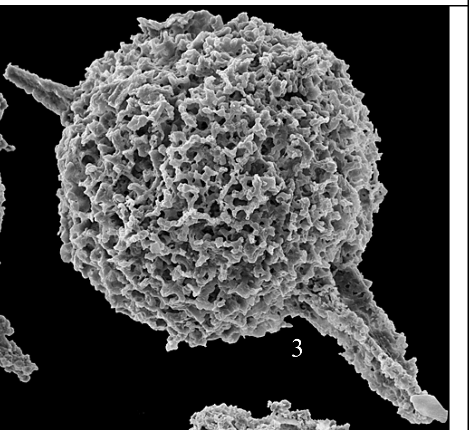
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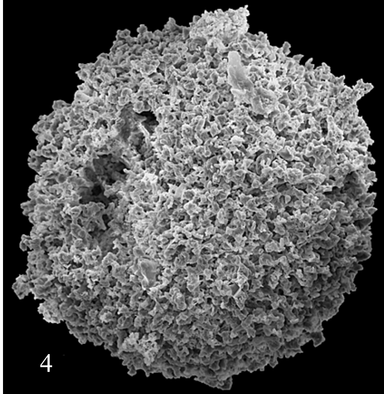
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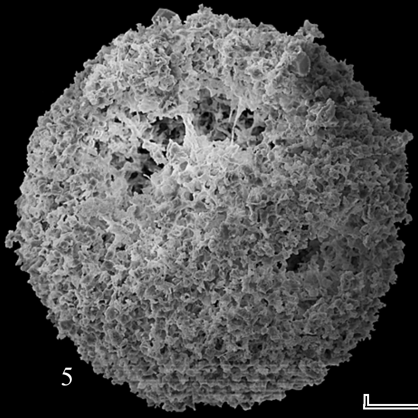
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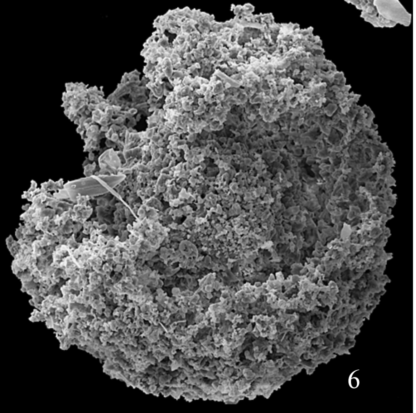
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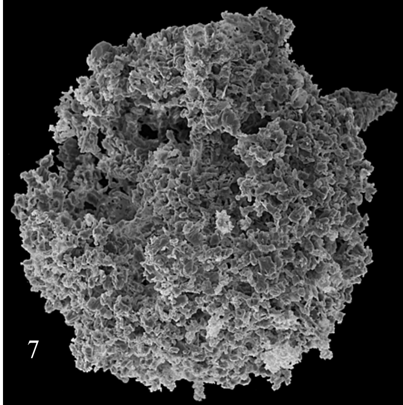
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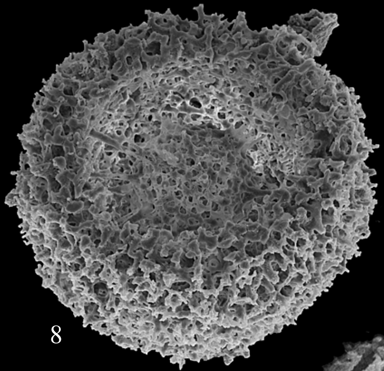
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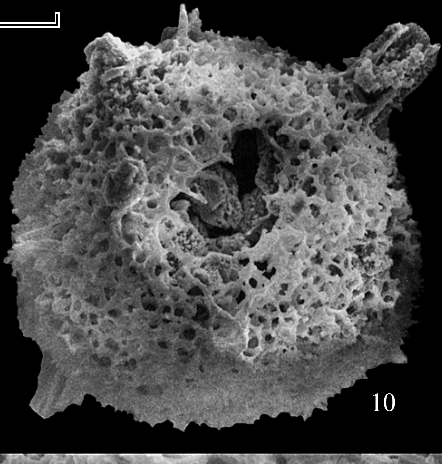
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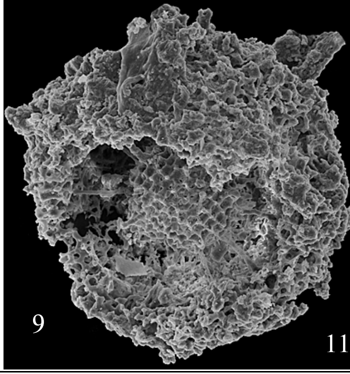
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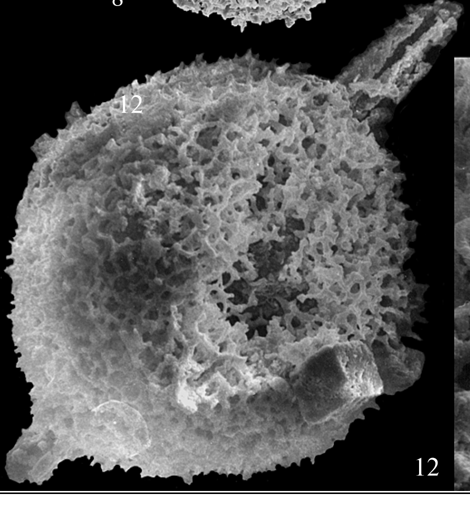

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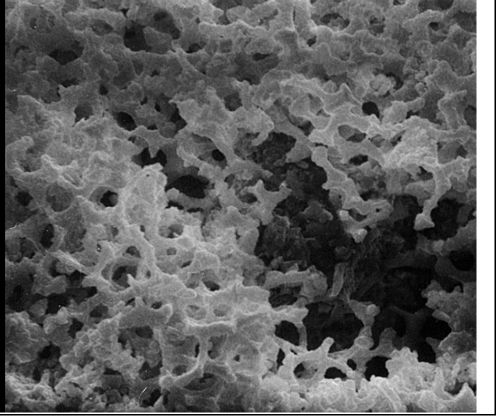
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walled. The pores of the internal sphere are large, circular, equal in size. The main spines are short and very short (L/D = 0.3–0.5), very massive, three-bladed, with a -shaped section of the spine base. One main spine is slightly longer than others.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	D	L	wL	tw	dp	wp	Ds	ts
12836	148.7	65.8	28.6	–	7.2	2.9	–	–
15773	184.0	48.0	24.0	4.0	6.0	2.0	60.0	4.0
15810	126.0	66.0	28.5	–	4.5	1.5	–	–

Specimen PIN, no. Holotype	D/tw	D/dp	D/Ds	Ds/ts	L/D	L/wL	dp/tw	dp/wp
12836	–	20.7	–	–	0.4	2.3	–	2.5
15773	46.0	30.7	3.1	15.0	0.3	2.0	1.5	3.0
15810	–	28.0	–	–	0.5	2.3	–	3.0

Comparison. The new species differs from *Spongentactinia crustescens* (Foreman, 1963) in the development of six short massive main spines.

Occurrence. Upper Devonian, Lower Famennian Substage, Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin and Lemvin Zone of the Polar Urals.

Material. Five specimens from the type locality (Fig. 6b, XI) and from an outcrop on the Palnik-Yu River in the Lemvin Zone of the Polar Urals (Fig. 6b, IX).

Spongentactinia marina Afanasieva et Amon, sp. nov.

Plate 38, figs. 4–10

Etymology. From the Latin *marina* (marine).

