Siliceous biota (radiolarians and sponges) and the Late Devonian biotic crisis: The Polish reference

VALENTINA VISHNEVSKAYA, ANDRZEJ PISERA, and GRZEGORZ RACKI

The radiolarian species *Astroentactinia paronae*, *A. stellata*, *Trilonche echinata*, *T. grandis*, *T. nigra*, *Haplentactinia inaudita*, and *H. rhinophyuosa* are common in late Frasnian to early Famennian rhythmic, calcareous-marly sequence of the southern Holy Cross Mts., Poland. They are known also from coeval abundant siliceous biota assemblages from the carbonate shelf of East European Platform including more than 150 taxa of radiolarians. However, in ecological terms, the moderately diverse Polish microfaunas (34 species of 12 genera) are more similar to these from Kolyma and Alaska, also marked by abundance of sphaerical entactiniids and near-absence of bilateral-symmetric Ceratoikiscidae and Palaeoscenididae. A succession of two distinctive siliceous sponges associations is established in the incipiently submerged Holy Cross carbonate platform: from an ephemeral, diverse, mostly rigid-skeletal lithistid-hexactinosan foreslope assemblage (initial phase of the late Frasnian Kellwasser Crisis), to long-lasting, basinal loose-skeletal hexactinellid-demosponge faunas (appearing abundantly just prior the Frasnian–Famennian boundary in the late *Palmatolepis linguiformis* Zone). Such regional blooms of marine siliceous biotas, parallel to temporary retreat of calcareous biota, are demonstrated worldwide for the Kellwasser Crisis. These suggest probable causal links with cooling pulses and at least regional, volcanically induced eutrophication.

Key words : Radiolaria, Porifera, palaeoecology, mass extinction, Frasnian, Famennian, Devonian, Poland.

Valentina Vishnevskaya [valentina@ilran.ru], Institute of the Lithosphere of Marginal Seas, Russian Academy of Sciences, Stromonetny per. 22, Moscow, 109180 Russia;
Andrzej Pisera [apis@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/53, PL-02-089 Warszawa, Poland;
Grzegorz Racki [racki@us.edu.pl], Wydział Nauk o Ziemi, Uniwersytet Śląski, ul. Będzińska 60, PL-41-200 Sosnowiec, Poland.

Introduction

In the Late Devonian a carbonate shelf formed as a wide, elongated belt on the pericratonic rim of the East European platform (Barskov 1994), stretching from the northern margin of Europe (Pechora basin) to the southeast (throughout Volga-Ural basin to Caspian-Dnieper-Donets basin), and then from the southern part of the Pripyat basin to the Polish fragment (Holy Cross Mountains, Silesian-Cracow region). The characteristic feature of these peripheral basins is the presence of abundant siliceous microbiota (e.g., Nazarov 1988; Żakowa and Radlicz 1990; Vishnevskaya et al. 1993; Afanasjeva 2000).

In the Holy Cross Mts., the first find of diverse Devonian polycystine radiolarians was made in marly Famennian strata (see Racka 1984). In the present paper, the microfaunas from the Frasnian–Famennian (F–F) passage at the Kowala section are systematically described for the first time (see also Vishnevskaya et al. 1997; Racki 1999). This led to a broader discussion of this group response to the late Frasnian biotic turnover, which is recorded primarily in collapse of stromatoporoid-coral reef ecosystems. The general term "Kellwasser (KW) Crisis", merging both the lower and upper anoxic KW events (Schindler 1993), is used here. Earlier, Nazarov and Ormiston (1985) stressed the dissimilarity of comparative evolutionary patterns between Palaeozoic radiolarians and the shelf-dwelling benthos. Similar conclusions were also presented by Kalvoda (1986), and Kiessling and Tragelehn (1994), whilst very recent diversity compilations by Afanasjeva (2000), Vishnevskaya and Kostyuchenko (2000), and Umeda (in press) present conflicting data. McGhee (1996) summarised dispersed evidence for an ecological shift toward the dominance of siliceous biota, primarily within the benthos, during the F–F extinction interval. In fact, the southern part of the Holy Cross Mts. is distinguished by a locally abundant and uniquely diverse late Frasnian siliceous sponge fauna (Rigby et al. 2001), replaced by species-poor Famennian assemblages, noted by Hurcewicz (1993). Thus, based on study of the reference Kowala succession (Fig. 1), the silicisponge associations are revisited herein in more details as well. Finally, a summary of the palaeoceanographic and evolutionary implications is presented for both the F–F microzooplankton and benthos (see Racki 1999).

V. Vishnevskaya and A. Pisera are responsible for radiolarian and sponge data, respectively, G. Racki for the stratigraphic setting, other discussions are joint.
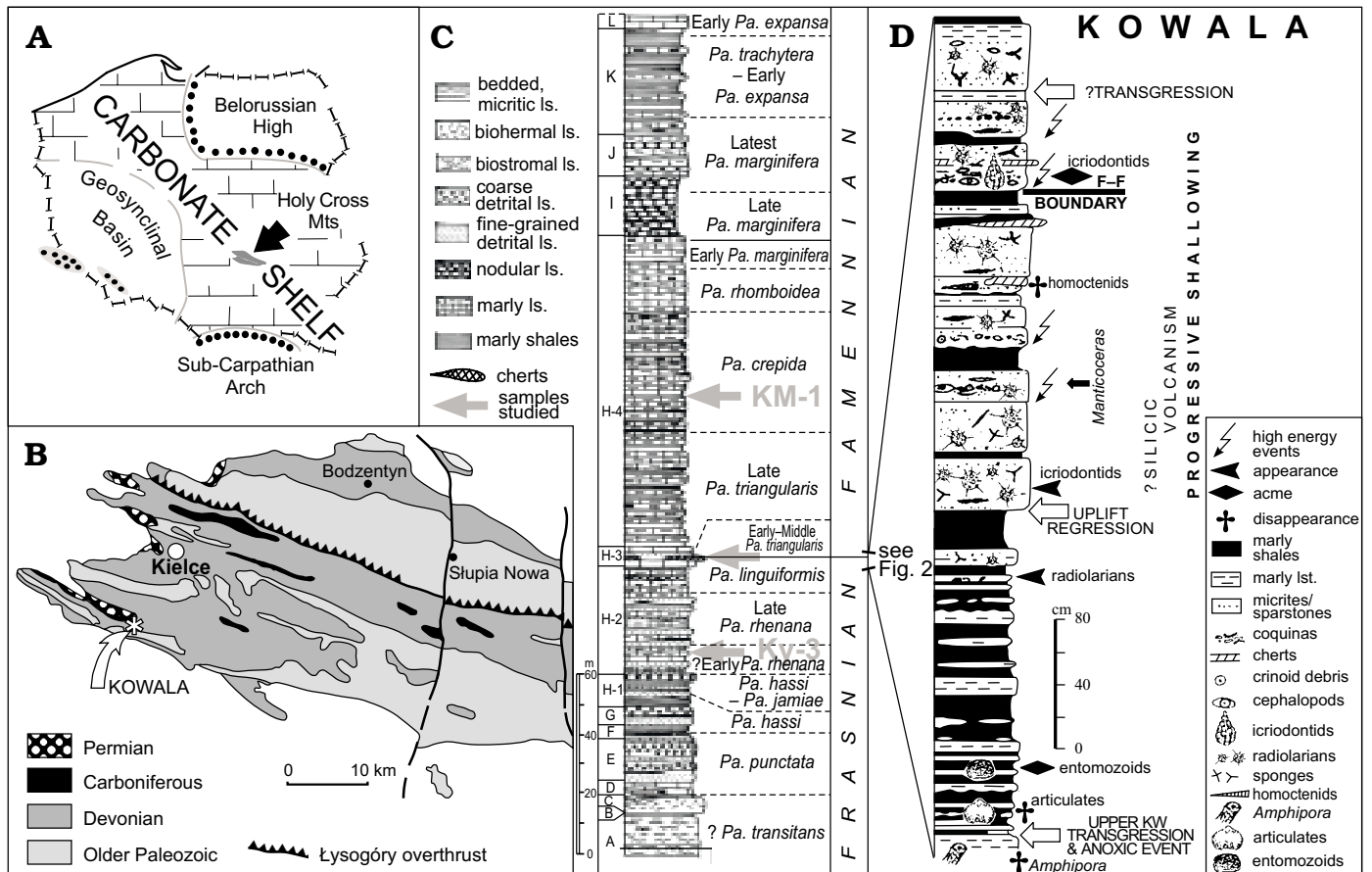
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Fig. 1. **A**, **B**. Location of the Kowala basin succession in Poland (**A**) and Holy Cross Mountains (**B**; see details in Racki 1993). **C**. Composite lithological section of the Late Devonian strata at Kowala (modified after Szulczewski 1996: fig. 8), the reference succession showing environmental evolution typical of intermittently drowned shelf from reef (units A–C) to slope (D–G) to intrashelf basin (H–L). Three sampled radiolarian-sponge intervals are arrowed. **D**. Sedimentary record of eustatic, anoxic and tectono-volcanic events around the Frasnian–Famennian boundary, with emphasis on selected biotic markers. Note blooms of siliceous biota, thought as promoted mostly by submarine exhalative volcanism paired with tectonically-driven shallowing, and a cooling pulse (see Racki 1999; Racki et al. 2002).

## Kowala basinal succession and siliceous faunas

Distinctive siliceous faunas have been found in the well-studied succession (e.g., Szulczewski, 1996; Joachimski et al. 2001; Racki et al. 2002) at active Kowala quarry (Holy Cross Mountains, Central Poland; Fig. 1A, B). The Kowala section is a typical representative of the Late Devonian infilling of the southern (Chęciny-Zbrza) intra-shelf basin, adjacent to the central palaeotopographic high (the Dyminy Reef). Within the over 150 m thick, dark to black rhythmic calcareous-marly suc-

cession (set H), four units are distinguished in the F–F strata (details in Racki et al. 2002; Figs. 1C, D and 2). There are:

H-1.—Variably-bedded, fossiliferous marly micrites are inter-stratified with graded detrital limestones (with broken reef-builders and brachiopod shelly partings), and/or thick (up to 1 m) slump layers.