Holotype. PIN, no. 5312/15722; Polar Urals, Lemvin Zone, Palnik-Yu River; Upper Devonian, Lower Famennian Substage.

Description. The test is very large, with two shells and six main spines. The outer shell is spongy, very thick-walled, with small and very small circular pores. The pore canals are very narrow. The interpore bars are very wide. The internal sphere is very large, porous, thick-walled. The pores of the internal sphere are large, equal in size, circular. The main spines are massive, three-bladed, with -shaped section of the spine base, although they seem very short because of disruption.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	D	L	wL	tw	dp	wp	Ds	ts
15722	216.0	28.8	28.8	31.7	4.8	8.6	72.0	3.8
15707	230.0	36.8	23.0	36.8	3.2	7.4	82.8	4.2
15801	220.0	32.2	35.0	30.0	5.0	7.5	80.0	4.0
15982	239.2	41.6	28.6	41.6	5.2	14.7	83.2	6.2
15989	225.0	–	–	27.5	3.0	9.0	–	–
15991	230.0	–	–	41.4	3.2	7.8	69.0	4.2

Specimen PIN, no. Holotype	D/tw	D/dp	D/Ds	Ds/ts	L/D	L/wL	dp/tw	dp/wp
15722	6.8	45.0	3.0	19.0	0.1	1.0	0.2	0.6
15707	6.3	71.9	2.9	19.7	0.2	1.6	0.1	0.4
15801	7.3	44.0	2.8	20.0	0.3	0.9	0.2	0.7
15982	5.6	46.0	2.9	13.4	0.2	1.5	0.1	0.4
15989	8.2	75.0	–	–	–	–	0.1	0.3
15991	5.6	71.9	3.3	16.4	–	–	0.1	0.4

Comparison. The new species differs from *Spongentactinia diplostraca* (Foreman, 1963) in the poorly developed main spines and very thick outer shell of the skeleton.

Occurrence. Middle Devonian, Upper Eifelian Substage, terminal Chotec Formation of the Prague Basin, Czechia; Upper Devonian, Lower Famennian Substage, Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin and Lemvin Zone of the Polar Urals.

Material. Six specimens from the type locality (Fig. 6b, IX), from borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth) Saremboi–Lekkeyaga Swell of the Timan–Pechora Basin (Fig. 6b, XI) and from the Hlubocepy section of the Prague Basin (Barrandian) of Czechia (Fig. 7).

Explanation of Plate 38

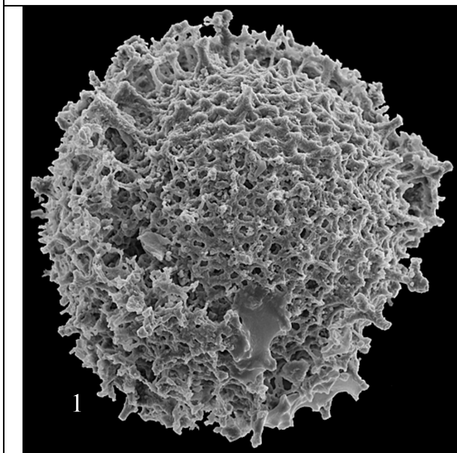
Spongentactinia polaris Afanasieva et Amon (1–3) and *Spongentactinia marina* Afanasieva et Amon (4–12).

Figs. 1–3. *Spongentactinia polaris* Afanasieva et Amon, sp. nov.: (1) holotype PIN, no. 5311/12836; scale bar, 33 μm; (2) specimen PIN, no. 5312/15773; scale bar, 56 μm; (3) specimen PIN, no. 5312/15810; scale bar, 49 μm.

Figs. 4–12. *Spongentactinia marina* Afanasieva et Amon, sp. nov.: (4) specimen PIN, no. 5323/15989; scale bar, 72 μm; (5) specimen PIN, no. 5323/15991; scale bar, 68 μm; (6) specimen PIN, no. 5323/15707; scale bar, 66 μm; (7) specimen PIN, no. 5323/15982; scale bar, 72 μm; (8) holotype PIN, no. 5323/15722; scale bar, 68 μm; (9) specimen PIN, no. 5312/15801; scale bar, 69 μm; (10) specimen PIN, no. 5311/12928; scale bar, 59 μm; (11, 12) specimen PIN, no. 5311/12918: (11) scale bar, 56 μm; (12) fragment, scale bar, 30 μm.

(1–3, 10–12) Upper Devonian, Lower Famennian Substage; Timan–Pechora Basin, Saremboi–Lekkeyaga Swell, borehole Zapadno-Lekkeyaginskaya-65 (2460–2467 m of depth), sample 86g. (4–8) Middle Devonian, Upper Eifelian Substage, upper part of the Chotec Formation; Czechia, Prague Basin (Barrandian), village of Hlubocepy, sample d-3/2. (9) Polar Urals, Lemvin Zone, Palnik-Yu River, sample 101/594.

Plate 39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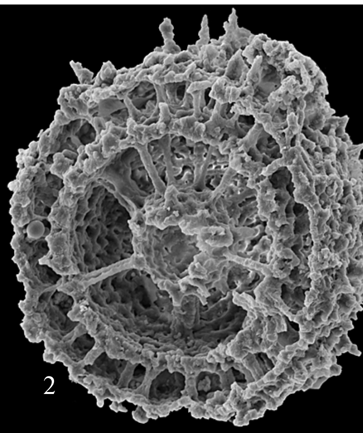
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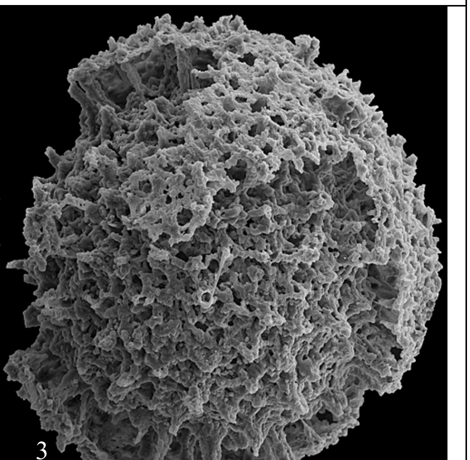
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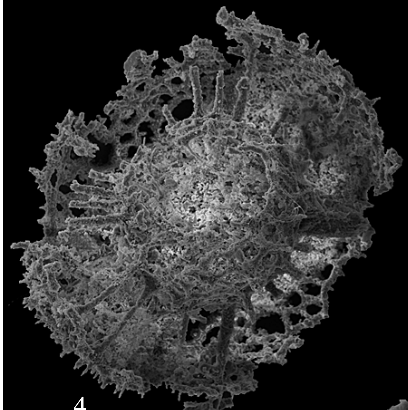
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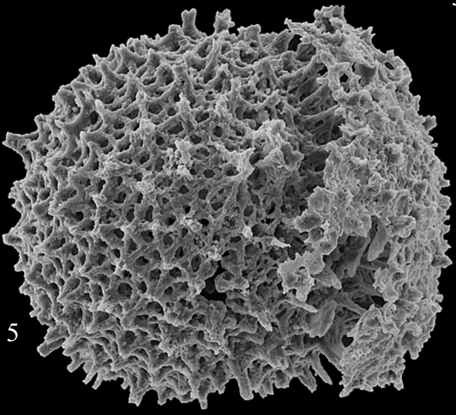
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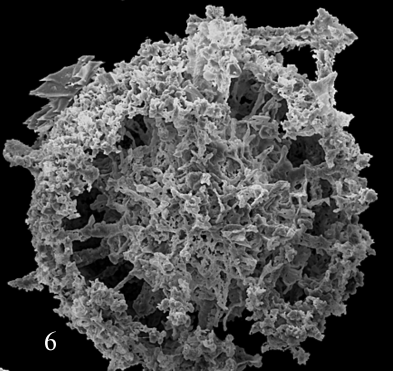
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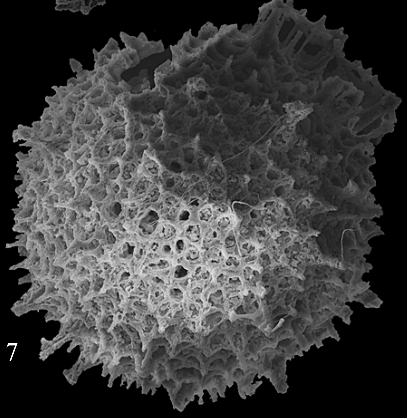
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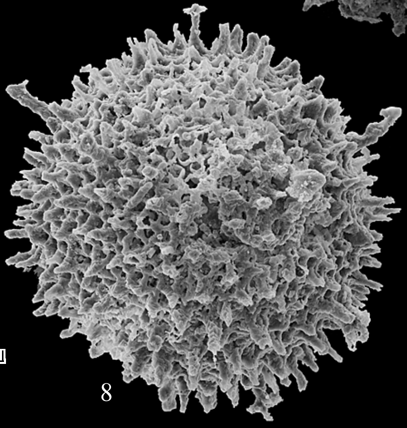
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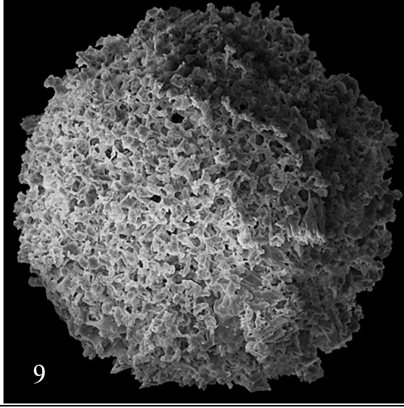
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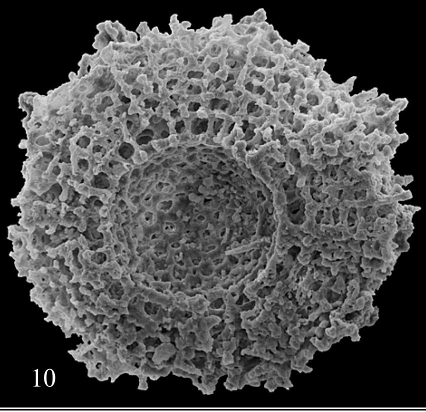
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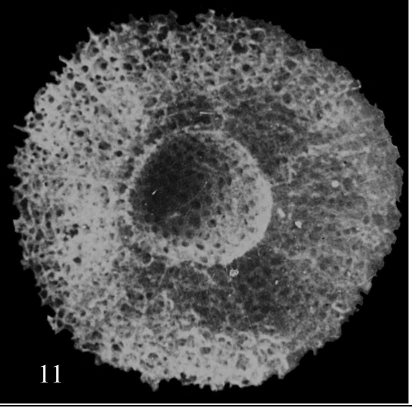

11

Subfamily Pluristratoentactiniinae Afanasieva, 1999

Genus *Pluristratoentactinia* Nazarov, 1981

Pluristratoentactinia Nazarov: Nazarov et al., 1981, p. 86; Nazarov, 1988, p. 61; Amon, 1999b, p. 70; Afanasieva, 2000a, p. 81.

Type species. *Pluristratoentactinia conspissata* Nazarov, 1981 (Nazarov et al., 1981, p. 87, pl. I, figs. 4–7).

Diagnosis. Test with two to six shells. From two to four intermediate spongy shells located between spongy outer shell and porous internal shell. Internal framework represented by spicule, six rays of which originating from median bar. Rays of spicule continued by main spines. Many by-spines positioned between layers of multilayer outer shell of skeleton.

Species composition. Three species from the Middle Devonian–Lower Permian: *Pluristratoentactinia conspissata* Nazarov, 1981 from the Middle Devonian of Czechia (Prague Basin), Upper Devonian of Russia (Kolyma Uplift, Polar and Southern Urals), Kazakhstan (Caspian Depression, Karachaganak Mountain Range), and Belarus (Pripyat Depression), and from the Lower Permian of Kazakhstan (Northern Mugodzhary and Caspian Depression, Karachaganak Mountain Range); *P. trisphaerata* sp. nov. from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of Russia (Polar Urals); *Pluristratoentactinia variabilis* (Ormiston et Lane, 1976) from the Lower Carboniferous of Germany (Rhine Shale Mountains), Russia (Southern Urals), and the United States (Oklahoma).

Pluristratoentactinia trisphaerata Afanasieva et Amon, sp. nov.

Plate 39, figs. 1–8

Etymology. From the Latin *tri* (three) and *sphaera* (sphere).

Holotype. PIN, no. 5312/15744; Polar Urals, Lemvin Zone, Palnik-Yu River; Upper Devonian, Lower Famennian Substage.

Description. The test is large or very large, with three shells. The external sphere is spongy, thin-walled. The pores of the outer shell are small, approximately equal in size, circular. The pore canals are narrow. The interpore bars are very wide, rounded, complicated by sculptural elements in the shape of very high pointed thorns. The intermediate sphere is large or very large, spongy, relatively thick-walled. The pores of the intermediate shell are small, approximately equal in size, rounded. The internal sphere is very large, thick-walled. The internal and intermediate spheres are complicated by numerous conical spines, which connect all shells of the skeleton. These spines are continued by numerous by-spines of the external sphere; they are very short, conical, hardly discernible from pointed thorns. Main spines are absent.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*Dm*	*Ds*	*tw*	*tm*	*ts*	*dp*	*wp*	*ht*
15744	135.0	90.0	36.0	3.0	6.0	1.8	3.0	4.5	15.0
15705	206.4	134.4	–	4.8	–	–	4.8	7.2	24.0
15747	191.3	138.7	–	3.8	–	–	3.8	5.6	15.0
15803	199.8	149.8	–	3.3	–	–	3.3	5.0	–

Specimen PIN, no. Holotype	*D/tw*	*D/dp*	*D/ht*	*D/Dm*	*Dm/tm*	*D/Ds*	*Ds/ts*	*dp/tw*	*dp/wp*
15744	45.0	45.0	9.0	1.5	15.0	3.8	20.0	1.0	0.7
15705	43.0	43.0	8.6	1.5	–	–	–	1.0	0.7
15747	50.3	50.3	12.6	1.4	–	–	–	1.0	0.7
15803	60.6	60.6	–	1.3	–	–	–	1.0	0.7

Comparison. The new species differs from *Pluristratoentactinia conspissata* Nazarov, 1981 in the development of one distinctly differentiated intermediate shell of the skeleton rather than from two to four intermediate shells, as in the species described by Nazarov et al. (1981).

Occurrence. Middle Devonian, Upper Eifelian Substage, terminal Chotec Formation of the Prague Basin, Czechia; Upper Devonian, Lower Famennian Substage of the Lemvin Zone of the Polar Urals.

Material. Eight specimens from the type locality (Fig. 6b, IX) and from the Hlubocepy section of the Prague Basin (Barrandian) of Czechia (Fig. 7).

Explanation of Plate 39

Pluristratoentactinia trisphaerata Afanasieva et Amon (1–8) and *Somphoentactinia multisphaerata* Afanasieva et Amon (9–11).