H-2.—Thinly bedded marly limestones with shale interbeds comprise frequent, irregular, subnodular intercalations, up to 45 cm thick. Sparse fossil assemblages include both planktic and benthic (mostly brachiopod) elements. Among the latter, diverse silicisponges are particularly characteristic of the lower part of this unit (see Rigby et al. 2001).

Fig. 2. Micropalaeontological characteristics of the upper Frasnian and Frasnian–Famennian passage at Kowala, based on the eastern quarry wall section ➤ from 1991 (section Kw). The material obtained from marly-shaly samples, supplemented by few conodont samples and thin sections for the unit H-3. Productive radiolarian (R) and spicule (S) samples studied (see Fig. 3 and Table 2) are arrowed. 1, tentaculitoids; 2, entomozoids; 3, large-sized palynomorphs; 4, goniatites; 5, ichtyolithes; 6, palmatolepid conodonts; 7, polygnathid conodonts; 8, ramose conodont elements; 9, phyllocarid remains; 10, benthic ostracods; 11, nanicellid foraminiferans; 12, sponge spicules; 13, rhynchonellid brachiopods; 14, chonetid brachiopods; 15, lingulids; 16, phosphatized burrow fills and pellets; 17, agglutinated foraminiferans; 18, icriodontid conodonts; 19, echinoderm remains; 20, ramose fossils (a, amphiporid stromatoporoids; b, others [fragmented ?auloporids]); 21, sphaerical microfossils (?mostly calcispheroids).
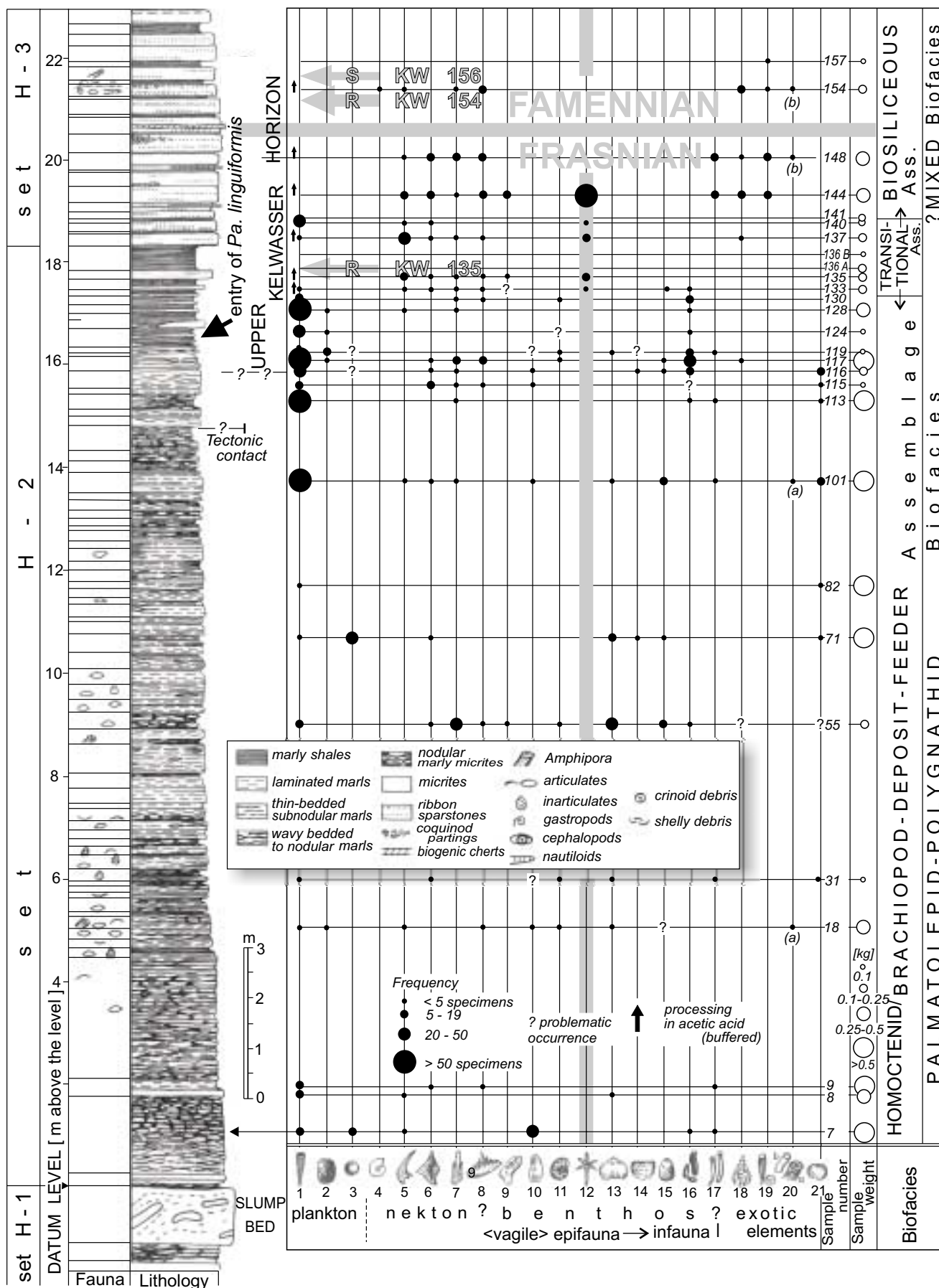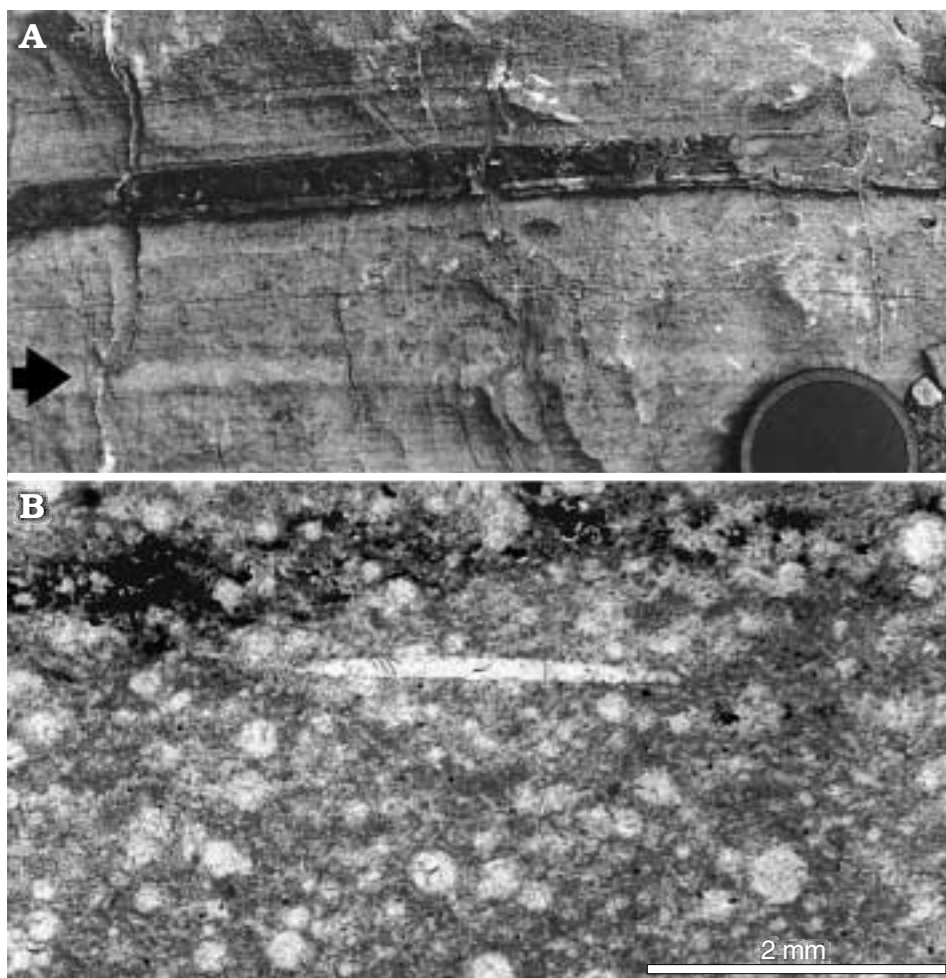
Fig. 3. Radiolarian-spiculite facies, set H-3, Frasnian–Famennian boundary beds at Kowala quarry, Poland (see Figs. 1C, D and 2; Racki 1999: fig. 2). **A**. Field photo of a laminated (marginally-agraded) limestone bed with black bedded chert ; arrowed is a lighter diagenetically unaffected band. **B**. Radiolarian-spiculite limestone packstone (sample Kw-154), with mostly incipiently neomorphozed micritic matrix and numerous pyrite aggregations in the upper part.

H-3.—Platy limestones, with beds up to 50 cm thick and thinner, usually less than 5 cm, shale partings. This calcareous unit, 6 to 8 m thick, is exceptional within the uniform basin succession. The chert-bearing ribbon beds are composed mostly of the variably neomorphosed ("grained") biomicritic and pressure-welded (stylolaminite) argillaceous bands, resulting in crudely laminated to ribbon-like appearance (Fig. 3). Crinoid-brachiopod, or cephalopod, lenses also occur, particularly in the middle portion of the unit.

H-4.—Thick monotonous series, more than 100 m thick, of thin- and rhythmically-bedded marly limestones and shales. With the exception of sporadic bioclastic material, mainly crinoid ossicles, an impoverished macrofauna is limited to bivalves (mostly *Guerichia*), and largely inarticulate brachiopods (*Orbiculoidea*).

As discussed by Racki et al. (2002), sets H-1 and H-2 belong to the *Palmatolepis rhenana* Zone, and the base of the *Palmatolepis linguiformis* Zone is questionably recognised in the uppermost (more clay-rich) part of the unit H-2. The F–F boundary is reliably placed in the lower segment of unit H-3, within the distinctive cherty bed (see Fig. 1C, D). The Lower *Palmatolepis triangularis* Zone shows a distinct thickness reduction to at most ca. 1.1 m.