Figs. 1–8. *Pluristratoentactinia trisphaerata* Afanasieva et Amon, sp. nov.: (1) specimen PIN, no. 5312/15747; scale bar, 52 μm; (2) holotype PIN, no. 5312/15744; scale bar, 43 μm; (3) specimen PIN, no. 5312/15803; scale bar, 47 μm; (4) specimen PIN, no. 5312/15940; scale bar, 108 μm; (5) specimen PIN, no. 5312/15804; scale bar, 47 μm; (6) specimen PIN, no. 5323/15705; scale bar, 68 μm; (7) specimen PIN, no. 5323/15927; scale bar, 44 μm; (8) specimen PIN, no. 5312/15934; scale bar, 58 μm.

Figs. 9–11. *Somphoentactinia multisphaerata* Afanasieva et Amon, sp. nov.: (9) specimen PIN, no. 5312/16000; scale bar, 64 μm; (10) holotype PIN, no. 5312/15728; scale bar, 46 μm; (11) specimen GIN, no. 4467/90; scale bar, 85 μm.

(1–5, 7, 8, 10, 11) Upper Devonian, Lower Famennian Substage. (6, 9) Middle Devonian, Upper Eifelian Substage, upper part of the Chotec Formation. Polar Urals, Lemvin Zone, Palnik-Yu River: (1–4, 8, 10) sample 101/594, (5, 7) sample 101/593). (11) Belarus, Pripyat Depression, borehole West Valaevskaya-1R (3539–3554 m of depth) (Nazarov, 1988, pl. 6, fig. 1). (6, 9) Czechia, Prague Basin (Barrandian), village of Hlubocepy, sample d-3/2.

Family Spongopolyentactiniidae Nazarov, 1975

Subfamily Somphoentactiniinae Kozur et Mostler, 1981

Genus *Somphoentactinia* Nazarov, 1975

Somphoentactinia: Nazarov 1975, pp. 92–93; 1988, pp. 62–63; Amon, 1999b, pp. 76–77; Afanasieva, 2000a, p. 84.

Type species. *Tetrentactinia somphozona* Foreman, 1963 (p. 283, pl. 7, figs. 6a, 6b); Upper Devonian, Lower Famennian Substage, Huron Member, Ohio Shale Formation (Over, 2007); 30 km south of Lake Erie, Ohio, United States.

Diagnosis. Test with two shells: external shell spongy, frequently differentiated into additional closely positioned shells, and internal latticed shell. Internal framework represented by spicule, six rays of which originating from very short median bar. Rays of spicule continued by main spines. They complicated in intersphere space by apophyses, continued on skeleton surface by many conical or rod-shaped spines.

Species composition. Four species from the Middle–Upper Devonian: *Somphoentactinia gavrilovi* Afanasieva, 2000 from the Upper Devonian of Russia (Timan–Pechora Basin); *S. multisphaerata* Afanasieva et Amon, sp. nov. from the Middle Devonian of Czechia (Prague Basin) and Upper Devonian of Russia (Polar Urals) and Belarus (Pripyat Depression); *S. somphozona* (Foreman, 1963) from the Middle Devonian of western Australia (Gogo Formation) and Upper Devonian of Russia (Timan–Pechora Basin; Kolyma Uplift; Polar, Middle, and Southern Urals), Kazakhstan (Northern Mugodzhary), Belarus (Pripyat Depression), western Australia (Gogo Formation), and United States (Ohio); and *S. teuchestes* (Foreman, 1963) from the Upper Devonian of the United States (Ohio).

Somphoentactinia multisphaerata Afanasieva et Amon, sp. nov.

Plate 39, figs. 9–11

Somphoentactinia sp.: Nazarov, 1988, p. 186, pl. 6, fig. 1.

Etymology. From the Latin *multus* (many) and *sphaera* (sphere).

Holotype. PIN, no. 5312/15728; Polar Urals, Lemvin Zone, Palnik-Yu River; Upper Devonian, Lower Famennian Substage.

Description. The test is large or very large, with two spongy shells. The external spongy shell is very thick, about one-third of the shell diameter. The outer shell of the skeleton is layered, distinctly divided into 6–10 primary concentric spheres enclosed into each other. These shells probably display an initial stage of differentiation of the external spongy layer. Radial bars connected to the bases of numerous external thorns extend through all spheres of the outer shell. The pores of the outer shell small, approximately equal in size, circular. The pore canals are very narrow. The interpore bars are very wide, rounded, complicated by sculptural elements in the shape of very high pointed thorns. The structure of the internal framework is uncertain. The internal sphere is very large, thick-walled. The pores of the internal sphere are large, equal in size, circular. The main spines are absent.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	*D*	*tw*	*dp*	*wp*	*ht*	*Ds*	*ts*
15728	163.2	49.9	3.3	3.3	9.9	69.9	4.0
15766	151.6	37.2	–	–	11.4	85.8	5.7
15927	142.2	–	4.7	3.2	14.2	–	–
15934	162.4	–	3.5	3.5	17.6	–	–
4467/90	291.8	90.9	5.7	5.7	11.3	104.7	5.1

Specimen PIN, no. Holotype	*D*/*tw*	*D*/*dp*	*D*/*ht*	*D*/*Ds*	*Ds*/*ts*	*dp*/*tw*	*dp*/*wp*
15728	3.3	49.5	16.5	2.3	17.5	0.1	1.0
15766	4.1	–	13.3	1.8	15.1	–	–
15927	–	30.3	10.0	–	–	–	1.5
15934	–	46.4	9.2	–	–	–	1.0
4467/90	3.2	51.2	25.8	2.8	20.5	0.1	1.0

Comparison. The new species differs from *Somphoentactinia somphozona* (Foreman, 1963) in the larger skeleton, the absence of the main spines, and in the layered structure of very thick (one-third of the shell diameter) outer shell, which is distinctly differentiated into 6–10 primary concentric spheres.

Occurrence. Middle Devonian, Upper Eifelian Substage, terminal Chotec Formation of the Prague Basin, Czechia; Upper Devonian, Lower Famennian Substage, Lemvin Zone of the Polar Urals and Pripyat Depression of Belarus.

Material. Six specimens from the type locality (Fig. 6b, IX), from borehole Zapadno-Valaevskaya-1P (3539–3554 m of depth) in the Pripyat Depression of Belarus (Fig. 20) and from the Hlubocepy section of the Prague Basin (Barrandian) of Czechia (Fig. 7).

Class Stauraxonaria Afanasieva et Amon, 2005

Order Palaeodiscata Afanasieva et Amon, 2005

Family Palaeodiscaleksidae Afanasieva, 2008

Genus *Palaeodiscaleksus* Afanasieva, 2008

Spongodiscus: Hinde, 1899a, p. 54.
Palaeodiscus: Afanasieva, 2000a, p. 91.
Palaeodiscaleksus: Afanasieva, 2008, p. 101.

Type species. *Spongodiscus punctus* Hinde, 1899a (p. 54, pl. IX, fig. 14); Middle Devonian, Givetian Stage, Yarrimie Formation (Aitchison, Stratford, 1997); New South Wales, Australia.

Diagnosis. Test discoidal, with one spongy shell. Structure of internal framework uncertain. Main spines very short, usually absent.

Species composition. Six species from the Devonian: *Palaeodiscaleksus acinus* (Hinde, 1899) from the Middle Devonian of Australia (New South

Wales); *P. cribrarius* (Hinde, 1899) from the Lower Devonian of Russia (Southern Urals), Middle Devonian of Australia (New South Wales) and Russia (Southern Urals), and Upper Devonian of Russia (Southern Urals and Rudny Altai); *P. punctus* (Hinde, 1899) from the Lower Devonian of Russia (Southern Urals), Middle Devonian of Australia (New South Wales) and Russia (Southern Urals and Rudny Altai), and Upper Devonian of Russia (Timan–Pechora Basin, Southern and Middle Urals); *P. saturniformis* Afanasieva et Amon, sp. nov. from the Middle Devonian of Russia (Rudny Altai); *P. scutulatus* (Hinde, 1899) from the Middle Devonian of Australia (New South Wales); and *P. tumefactus* Afanasieva et Amon, 2008 from the Lower and Middle Devonian of Russia (Southern Urals) and the Upper Devonian of Russia (Timan–Pechora Basin, Southern and Middle Urals).

Remarks. Members of this genus were initially assigned after Hinde (1899a, p. 54) to the genus *Spongodiscus* (Ehrenberg, 1854a, 1854b). However, subsequent studies have shown essential differences between ancient coarse-spongy discoidal radiolarians and convergently similar Recent members of this genus, which was established by Ehrenberg (1854a, 1854b) in the Recent beds of the Atlantic Ocean and Mediterranean Sea. According to the data of Alekseev (1989, 1998; Alekseev et al., 2001), the mean duration of genera is approximately the same as that of the geological age. In the Paleozoic, genera possibly existed for a longer time. However, it is hardly probable that such a complex organism as radiolarian constantly existed for 65 ages from the Middle Devonian to the Recent, i.e., for almost 380 m.y.

In addition, the generic name *Palaeodiscus* (Afanasieva, 2000a, p. 91) was repeatedly preoccupied. The earliest homonym is the genus *Palaeodiscus* Salter, 1857 (Salter, 1857, p. 332), a Silurian sea urchin; thus, the genus *Palaeodiscus* Afanasieva, 2000 is a junior homonym. Therefore, according to the principle of homonymy (*International Code* ..., 2000, article 52.1), a new replacement name, *Palaeodiscaleksus* Afanasieva, 2008 was established (Afanasieva, 2008); it descends to the old name *Palaeodiscus* (from the Greek *palaios* (ancient) and *diskos* (disk)) and in honor of A.S. Alekseev, who was the first to pay attention to the fact that the former name was preoccupied. Since *Palaeodiscus* Afanasieva, 2000 is the type genus of the family Palaeodiscidae Afanasieva, 2000, the last name should also be replaced according to article 39 of the ICZN (*International Code* ..., 2000) by the new family name Palaeodiscaleksidae Afanasieva, 2008 (Afanasieva, 2008).

Palaeodiscaleksus saturniformis Afanasieva et Amon sp. nov.

Plate 40, figs. 1–6

Etymology. From the Latin *Saturnus* (Saturn) and the morpheme *-formis* (-shaped).

Holotype. PIN, no. 5253/50712; Rudny Altai, Zmeinogorskii District, Shipunikha River; Middle Devonian, Upper Givetian, Shipunikha Formation.

Description. The test is large or very large, discoidal. The skeletal disk is considerably flattened ($D/H = 7.4–16.5$), with a slightly convex middle part. The pores are small, mostly equal in size, circular. The interpore bars are very wide, flattened.

Measurements, μm, and ratios:

Specimen PIN, no. Holotype	D	H	dp	wp	D/H	D/dp	dp/wp
50712	140.0	8.8	3.0	3.8	15.9	46.7	0.8
50704	185.0	25.0	–	–	7.4	–	–
50709	212.5	21.3	–	–	10.0	–	–
50710	131.6	–	2.4	3.8	–	54.8	0.6
50711	188.1	–	3.3	4.9	–	57.0	0.7
50713	165.0	10.0	3.6	3.8	16.5	45.8	0.9

Comparison. The new species differs from *Palaeodiscaleksus cribrarius* (Hinde, 1899) and *P. punctus* (Hinde, 1899) in the slightly convex middle part of the skeleton and the extremely flattened peripheral part resembling the ring of Saturn, which caused the name of the new species.

Occurrence. Middle Devonian, Upper Givetian, Shipunikha Formation; Shipunikha River Zmeinogorsk District of the Rudny Altai.

Material. Six specimens from the type locality (Fig. 22b, III).

Class Nassellaria Ehrenberg, 1847

Order Pylomariata Afanasieva, 1999

Superfamily Pylentonemoidea Deflandre, 1963

Family Pylentonemidae Deflandre, 1963

Subfamily Archocyrtiinae Kozur et Mostler, 1981

Genus *Archocyrtium* Deflandre, 1972

Archocyrtium: Deflandre, 1960, pp. 212–218 (nomen nudum); 1972, p. 15; Holdsworth, 1973, pp. 122–123 (part.), 1978, p. 786; Afanasieva, 1986, p. 29; Cheng, 1986, p. 123; Nazarov, 1988, pp. 69–70; Afanasieva, 2000a, p. 103.

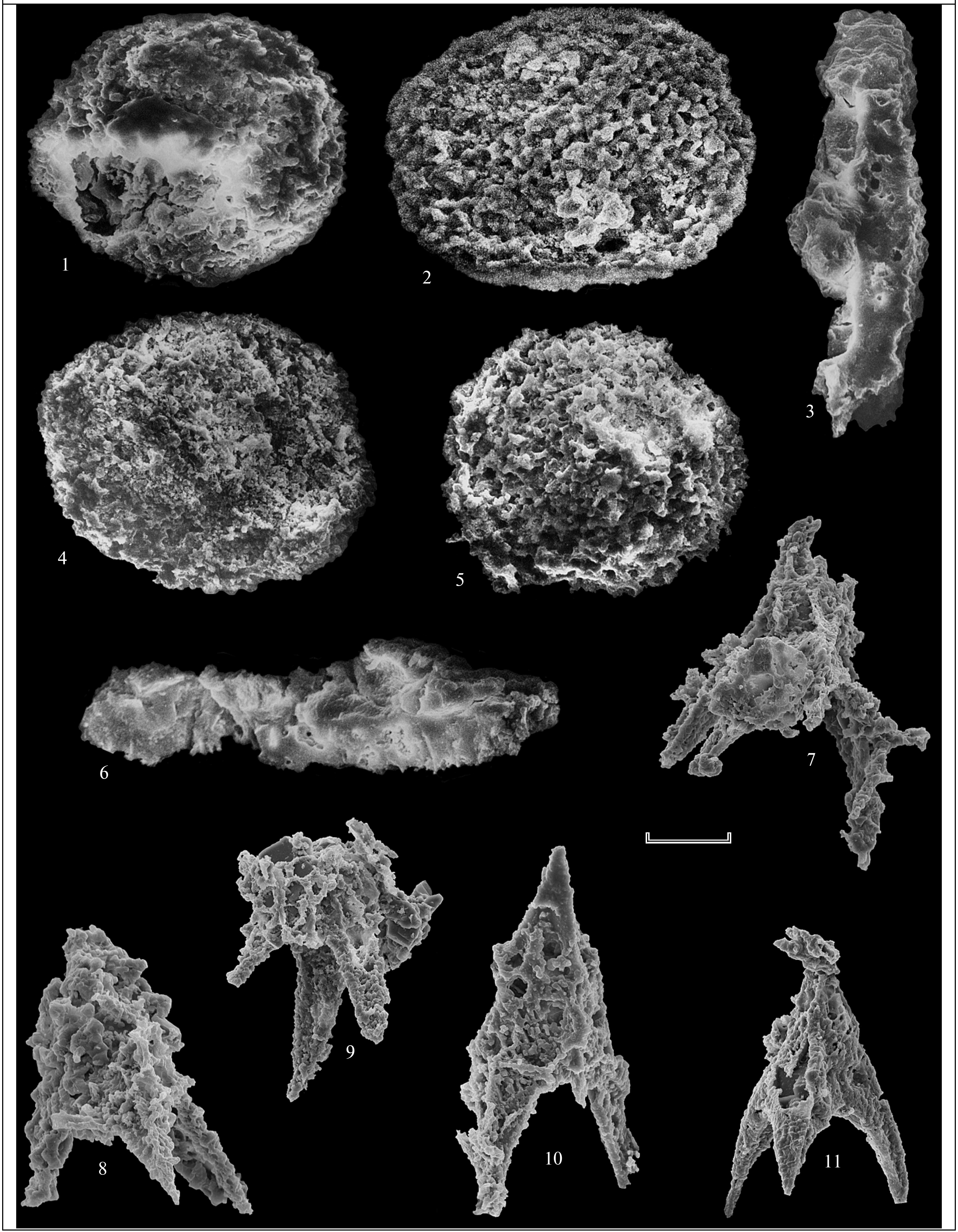
Cyrtentactinia: Foreman, 1963, pp. 284–285 (part.).