The H-1 to H-2 sequence reveals a decreasing contribution of the Dyminy Reef—derived carbonate debris in basinal deposition (see the micropalaeontological record in Fig. 2), but the central high persisted to at least the Famennian Early *Palmatolepis crepida* Zone, as evidenced by distal turbidites. These conditions implied that both the anoxic KW events are difficult to recognize strictly within the hemipelagic sequence of the oxygen-deficient basin (Joachimski et al. 2001; Racki et al. 2002). The Famennian part of this succession is more lithologically monotonous and generally scarcely fossiliferous. The principal factor controlling vertical ecological pattern seems to be the oxygen content of seawater (Szulczewski 1992).

The F–F sequence has been sampled several times since 1988 in different walls of the active quarry. The study is mostly based on section "Kw" in the easternmost part which was sampled in 1991 (Fig. 2). Many variably preserved, frequently pyritised sponge spicules and calcified radiolarian specimens were discovered in the broadly-defined F–F passage beds (see Figs. 4–12), although most samples processed contain only undeterminable remains. Silicisponges and radiolarians are the only obvious sources of silica for the locally intensive silicification of bioclasts and cherts (Karwowski et al. 1993). A diverse late Frasnian sponge fauna, described by Rigby et al. (2001), is supplemented herein by
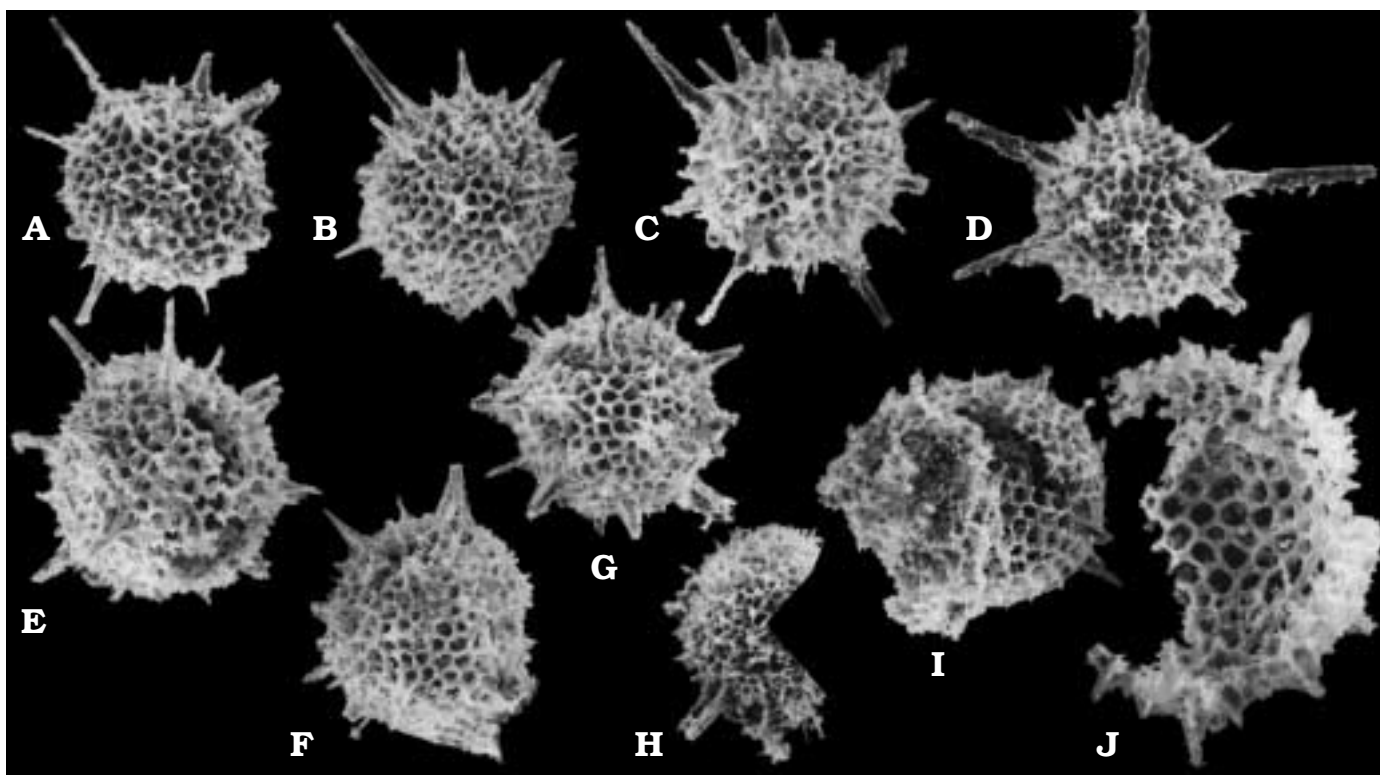
Fig. 4. Entactiniid radiolarians from the Kowala Quarry, set H-3, earliest Famennian (Middle *Pa. triangularis* Zone), sample Kw-154, all × 150 except **J** × 240. **A–C**. *Astroentactinia stellaepolus*. **D**. *Stigmospherostylus diversita*. **E**, **G**. *Astroentactinia stellata*. **F**. *Astroentactinia* cf. *crassata*. **H**. *Stigmospherostylus* cf. *micula*. **I**, **J**. *Helioentactinia* cf. *perjucunda*.

analysis of spicule associations, particularly from sample Ky-3 (Fig. 1C). In the most productive radiolarian sample (Kw-154; Fig. 2 and Tables 1, 2), the conodont species *Polygnathus buzmakovi, Po.* cf. *semicostatus*, *Po. brevilaminus*, *Palmatolepis subperlobata*, ?*Alternognathus pseudostrigosus*, and *Icriodus alternatus* were identified by V. Aristov, establishing an earliest Famennian age (Middle *Pa. triangularis* Zone). Less abundant radiolarians occur also in the uppermost Frasnian sample Kw-135 from the topmost set H-2 (upper *Pa. linguiformis* Zone). In addition, numerous radiolarians and spicules were previously discovered in the "*Cardiola*"-bearing marly limestone sample KM-1 from Famennian set H-4 (undivided *Pa. crepida* Zone; see Racka 1984; Hurcewicz 1993). The siliceous faunal association commonly occurs throughout the Famennian rhythmic basin sequence (Żakowa and Radlicz 1990).

Review of taxonomy and distribution of radiolarians

Below we review the taxa identified tentatively from the poorly preserved material from Kowala; they possibly encompass several new species. Other species are summarized in Table 1. The genera *Entactinia* Foreman, 1963 and *Entactinosphaera* Foreman, 1963 are treated here as junior synonyms of *Stigmospherostylus* Rust, 1892 and *Trilonche* Hinde, 1899 respectively, following Aitchison and Stratford (1997: 380). This problem, according to one of us (V.V.) needs, however, further consideration because of the different number of spines and spheres in *Entactinia* and *Entactinosphaera,* than in *Stigmospherostylus* and *Trilonche*, the difference considered generally as of generic level.

Stigmospherostylus **cf. *micula* Foreman, 1963** (Fig. 4H).— The specimens from the basal Famennian of Kowala differ from the holotype in having a thicker wall and massive spines *Sigmospherostylus micula* is described from the Famennian (USA) and middle Frasnian (Pechora Basin, Russia).

?*Radiobisphaera assidera* **(Nazarov, 1975)** (Fig. 6G).— The tests distinctly differ from *R. assidera* (see Fig. 4B, C) in having six thick long spines, numerous thin, short, and one long, massive, main spine. Found in the F–F passage beds of Kowala Quarry (Poland).

?*Trilonche echinata* **Hinde, 1899** (Fig. 6D, J).—The tests from F–F passage beds at Kowala Quarry are two-spherical with six strongly three-bladed main spines, but numerous short spines are distributed not so densely as in typical *E. echinata*, and we can count not more then 6–7 short thin spines between the two main spines.

Trilonche **cf. *echinata* Hinde, 1899** (Fig. 6F, K).—The F–F tests from the Kowale Quarry are markedly distinguished from *T. echinata* in having sharply-pointed spines.

Table 1. Summary of radiolarian species from the Frasnian–Famennian transition at Kowala.