Type species. *Archocyrtium riedeli* Deflandre, 1972; Lower Carboniferous, Tournaisian–Visean stages; Montagne Noire, France.

Diagnosis. Test subspherical, wall porous. Internal framework represented by four-rayed spicule. Test having four well-developed three-bladed main spines, three of which surrounding pylome and one aboral spine occupying axial position. Three main spines surrounding pylome connected to each other by narrow band of nonporous skeletal tissue.

Species composition. Six species from the Silurian–Lower Carboniferous: *Archocyrtium amoenus* Afanasieva et Amon, sp. nov. from the Upper Devonian of Russia (Polar Urals); *A. coronaesimile* Won, 1983 from the Lower Carboniferous of Germany (Rhine Shale Mountains); *A. cibdelosphaera* (Foreman, 1963) from the Upper Devonian of Russia (Polar Urals) and the United States (Alaska, Ohio) and

Plate 40



Explanation of Plate 40

Palaeodiscaleksus saturniformis Afanasieva et Amon (1–6) and *Archocyrtium amoenus* Afanasieva et Amon (7–11).

Figs. 1–6. *Palaeodiscaleksus saturniformis* Afanasieva et Amon sp. nov.: (1) specimen PIN, no. 5253/50704; scale bar, 34 µm; (2) specimen PIN, no. 5253/50713; scale bar, 33 µm; (3) specimen PIN, no. 5253/50710; scale bar, 33 µm; (4) specimen PIN, no. 5253/50711; scale bar, 44 µm; (5) holotype PIN, no. 5312/50712; scale bar, 33 µm; (6) specimen PIN, no. 5253/50709; scale bar, 33 µm.

Figs. 7–11. *Archocyrtium amoenus* Afanasieva et Amon, sp. nov.: (7) specimen PIN, no. 5312/15886; scale bar, 33 µm; (8) specimen PIN, no. 5312/15881; scale bar, 21 µm; (9) specimen PIN, no. 5312/15896; scale bar, 35 µm; (10) holotype PIN, no. 5312/15839; scale bar, 25 µm; (11) specimen PIN, no. 5323/15828; scale bar, 40 µm.

(1–6) Middle Devonian, Upper Givetian Substage, Shipunikha Formation; Rudny Altai, Zmeinogorskii District, Shipunikha River. (7–11) Upper Devonian, Lower Famennian Substage; Polar Urals, Lemvin Zone, Palnik-Yu River: (7–9) sample 101/593, (10, 11) sample 101/594.

Lower Carboniferous of France (Montagne Noire) and Turkey; *A. parvum* Deflandre, 1972 from the Upper Devonian of the United States (Alaska, Ohio) and Lower Carboniferous of France (Montagne Noire), Turkey, and Russia (Penzhinsky Mountain Range); *A. riedeli* Deflandre, 1960 from the Upper Devonian of Russia (Middle and Polar Urals) and the United States (Alaska, Ohio) and Lower Carboniferous of France (Montagne Noire), Turkey, and Russia (Penzhinsky Mountain Range); and *A. tersae* Deflandre, 1972 from the Silurian of France (Brétignolles).

Archocyrtium amoenus Afanasieva et Amon, sp. nov.

Plate 40, figs. 7–11

Etymology. From the Latin *amoenus* (delightful).

Holotype. PIN, no. 5312/15839; Polar Urals, Lemvin Zone, Palnik-Yu River (Pal'nikskoe deposits); Upper Devonian, Lower Famennian Substage.

Description. The skeleton is elongated conical. The total height of the skeleton is large, less often, small. The central spherical part of the test (cephalis) is very small, thick-walled, with very large pores. The pore canals are wide. The interpore bars are wide, rounded. The test has four main spines, three of which surround the pylome and one aboral spine is in the axial position. The main spines are long ($L/D = 1.5–2.3$), very massive, straight, three-bladed, with a -shaped section of the spine base.

Measurements, µm, and ratios:

Specimen PIN, no. Holotype	*H*	*D*	*L*	*wL*	*tw*	*dp*	*wp*
15839	121.9	27.3	45.5	18.2	1.8	5.5	2.7
15828	141.9	35.5	54.6	27.3	–	–	–
15881	88.2	22.1	45.6	17.6	–	–	–
15886	150.2	34.7	80.8	25.4	–	–	–
15896	–	47.5	68.8	23.8	2.5	6.3	2.8

Specimen PIN, no. Holotype	*D*/*tw*	*D*/*dp*	*L*/*D*	*L*/*wL*	*dp*/*tw*	*dp*/*wp*
15839	15.2	5.0	1.7	2.5	3.1	2.0
15828	–	–	1.5	2.0	–	–
15881	–	–	2.1	2.6	–	–
15886	–	–	2.3	3.2	–	–
15896	19.0	7.5	1.5	2.9	2.5	2.2

Comparison. The new species differs from *Archocyrtium cibdelosphaera* (Foreman, 1963) and *A. riedeli* Deflandre, 1960 in the elongated conical skeleton with a very small cephalis with very large pores and very massive, straight main spines.

Occurrence. Upper Devonian, Lower Famennian Substage; Lemvin Zone of the Polar Urals.

Material. Five specimens from the type locality (Fig. 6b, IX).

CONCLUSIONS

We have accumulated extensive new material of Devonian radiolarians, which requires comprehension from a new standpoint of modern information on taxonomy, paleoecology, paleobiogeography, evolution, and biostratigraphy of this group. This has opened new opportunities in specification and detailed elaboration of radiolarian zones of the Devonian System within the framework of the integrated radiolarian scale of the Paleozoic of Russia.

The present study is the first comprehensive investigation of Devonian radiolarians, using modern techniques and approaches. The new approach to the resolution of the problems of biodiversity, evolutionary patterns, paleobiogeographic distribution, and biostratigraphic potential of Devonian radiolarians consists of the complex study of this faunal group from different points of view, taking into account all evolutionary changes in various taxonomic groups of radiolarians on the geological time scale.

(1) The history of study of Devonian radiolarians of Russia, since the monograph of Rüst (1892) is considered, geographical distribution of radiolarians is analyzed.

(2) The results of original studies and revisions have provided improvement and detailed elaboration of the radiolarian scale for the Devonian System and establishment of 18 Devonian biostratigraphic assemblages and subassemblages of radiolarians, including 11 new assemblages.

(3) Late Emsian–Middle Frasnian radiolarians of the Southern Urals are found for the first time and described. The new Late Emsian radiolarian assemblage is represented by 20 species of 11 genera, the Late Eifelian assemblage includes 17 species of

11 genera, and Middle Frasnian radiolarians are represented by 13 species of seven genera of spherical, discoidal, spindle-shaped, pylomate, and spiny radiolarians.

The following new Devonian radiolarian-based biostratons which are distributed and valid in the Southern Urals and Northern Mugodzhary are established:

- beds with *Primaritripus buribayensis–Entactinia rostriformis* are dated within the Late Emsian in the range of the *patulus* Conodont Zone;
- beds with *Primaritripus kariukmasensis* from the Upper Eifelian are characteristic of the *australis–kockelianus* conodont zones;
- beds with *Primaritripus chuvashovi* are dated Middle Frasnian and correspond to the *punctata* Conodont Zone.

(4) A diverse Late Eifelian radiolarian assemblage (31 species of 15 genera) has been found in the extreme western marginal area of the Russian Platform in the Prague Basin of Czechia. We propose to regard the new Late Eifelian radiolarian association as a characteristic biostratigraphic assemblage, beds with *Apophisisphaera hystricuosa–Spongentactinia fungosa*, which correspond to the range of the *Tortodus kockelianus* Conodont Zone.

The analysis of changes in the composition of radiolarian assemblages upward in the section has shown that 54.8% of radiolarians became extinct near the boundary with Givetian black shale of the Kacak Member. Particular attention should be paid to the predominant disappearance of relatively more deep-water spherical spongy species of Spumellaria (90.9%) on a background of extinction of 30.8% of spherical porous Sphaerellaria and 42.9% of spiny Aculearia.

(5) The *Spongentactinella windjanensis–Bientactinosphaera nigra* assemblage is dated Givetian.

(6) The results of original studies and revisions allowed the establishment of the following seven radiolarian assemblages within the Frasnian Stage:

- *Polyentactinia circumretia–Bientactinosphaera egindyensis* for the Middle and Upper Frasnian of the Southern Urals, Northern Mugodzhary, and Rudny Altai;
- *Bientactinosphaera pittmani–Russirad kazintsovae* for the Upper Frasnian of the Timan–Pechora Basin;
- *Radiobisphaera domanicensis–Radiobisphaera menneri* for the Middle Frasnian (Domanik Formation) of the Southern Urals and Volga–Ural Basin;
- *Moskovistella allbororum–Ceratoikiscum ukhtensis* for the Middle Frasnian (Domanik Formation) of the Timan–Pechora Basin and Rudny Altai;
- *Primaritripus chuvashovi* for the Middle Frasnian of the Southern Urals;
- *Helenifore gogoense–Retisphaera concinna* for the Lower Frasnian of Australia;
- *Palaeodiscaleksus punctus–Astroentactinia biaciculata* for the Lower Frasnian of the Timan–Pechora Basin.

(7) A distinctive feature of the Early Frasnian *Palaeodiscaleksus punctus–Astroentactinia biaciculata* assemblage of the northern Timan–Pechora Basin is the appearance in deposits of the external shelf of abundant, but homogenous discoidal radiolarians (two species of two genera). In the southern Timan–Pechora Basin, the radiolarian assemblage is more diverse (nine species of six genera), but scarce.

(8) A new study and comparative analysis of Early Famennian radiolarians from the Lemvin Zone of the Subpolar Urals and western slope of the Middle Urals as well as revision of Famennian radiolarians from the Saremboi–Lekkeyaga Swell of the northeastern Timan–Pechora Basin and northern Caspian Region provided the establishment of five radiolarian assemblages within the Famennian Stage:

- *Tetrentactinia barysphaera–Ceratoikiscum famennium*, Pripyat Depression, Evtropiny Noski of the Malaya Pechora allochthon of the western slope of the Northern Urals, Southern Urals, and Northern Mugodzhary;
- *Tetrentactinia barysphaera–Retientactinosphaera magnifica*, northeastern Timan–Pechora Basin;
- *Tetrentactinia barysphaera–Caspiaza spinifera*, Lemvin Zone of the Polar Urals;
- *Haplentactinia alekseevi–Haplentactinia vilvaensis*, western slope of the Middle Urals;
- *Tetrentactinia barysphaera–Holoeciscus auceps*, northern slope of the Caspian Depression.

(9) The Early Famennian radiolarian assemblage with *Tetrentactinia barysphaera–Retientactinosphaera magnifica* of the northeastern Timan–Pechora Basin includes 27 species of 16 genera. A new rich association of Early Famennian radiolarians with *Tetrentactinia barysphaera–Caspiaza spinifera* from the Lemvin Zone of the Polar Urals consists of 54 species of 26 genera. A very unusual association of Early Famennian radiolarians with *Haplentactinia alekseevi–Haplentactinia vilvaensis* from the western slope of the Middle Urals is distinguished by the development of five species of two genera of latticed Spumellaria and one species of Aculearia.

(10) The analysis of morphological and paleoecological features of the so-called “primitive” small pelagic foraminifers of the “Ural” Assemblage of the microfauna, established by Bykova (1955), allowed us to assign some species of the genera *Archaesphaera, Parathurammina*, and *Bisphaera* to the radiolarian genera *Astroentactinia, Borisella*, and *Trochodiscus*. Forcible arguments in favor of the assignment of planktonic forms of the “Ural” Assemblage to radiolarians are (1) the skeleton structure, which, even taking into account the carbonate composition, sharply differs in morphology from foraminifer shells, (2) paleoecological features of the microorganisms in

question, i.e., confinement to the pelagial of open seas and oceans with normal salinity.

(11) Middle–Late Devonian radiolarians have been found and described for the first time from deposits of the Upper Givetian–Upper Frasnian in six sections of the Shipunikha and Zmeinogorsk zones of the Rudny Altai. Radiolarians are represented by 42 species of 15 genera of spherical, discoidal, and spiny forms. The new study of radiolarians allowed us (1) to reveal Late Givetian radiolarians, including a new species, *Palaeodiscaleksus saturniformis* sp. nov.; (2) show the Middle Frasnian age of the Lower Kamenevsk Subformation in the Goryunovo gully; (3) confirm Late Frasnian age of the Upper Kamenevsk Subformation in the section on the Gryaznukha River in the vicinity of Razdol'naya Hill; (4) determine Late Frasnian radiolarians near the village of Uspenka; and (5) reconstruct paleobiogeographic environments of radiolarians.

(12) The new data obtained on the taxonomic composition of radiolarian associations provided more detailed paleogeographic characteristics of sedimentation conditions in the Devonian Period, which was particularly rich in geological events. The prevalence in oryctocoenoses of discoidal forms is evidence of normal marine, but relatively shallow-water conditions of sedimentation in the Late Givetian of the Rudny Altai, in the Late Emsian, Late Eifelian, and Middle Frasnian water areas of the Southern Urals, and in the Early Frasnian in the northern Timan–Pechora Basin.

(13) Changes in the composition of the pelagic biota of radiolarians and ammonoids within the Frasnian Age in the Timan–Pechora Basin are analyzed. It is shown that the zones of increased bioproductivity are under control of climatic and tectonic factors. Within the equatorial and tropical belts above the deep fractures of rift zones of the past and present, unique life conditions are formed. The rift zones are sources of nutritive matter of endogenous nature.