Species [illustration]	Diagnostic characters	Occurrence at Kowala*	Distribution
Stigmospherostylus additiva (Foreman, 1963)	One-spherical test with six equal, thick, massive spines; inner spicule also has six spines	F–F passage beds	Famennian of eastern USA, Frasnian of Pechora Basin (Russia), Gogo Formation of Western Australia
Stigmospherostylus diversita (Nazarov, 1973) (Fig. 4D)	One-spherical test bears numerous spines of equal size	F–F passage beds	Frasnian of Pechora Basin and South Urals
Stigmospherostylus crustescens (Foreman, 1963) (Fig. 9B)	One-spherical test with six to eight thick, massive spines	Basal Famennian	Famennian of eastern USA and Pechora Basin
Trilonche aculeatissima (Aitchison, 1993) (Fig. 6A)	Two-spherical test with six main massive spines and numerous, needle-like, thinner by-spines. The main spines are equal in size and three-bladed	Basal Famennian	Frasnian of Western Australia
Trilonche australis (Aitchison, 1993) (Fig. 6I)	Two-spherical test with six robust three-bladed main spines and numerous small very short fragile by-spines. One main spine is longer than others and slightly dominant	Basal Famennian	Frasnian of Western Australia and Pechora Basin
Trilonche grandis (Nazarov, 1975) (Fig. 9A)	Two spheres with six main, long, three-bladed spines approximately equal in size	F–F passage beds	Frasnian of Pechora Basin and Urals , Western Australia
Trilonche guangxiensis (Li and Wang, 1991) (Fig. 9C–E)	Two-spherical test with four or six long three-bladed spines, and numerous very short spines	F–F passage beds	Frasnian of Guangxi (China), Pechora Basin
Trilonche echinata Hinde, 1899 (Fig. 6B, C, E, H)	Two-spherical test with six strongly three-bladed, main spines and numerous, short, rod-like by-spines	F–F passage beds	Worldwide in Upper Devonian: Frasnian of Western Australia, Volga-Pechora Basin and Urals, Famennian of eastern USA
Trilonche eostrongila (Foreman, 1963)	Two-spherical test with six strongly three-bladed main spines, which are continuations of inner spines of central spicule, and numerous short rod-like by-spines	Basal Famennian	Famennian of eastern USA
Trilonche nigra Hinde, 1899	Two-spherical test with six or nine long, three-bladed spines, and numerous very short spines	F–F passage beds	Worldwide; Middle–Upper Devonian of Western Australia, Frasnian of Volga-Pechora Basin, Eifelian–Givetian of the South Urals
Trilonche assidera (Nazarov, 1975) (Fig. 5B, C)	Test with two spherical walls, but an outer sphere armed by numerous short spines and one long massive main spine	F–F passage beds	Eifelian–Givetian of South Urals, Frasnian of Pechora Basin, South Urals, Western Australia and Guangxi (China)
Astroentactinia corynacantha (Nazarov and Ormiston, 1983) (Fig. 5A, D)	Spherical test with numerous main conical spines, one significantly longer than others; this long spine is massive, sub-bladed	F–F passage beds	Frasnian of Western Australia, Pechora Basin
Radiobiosphaera menneri Afanasjeva, 2000 (Fig. 5G, H)	Two-spherical test bears two polar spines, one of which is massive and short, the other a thin and long, of conical form	F–F passage beds	Frasnian of Pechora Basin
Astroentactinia crassata Nazarov, 1975 (Fig. 4F)	Spherical test with numerous spines, which are massive and short, of conical form	F–F passage beds	Frasnian of Urals and Pechora Basin
Astroentactinia stellata Nazarov, 1975 (Fig. 3E, G)	Spherical test with numerous main external spines, which are approximately of equal size	F–F passage beds	Frasnian of Urals (Russia), Western Australia
Helioentactinia stellaepolus Aitchison, 1993 (Fig. 4A–C)	Spherical test has got numerous short spines; one of the main spines is longer, but thin, sharp and conical	F–F passage beds	Frasnian of Urals and Western Australia
Polyentactinia tenera Aitchison, 1993 (Fig. 9F)	Spherical test with spongy shell, armed by several long rod-like main spines. No obvious development of by-spines	Basal Famennian	Frasnian of Western Australia
Spongentactinia somphormis (Foreman), 1963	Shell has spongy-like skeleton with well visible irregular pores	Basal Famennian	Famennian Huron Formation (eastern USA)

*F–F boundary beds refer to the uppermost Frasnian (= sample Kw-135; upper *Pa. linguiformis* Zone) and basal Famennian (= sample Kw-154; Middle *Pa. triangularis* Zone).
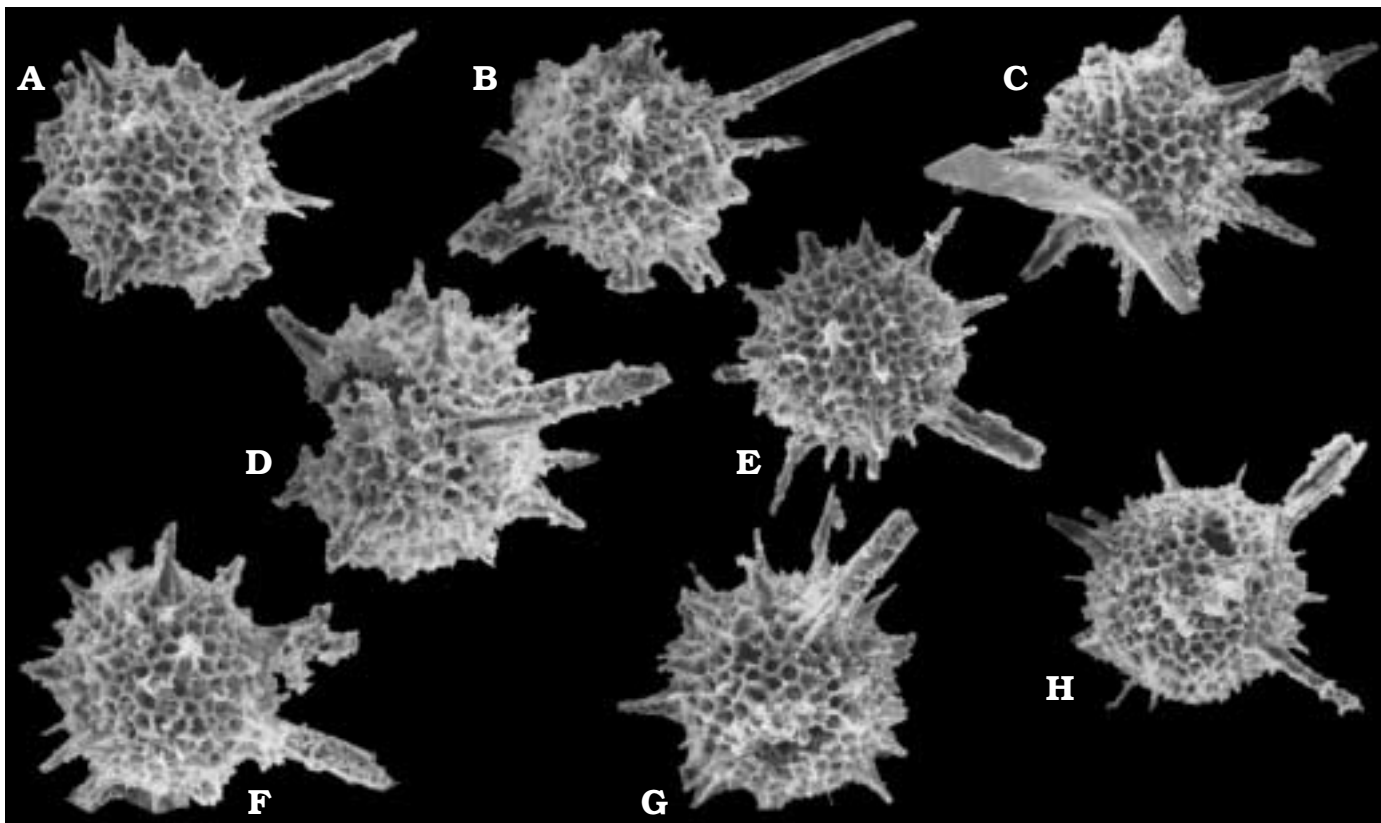
Fig. 5. Entactiniid radiolarians from the Kowala Quarry, set H-3, earliest Famennian (Middle *Pa. triangularis* Zone), sample Kw-154, all × 150. **A**, **D**. *Astroentactinia corynacantha*. **B**, **C**. *Trilonche assidera*. **E**, **F**. *Astroentactinia* aff. *paronae*. **G**, **H**. *Radiobiosphaera menneri*. All SEM micrographs.

Astroentactinia **aff.** *paronae* (Hinde, 1899) (Fig. 5E, F).— This F–F spherical test from Kowala Quarry is distinguished by numerous (up to 16) spines, one of which long, three-bladed in the base and sharpen conical form in the end. *A. paronae* is widely distributed in Givetian of Australia, Frasnian of Volga and Pechora Basin and South Urals.

Polyentactinia **cf.** *rudihispida* **Nazarov and Ormiston, 1993** (Fig. 8F).—The Famennian (*Pa. crepida* Zone) specimens from Kowala differ from the species reported from the Frasnian and Famennian of Pechora and Pripyat Basins in having spherical test with spongy shell, armed by numerous, pronounced, long, conical, main spines.

Haplentactinia **aff.** *flagelifera* **Nazarov, 1988** (Fig. 8A–E).— The lower Famennian (*Pa. crepida* Zone) specimens under study differ from Famennian species, illustrated by Nazarov (1988), in having subspherical test with spongy-porous shell, bearing several long, rod-like, main spines. The spines are characterized by development of numerous apophyses and penetrating the shell body.

Haplentactinia **cf.** *inaudita* **Nazarov, 1988** (Fig. 7F–H).— The poorly-preserved basal Famennian tests from Kowala Quarry are characterized by spongy or triangular porous shell, armed with several long, rod-like, main spines. The spines are characterized by development of numerous apophyses. *H. inaudita* is known from the Frasnian of Russia (Urals, Pechora).

Helioentactinia **cf.** *perjucunda* **Nazarov and Ormiston, 1983** (Fig. 4I, J).—The basal Famennian specimens from Kowala Quarry are two-spherical with numerous short, three-bladed spines, but the inner sphere is thin-walled, one-half the diameter of the main shell. The outer shell is thicker with large and sometimes smaller pores. *H. perjucunda* occurs in the Frasnian of Western Australia, Pechora Basin and the South Urals, and in the Famennian of Pripyat and Pechora regions.

Haplentactinia **cf.** *rhinophyusa* **Foreman, 1963** (Fig. 7A–C, E).— This test is spherical with six long, rod-like, gently tapering spines. The shell has loosely developed irregular triangular and angular lattice pores. The studied basal Famennian specimens differ from typical tests of *H. rhinophyusa*, occurring in the Frasnian of Russia and Western Australia and North American Famennian, in having spines with numerous apophyses.

Secuicollacta **ex gr.** *amoenitas* **Nazarov, 1988**.—The shell has tangential orosphaerid-like skeleton with well-developed irregular pores. The specimens are found in the lower Famennian (*Pa. crepida* Zone) of the Kowala Quarry. *S. amoenitas* is known from the Famennian of Pripyat Basin (Belorussia).