(14) General patterns of the life of radiolarians in the Devonian of the Russian Platform are considered. Siliceous organisms (radiolarians and sponges) widely developed in eastern water areas of the Russian Platform, which were characterized by a high content of silica in marine water due to the rise of highly siliceous waters along fractures. Based on changes in the quantitative ratio of spherical Sphaerellaria and Spumellaria (**S**) and spiny Aculearia (**A**), the paleoclimatic coefficient **PC = S/A** has been established, according to which the prevalence in deposits of spiny radiolarians over spherical taxa is evidence of colder waters in habitats (**PC ≤ 1**) and vise versa.

(15) The Domanik Formation is characterized by regular alternation of two main rock variants: on the one hand, black bituminous siliceous differences enriched by organic matter, but completely free from skeletal remains and, on the other hand, limestone layers literally overfull of skeletons of diverse organisms, but with a low content of C_{org}.

(16) The model for the cyclic formation of rocks of the Domanik type under conditions of hydrosulphuric contamination of bottom waters, which is manifested at all levels from a sequence as a whole to a particular member, group of beds, beds, layers, and even vary thin layers seen only in thin sections is elaborated; this reflects the pulsation pattern of evolution of the basin.

(17) It is shown that the skeletons of radiolarians, tentaculites, and spicules of sponges were replaced by pyrite in conditions of hydrosulphuric contamination. Apparently, pyritization developed along biomineralogical borders and growth directions of skeletons of various organisms.

(18) Features of the formation of the Timan–Pechora Sedimentation Basin in the Frasnian Age and changes connected with them in the development and extinction of radiolarians and ammonoids are evidence of distinct influence of eustatic and local tectonic events on the formation of biodiversity. On the one hand, a general increase in sea level in the Domanik Time and an increase in area of the deep shelf in conditions of a tropical climate caused successful development of microplankton, including radiolarians. On the other hand, anoxic conditions near the bottom resulted in changes in communities of planktonic and benthic organisms. In conditions of hydrosulphuric contamination of bottom waters, benthic faunas are completely absent; ammonoids are dominated by highly specialized planktonic forms, and diverse radiolarians are widespread.

(19) The effect of seasonal rhythmics of the galactic year on bursts of life and mass extinctions of radiolarians is shown. The sequence of galactic seasons is reflected in radiolarian evolution. The Devonian Period covers the final spring season of the galactic year Phosphatian, during which the rate of speciation increased by many times and the Paleozoic maximum of the number of taxa was reached.

(20) It is presumed that evolutionary innovations could have been distributed through lateral gene transfer by bacteria and symbiotic algae.

(21) Features and basic distinctions in appearance and distribution in Devonian basins of radiolarians with two porous spheres and one main spine are considered. It is shown that, during invasion and adaptation of species to a new environment, there is struggle for ecological niches between coenophobic and coenophilic species.

Four solitary population waves have been established and a scenario of expansion in the Devonian of the radiolarian morphotype considered is developed. However, the capability for the formation of a solitary population wave is only manifested in phylogenetically young juvenile taxa. They have a high activity of mobile genetic elements and capable of the hyperbolic growth of abundance and rapid adaptation to new ecological niches in new territories.

Wave expansion of morphological novelties and dynamics of a biological burst in the zone of invasion is characterized by a hyperbolic growth of population density and provides a perfect means for paleoecological reconstruction and improvement of regional biostratigraphic schemes.

(22) Comparative analysis of species and generic compositions of four key radiolarian associations of the Famennian, which inhabited marginal and epicontinental marine basins of the supercontinent of Euramerica, has shown a high frequency of the basic core of associations at the level of 39.0–63.4% of genera and 23.3–48.3% of species and regular migration patterns of dominant taxa. These migration patterns allowed us to establish in the Famennian four migration streams: Northwestern (North America ⇄ Polar Urals), Southern (North America ⇄ Pripyat Depression), Eastern (Pripyat Depression ⇄ Polar Urals), and Northeastern (Polar Urals ⇄ Middle Urals).

(23) Quantitative dominance of Spumellaria in all Famennian radiolarian associations is shown. A trend towards an increase in taxonomic diversity of Spumellaria in the Famennian in the ancient northeast from the marginal epicontinental paleoseas of Euramerica to open waters of the Ural Paleocean has been recognized.

(24) The genera *Bisphaera, Entactinia, Entactinosphaera, Stigmosphaerostylus*, and *Trilonche* are revised.

It is shown that the main difference of the genus *Entactinia* Foreman, 1963 from *Stigmosphaerostylus* Rüst, 1892 is in the structure of the outer shell of the skeleton, internal spicule, and the number of the main spines; this suggests that they should by assigned, respectively, to the families Entactiniidae and Haplentactiniidae and the classes Sphaerellaria and Spumellaria.

The genus *Trilonche* Hinde, 1899 should be considered within the framework of the initial diagnosis of the morphotype with two porous spheres and three main spines.

The species established by Foreman (1963) in the genus *Entactinosphaera* are presently assigned based on morphological characters to seven genera of three orders of two radiolarian classes: the class Sphaerellaria, order Entactiniata (*Bientactinosphaera* Afanasieva, 2000, *Entactinosphaera* Foreman, 1963, *Helioentactinia* Nazarov, 1975, *Radiobisphaera* Won, 1997) and the class Spumellaria, order Cancelliata (*Retientactinosphaera* Afanasieva, 2011, *Magnisphaera* Won, 1997) and order Spongiata (*Spongentactinia* Nazarov, 1975).

As the genus *Bisphaera* Won, 1997 was revised, it was shown that it is a junior homonym of the genus *Bisphaera* Birina, 1945 and its species should be assigned based on morphology to four genera of the order Entactiniata: *Bientactinosphaera* Afanasieva, 2000, *Helioentactinia* Nazarov, 1975, *Ornatoentactinia* Afanasieva, 2000, and *Radiobisphaera* Won, 1997.

The diagnoses of the genera *Entactinia, Entactinosphaera, Radiobisphaera*, and *Somphoentactinia* are amended.

(25) Ten new species from the Upper Eifelian of the Prague Basin, from the Upper Givetian of the Rudny Altai, from the Domanik Formation of the Middle Frasnian of the Timan–Pechora Basin, from the Upper Frasnian of the eastern slope of the Middle Urals, and from the Lower Famennian of the Pripyat Depression, Timan–Pechora Basin, Polar Urals, and western slope of the Middle Urals are described, including *Archocyrtium amoenus* sp. nov., *Bientactinosphaera zuraevi* sp. nov., *Entactinia bella* sp. nov., *Haplentactinia kuzminae* sp. nov., *Haplentactinia vilvaensis* sp. nov., *Palaeodiscaleksus saturniformis* sp. nov., *Pluristratoentactinia trisphaerata*, sp. nov., *Somphoentactinia multisphaerata* sp. nov., *Spongentactinia marina* sp. nov., and *Spongentactinia polaris* sp. nov.

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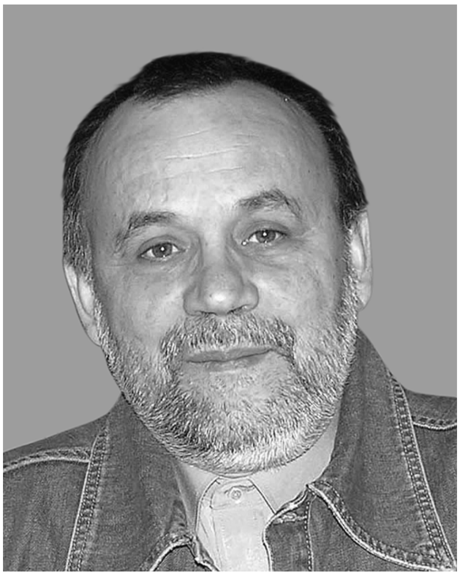

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