Spongentactinella **sp.** (Fig. 7D).—The characteristic test is conspicuous for thick spongy shell, armed with several short external spines. Inner spicule located excentrically. This
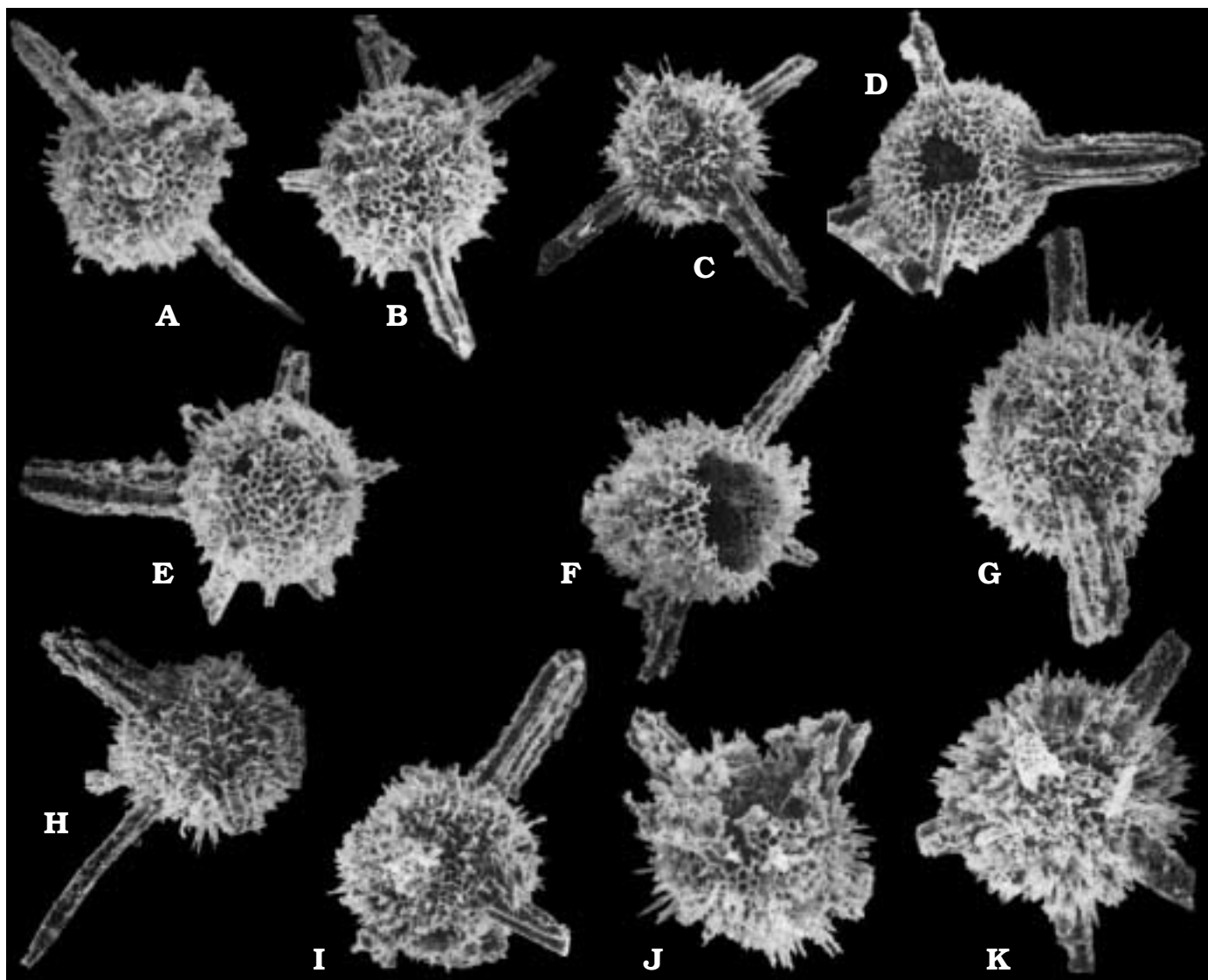
Fig. 6. Entactiniid radiolarians from the Kowala Quarry, set H-3, earliest Famennian (Middle *Pa. triangularis* Zone), sample Kw-154, all × 150. **A**. *Trilonche aculeatissima*. **B**, **C**, **E**, **H**. *Trilonche echinata*. **D**, **J**. ?*Trilonche echinata*. **F**, **K**. *Trilonche* cf. *echinata*. **G**. ?*Trilonche assidera*. **I**. *Trilonche australis*. All SEM micrographs.

taxon occurs in ?topmost Frasnian through basal Famennian at Kowala.

***Albaillella* sp.** (Fig. 9G, H).—At Kowala, poorly-preserved bilateraly-symmetric specimens are present in Famennian samples only (*Pa. triangularis* to *Pa. crepida* zones).

***Ceratoikiscum* cf. *famenium* Nazarov, 1988**.—Basal Famennian specimens from Kowala, composed of three crossing spines in form of triangular frame, with well-developed spongy patagium, differ from Famennian species, illustrated by Nazarov (1988), in having massive spines.

***Ceratoikiscum* cf. *planistellare* Foreman, 1963**.—The coeval shells of this genus at Kowala are marked by the absence of spongy patagium. *C. planistellare* is known from the North American Famennian Huron Formation, as well as from the Frasnian of Western Australia and Timan-Pechora Province.

Radiolarian assemblages and the Frasnian–Famennian mass extinction

Radiolarians and sponge spicules co-occur in all areas of the Late Devonian Pechora, Volga-Ural and Polish intrashelf basins. The richest Frasnian radiolarian associations were reported in the Pechora and Volga-Ural peri-cratonic basins (Bykova and Polenova 1955; Maksimova 1970; Nazarov 1988; Vishnevskaya et al. 1993; Afanasjeva 2000), and include more than 130 species. In addition, a siliceous radiolarian fauna was recently discovered in the shallow-water evaporite-carbonate facies of the Moscow Syneclise (Vishnevskaya 1998). Earlier, Zavidonova (1951: 125, fig. 2) in-
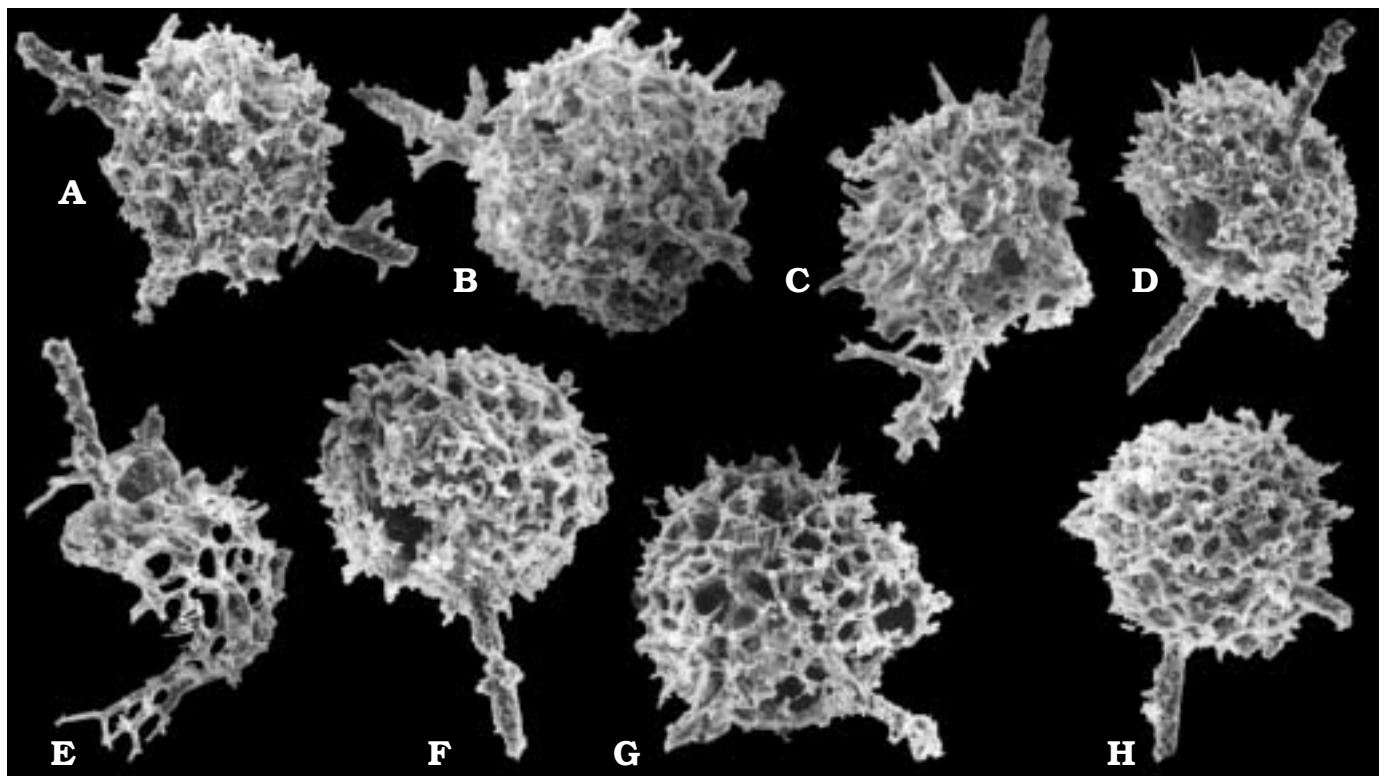
Fig. 7. Entactiniid radiolarians from the Kowala Quarry, set H-3, earliest Famennian (Middle *Pa. triangularis* Zone), sample Kw-154, all × 75. **A–C**, **E**. *Haplentactinia* cf. *rhinophyusa*. **D**. *Spongentactinella* sp. **F**, **G**. *Haplentactinia* cf. *inaudita*. All SEM micrographs.

terpreted radiolarians of the Moscow basin as spherical ooids with visible concentric and radial structures. The first investigations of Givetian?–Frasnian carbonate strata in boreholes of the Kaluga and Moscow areas have shown the presence of rare, predominantly multi-layered spherical radiolarians with spongy shell skeletons, belonging to *Pluristratoentactinia* and *Tetraentactinia*. The existence of radiolarians in evaporites is not surprising, as the presence of Quaternary radiolarian clay with gypsiferous mud was described from the Tyrrhenian Sea (Castellarin and Sartori 1978).

Famennian radiolarian assemblages were established in various facies settings of Pechora (30 species, Afanasjeva 2000), Pripyat (Nazarov 1988) and south Polish intrashelf settings (Vishnevskaya et al. 1997). Interbedded bituminous domanikoid facies (*sensu* Vishnevskaya 1998) of the *Pa. crepida* Zone in the north Pechora basin (Barents Sea and Nowaya Zemlja regions) are probably a record of transgression (Schekoldin 1997; Veimarn et al. 1998). Rare bilateral-symmetric radiolarian taxa confirm this assumption. However, shallowing during the same time probably took place in the Pripyat basin. A regressive pulse (Becker 1994), considered as beginning of the Condroz event and coinciding with the end of *Pa. crepida* Zone, was accompanied by accumulation of black shales in the shelf basins of Western Europe (Germany, France).

Analysis of brachiopod communities indicates direct connections between the Lvov depression, Baltic trough and possibly Polish epeiric sea, while the connection with the Dniepr-Donetsk depression and Central Devonian Field seas was not permanent. Thus, moving from east to west along the Late Devonian East European carbonate basins, we observe shallower facies and disappearance of domanikoid bituminous deposits (see Vishnevskaya 1998: fig. 3). The high-diversity Pripyat radiolarian assemblage occurs in carbonate-clay sequences (75–250 m) representing the *Pa. triangularis* to *Pa. crepida* zones. It contains about 70 species and 18 genera (Nazarov 1988: 132). The particular character of this assemblage is domination of spongy spherical species with long spines ornamented with numerous apophyses, as well as occurrence of bilateraly-symmetric Ceratoikiscidae and Palaeoscenidiidae.

The Polish late Frasnian–Famennian assemblages are taxonomically uniform and invariably dominated by abundant spherical morphotypes, even if the youngest microfauna obtained (from the *Pa. crepida* Zone) is far less differentiated. In summary, the assemblages from Kowala include 34 taxa of 12 genera (Tables 1, 2), showing strict affinities with Frasnian faunas of Russia and Australia, as well as to those from the Famennian of Beloruss and USA. The most distinctive cosmopolitan genera are *Stigmospherostylus*, *Trilonche*, *Astroentactinia*, *Helioentactinia*, *Polyentactinia,* and *Haplentactinia* (see Figs. 4–9). In contrast to the diverse entactiniid association, the bilaterally symmetrical groups (*Ceratoikiscum* and *Albaillella*; Fig. 9G, H) occur only sporadically in the Holy Cross microfaunas. Also in contrast to the F–F radiolarian associations from Prypjat and Pechora, the coeval less differenti-

Table 2. Taxonomic composition of the Late Devonian radiolarian assemblages at Kowala (semiquantitative scale: a, abundant; c, common, r, rare).

Stratigraphic position	topmost Frasnian	basal Famennian	Lower Famennian
Conodont zones	*Pa. linguiformis*	Middle *Pa. triangularis*	*Pa. crepida*
List of radiolarian species	Sample Kw-135	Sample Kw-154	Sample KM-1
Stigmospherostylus additiva	c	a	
Stigmospherostylus crustescens		r	
Stigmospherostylus diversita	a	r	
Stigmospherostylus herculea		a	
Stigmospherostylus cf. *micula*		c	
Trilonche aculeatissima		a	
Trilonche assidera	c	r	
?*Trilonche assidera*	c	a	
Trilonche australis		c	
Trilonche echinata	c	a	
?*Trilonche echinata*	c	a	
Trilonche cf. *echinata*	a	a	
Trilonche eostrongyla		r	
Trilonche grandis	c	a	
Trilonche nigra	c	a	
Trilonche guangxiensis	r	c	
Radiobiosphaera menneri	a	c	
Astroentactinia corynacantha	c	r	
Astroentactinia crassata	c	c	
Astroentactinia aff. *paronae*	c	a	
Astroentactinia stellaepolus	a	a	
Astroentactinia stellata	c	c	
Helioentactinia cf. *perjucunda*		r	
Polyentactinia cf. *rudihispida*			a
Polyentactinia tenera		a	
Haplentactinia aff. *flagelifera*			c
Haplentactinia cf. *rhinophyusa*		c	
Haplentactinia cf. *inaudita*		c	
Spongentactinia somphormis		a	
Spongentactinella sp.	r	c	
Secuicollacta ex gr. *amoenitas*			a
Ceratoikiscum cf. *famenium*		r	
Ceratoikiscum cf. *planistellare*		r	
Albaillella sp.		r	r

Fig. 8. Entactiniid radiolarians from the Kowala Quarry, set H-4, early Famennian (*Pa. crepida* Zone), sample KM-1, all × 75. **A–E**. *Haplentactinia* aff. *flagelifera*. **F**. *Polyentactinia* cf. *rudihispida*. All SEM micrographs.

representatives of the bilaterally symmetrical group, took place in the Famennian interval studied (Table 2). Thus, no devastating influence of the KW biocrisis can be recognized in the continuous radiolarian succession, contrary to conclusion by Umeda (in press). In fact, all previous F–F diversity data were based on microfaunas from separated areas (e.g., Afanasjeva 2000).

Frasnian to Famennian siliceous sponge faunas

Sponges are important components of some Late Devonian benthic assemblages in south Polish epeiric seas (Hurcewicz 1993). In general terms, clear differences exist between Frasnian (pre-extinction) and Famennian (post-extinction) faunas. Most Frasnian siliceous sponges exhibit complete preservation, and belong to groups marked by a rigid fused skeleton.

ated Polish microfaunas are surprisingly ecologically similar to these from Kolyma and Alaska, because they are characterized by abundance of spherical forms and near-absence of bilaterally symmetrical Ceratoikiscidae and Palaeoscenididae. From purely morphological aspect, the F–F radiolarian assemblage of Poland is comparable with Givetian shallow-water radiolarian assemblages of Moscow and Pripyat regions (Vishnevskaya 1998), where multi-layered spherical *Pluristratoentactinia* and *Tetrentactinia* dominated.

It is necessary to emphasize that if genera such as *Stigmospherostylus*, *Trilonche* and *Astroentactinia* are invariably dominant in F–F transition of Poland, the appearance of several new genera, such as *Helioentactinia*, *Polyentactinia*, *Haplentactinia*, *Spongentactinia*, *Secuicollacta*, as well as
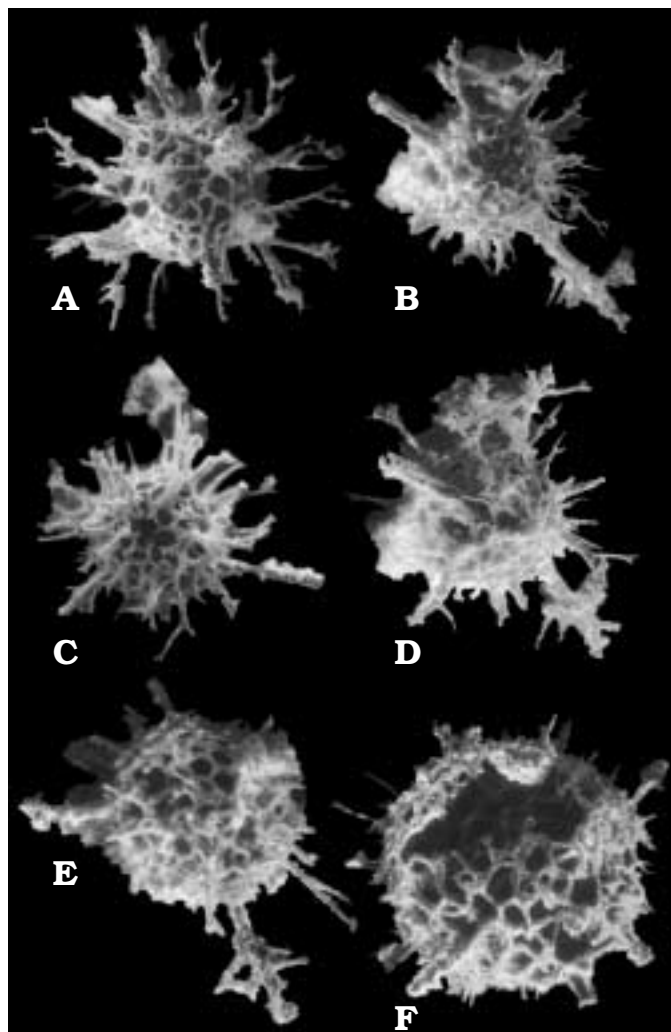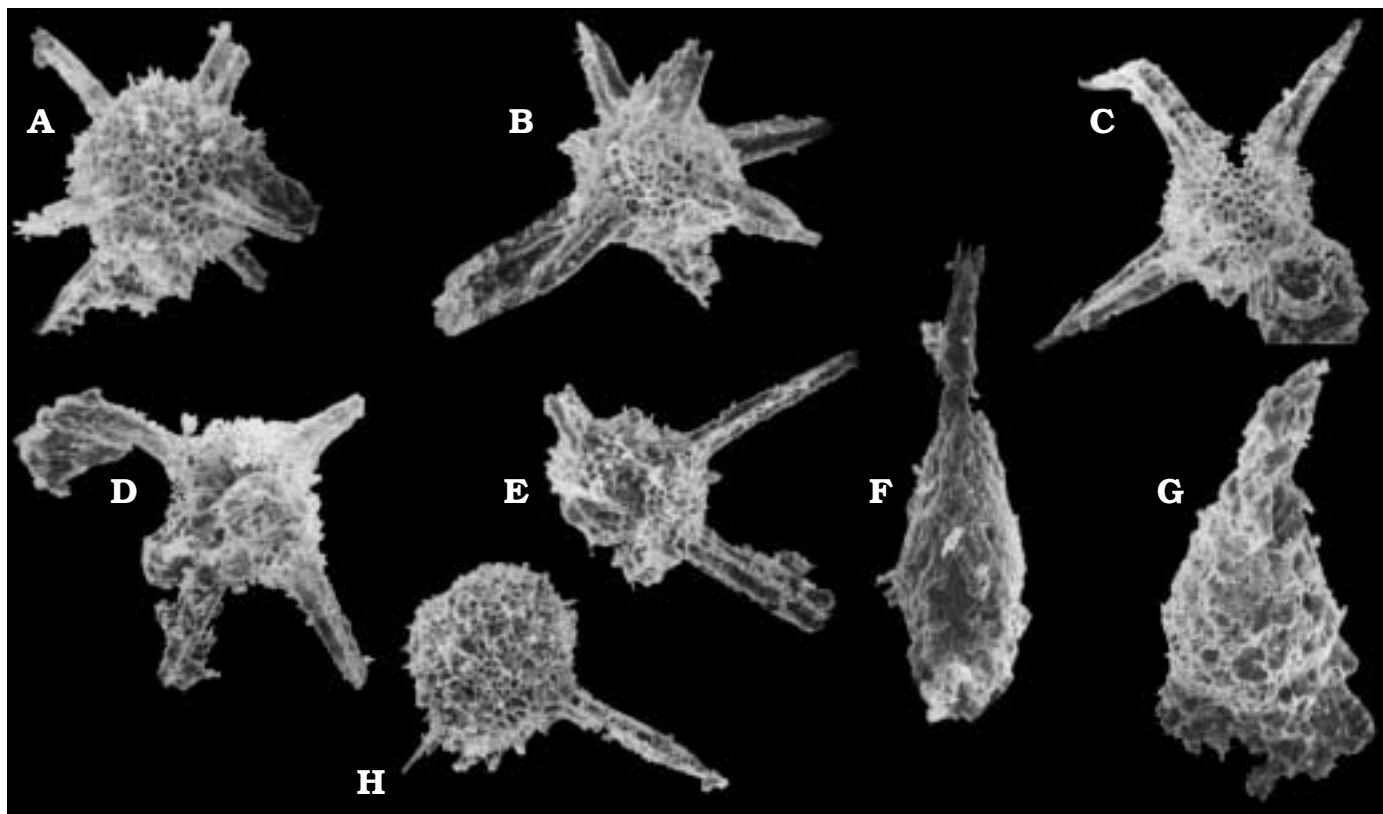
Fig. 9. Entactiniid (**A–F**) and albaillellid (**G**, **H**) radiolarians from the Kowala Quarry, set H-3, earliest Famennian (Middle *Pa. triangularis* Zone), sample Kw-154, all × 75. **A**. *Trilonche grandis*. **B**. *Stigmospherostylus crustescens*. **C–E**. *Trilonche guangxiensis*. **F**. *Polyentactinia tenera*. **G**, **H**. *Albaillella* sp. All SEM micrographs.

Exclusively groups having loose, dispersed spicules that occur in insoluble residues represent Famennian sponges. Pre-extinction associations are significantly more diverse, as exemplified by a distinctive late Frasnian fauna from the Jaźwica and Kowala quarries (see Rigby et al. 2001), including 15 species representing 11 genera. Less diverse are associations described by Hurcewicz (1985) from Wietrznia and Kowala. Examination of the original collection of the latter author, however, revealed that this sponge fauna remains somewhat uncertain, because, for example, specimens identified as representatives of Recent genus *Reniera* from Wietrznia are in fact silicified fragments of receptaculitid algae, and some others clearly do not display spicule types as illustrated.

A diverse assemblage of sponges, including the youngest Devonian desma-bearing astylospongiid demosponges known, and the oldest well preserved and most diversified hexactinosan hexactinellid sponges, has been collected from upper Frasnian (*Pa. rhenana* Zone) deposits at Jaźwica (as well as from set H-1 at Kowala; Fig. 1C). The latter, typical of Mesozoic to Cenozoic biotas, is distinguished by hexactine skeletons fused in a regular, solid three-dimensional network. In addition, spicules occuring in residues (Figs. 10, 11) prove the presence of loose-skeletal hexactinellids (various hexactines and their derivatives) and demosponges (oxeas, strongyles and tetraxones), as well as anthaspidellid lithistids (dendroclones) not known from bodily preserved sponges.

The diverse faunas were found in calcareous (usually nodular) and marly rocks, interpreted as hemipelagic fore-reef deposits. Hurcewicz (1985), who regarded sponge aggregations from Kowala as a "sponge reef", was in error, because they merely represent an accumulation of downslope redeposited specimens. Taxonomically similar Frasnian assemblages (but in terms of higher taxonomic levels) are known from other European sites (see review in Rigby et al. 2001), but several faunas remain as yet unstudied and noted only as spiculite and spongiolite microfacies, as exemplified by sponge wackestones/bafflestones (MF2 of Preat et al. 1998) of the Montagne Noire. This aplies also to Moravian (Hladil and Kalvoda 1993) and South Chinese (Ma and Bai 2002) F–F sponge-rich communities. In late Frasnian deeper-water settings of the Subpolar Urals, ecologically matching ?biostromal deposits also occur, formed by undetermined lithistids (Yudina et al. 2002: fig. 5A), probably taxonomically unlike those from Poland and Germany. In Nevada, late Frasnian (Late *Pa. rhenana* Zone) sponge spicules include umbellate hemidiscosan microscleres of hexactinellids (Boundy-Sanders et al. 1999). Diverse F–F sponge foreslope faunas from Western Australian reef complex are a peculiar regional character (e.g., Wood 2000) but remain poorly known in taxonomic terms.

Latest Frasnian and early Famennian stressed benthic habitats of submerged carbonate shelves seem to be very suitable for silicisponge thriving. This is highlighted by an acme of
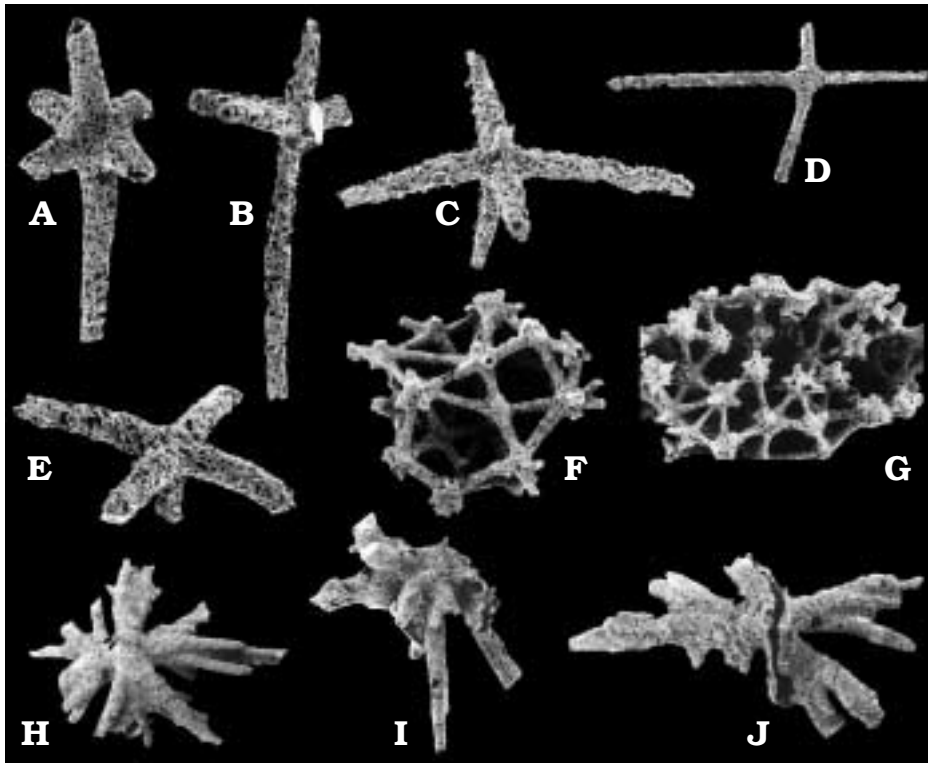
Fig. 10. Hexactinellid and lithistid spicules from Kowala Quarry, set H-2, late Frasnian. **A**, **H**, **E**. Hexactines (**A** × 43; **H** × 49; **E** × 75). **B**. ?Stauractine, × 21. **G**. Dermal pentactine, × 64. **I**. fragments of fused skeleton of hexactinosan sponge, × 21. **J**. Fragment of fused skeleton of astylospongiid lithistid, × 32. **C**, **D**, **F**. dermal spicules (strongly modified pentactines) of docodermatid hexactinellid. (**D** × 13; **C** × 15; **F** × 17). All SEM micrographs.
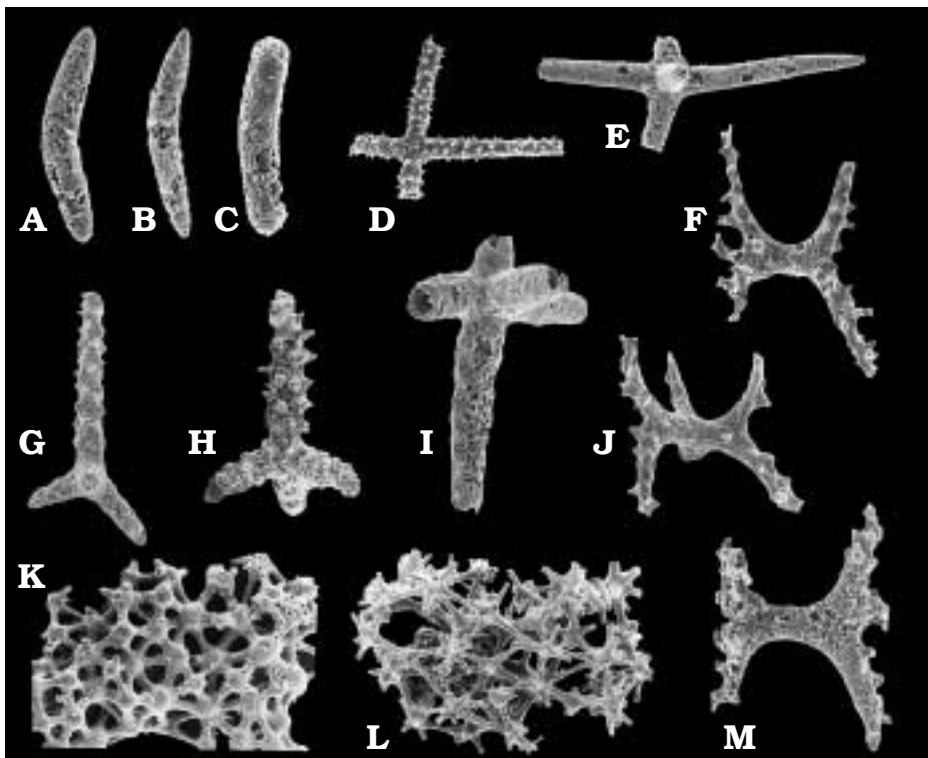

Fig. 11. Demosponge (including lithistid) and hexactinelid spicules from Kowala Quarry, set H-2, late Frasnian, sample Ky-3. **A**, **B**. Strongyloxeas, × 70. **C**. Strongyl, × 70. **D**. Stauractin, × 54. **E**. Pentactine, × 36. **F**, **J**, **M**. Desmas (dendroclones) of antahspidellid lithistids, × 70. **G**. Tetraxon, × 70. **H**. Tetraxon, × 54. **I**. Hexactine, × 36. **K**, **L**. Fragments of astylospongiid lithistid skeleton, × 27 All SEM micrographs.

loose-skeletal hexactinellids in shallow-marine Appalachian habitats (37 species; see McGhee 1996: 67). However, faunas from the broadly-defined F–F passage (*Pa. linguiformis* to Middle *Pa. triangularis* zonal interval) at Kowala seem to be taxonomically impoverished, even if they were the main benthic element of siliceous-dominated "crisis" biotas (Racki et

al. 2002). Residua from conodont samples (sets H-2 and H-3; see Figs. 1C, D and 2) contain commonly, and occasionally numerous spicules evidencing loose-skeletal groups of Hexactinellida, and rare Demospongea (Fig. 12). A similar sponge association, comprising taxa with loose hexactines and rare demosponge tetraxones, was recorded by Hurcewicz
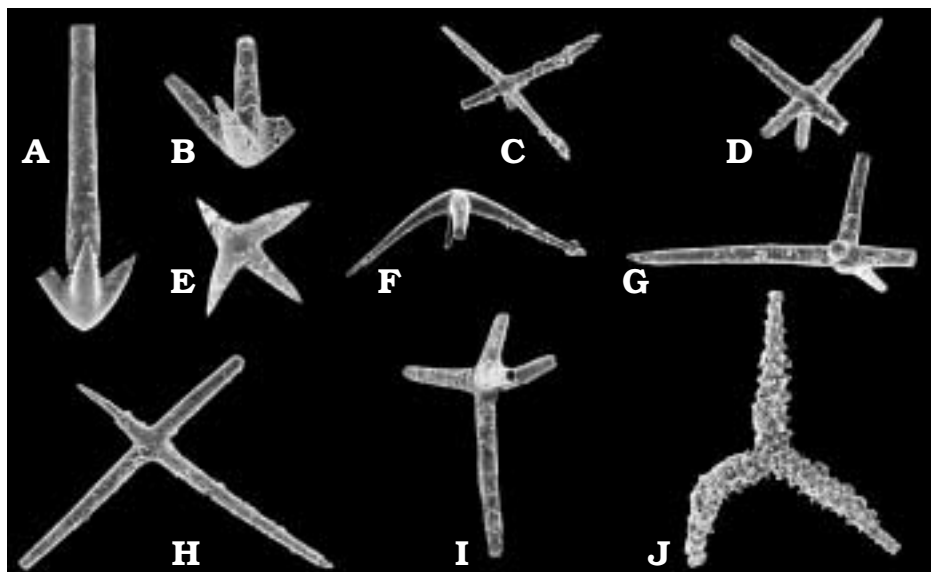
Fig. 12. Hexactinellid and demosponge spicules from the Kowala Quarry, set H-3, earliest Famennian, sample Kw-156, all × 38. **A**, **B**, **E**. Anchoring spicules of hexactinellids. **C**, **D**, **F–H**. ?Dermal pentactines. **I**. Hexactine. **J**. Undetermined demosponge spicule. All SEM micrographs.

(1993) from slightly upper Famennian rocks in this Holy Cross region. Although more precise taxonomic determinations are impossible for this material, replacement of the ephemeral rigid-skeletal lithistid-hexactinosan foreslope association by persistent loose-skeletal hexactinellid and rare demosponge basinal faunas near the F–F bounary is the prominent biotic character of the Late Devonian evolution in the stratified Chęciny-Zbrza basin (see also Hurcewicz 1993). Thus, sparse colonization of muddy bottoms by siliceous sponges was presumed to have occurred in deep-water and oxygen-depleted environments (May 1995: 44), well known also from other marine basins and ages. Dictyospongid hexactinellids (loose spicules), anthaspidellid and ?astylospongiid lithistids were the most distinctive elements of the black "Schistes de Porsguen" in the Famennian of the Rade de Brest (Pickett and Plusquellec 1998).

Flourishing of heterotrophic siliceous sponges through the Phanerozoic might be causally linked to increased nutrient levels in submerged and tectonically disturbed mid-shelf and proximal foreslope areas (Brunton and Dixon 1994). From an evolutionary viewpoint, the apparent gap in the geological record of Hexactinosa between the Late Devonian and Triassic (Pisera 1999) may be associated with ecological requirements for these sponges (Rigby et al. 2001). Today they are dwellers of relatively deep-water, quiet environments, under low competition and low light (Pisera 1997). Thus, their fossil record is probably controlled by frequency and preservation potential of comparable depositional systems (see also Gammon et al. 2000). Because the sedimentary record refers mainly to shallow shelf or marginal basinal settings, the probability of finding of Palaeozoic and early Mesozoic hexactinosan sponges, as they were relatively subordinate benthic components, is also proportionaly small. Furthermore, silica limitation may have forced neritic sponges with desmas to either lighten their skeletons, or to move to deeper, silica-rich environments (Maldonado et al. 1999).

Implications

The appearance of the diverse sponge faunas in the Chęciny-Zbrza basin succesion seems to be roughly correlated with the major *Palmatolepis semichatovae* transgression (introductory Late Devonian sea-level highstand), and accelerated submerged of the Dyminy Reef manifested in hemipelagic rhythmic deposition of the marly set H in the Kowala area (see Racki 1993; Racki et al. 2002; Fig. 1C). Thus, the regional record of an initial phase of the late Frasnian KW Crisis is conspicuous by flourishing distinctive brachiopod-sponge-coral faunas in deep-slope, episodically storm-influenced habitats (Rigby et al. 2001).

The uppermost clayey part of unit H-2 (ca. 1.5 m thick; see Figs. 1D and 2) at Kowala is marked by gradual disappearance of shelly benthos (especially "euryoxic" rhynchonellids) and exotic, reef-derived bioclasts (e.g., ramose stromatoporoids). This is accompanied by the entry of pelagic palmatolepid conodonts (*Palmatolepis linguiformis*), higher homoctenid frequency and a weak entomozoid acme (*Entomoprimitia* [*Entomoprimitia*] *splendens*) probably corresponding to onset of the Upper KW transgresive/anoxic pulse (Racki et al. 2002). A more prominent biotic shift is approximated with the lithologic change from unit H-2 to H-3. Lithofacies turnover is emphasised by the overall switch in both benthic and pelagic settings from mostly calcareous to long-lasting siliceous, radiolarian and basinal loose-skeletal hexactinellid-demosponge biotas. This may be a biotic signature of an oceanic cooling event, invoked for the F–F biotic crisis (e.g., McGhee 1996; Copper 1998). Such a climate setting is indeed suggested by new oxygen isotopic data for both the Kellwasser intervals (Joachimski and Buggisch 2000). Notably, the F–F ecosystem perturbations were a prelude to progressive Famennian–Carboniferous cooling. Thus, climatically controlled equatorial and marginal upwelling may have promoted biosiliceous production in some regions (e.g.,

Kalvoda 1986), even if palaeoclimate numerical modelling does not support the idea of large-scale upwelling in Late Devonian greenhouse seas (Ormiston and Oglesby 1995; see also Kidder and Erwin 2001). Possible causal feedbacks between Earth-bound catastrophic changes in the mid-Late Devonian ocean-atmosphere system, particularly abrupt climate changes, anoxia and eutrophication/productivity links, have been widely discussed (e.g., Schindler 1993; Ormiston and Oglesby 1995; McGhee 1996; Copper 1998; Racki 1999; Joachimski and Buggisch 2000; Joachimski et al. 2001; Racki et al. 2002).

Onset of radiolarian-spiculite calcareous deposition through the F–F transition in the Holy Cross (and Moravian, see Hladil et al. 1991; Hladil and Kalvoda 1993) basins was clearly linked to a sustained shallowing trend interrupted by higher-energy episodes, but probably also with tectonic uplift and/or oceanic overturn during the anoxic Upper KW Event (Racki et al. 2002). Regional tectonic rejuvenation pulses along the southern flank of the submerged Dyminy reef were probably an echo of spasmodic initiation of the Pripyat-Dniepr-Donets rifting in the neighbouring East European Craton. Co-occurrence of abundant Famennian radiolarians with quartz silt and mica also implies possible volcanic activity and ash leaching (Żakowa and Radlicz 1990). This was only a prologue to the Early Carboniferous volcanism-controlled Culm-type biosiliceous deposition, widespread over the south Laurussian shelf (e.g., Chlebowski in Żakowa et al. 1983).

Silicisponges may have out-competed calcareous benthos even in inner shelf habitats because of elevated discharge of land-derived nutrients that included high quantities of dissolved silica and a calm hydrodynamic setting (Gammon et al. 2000). Prolific sponge colonization may likewise be promoted by shallow-water hydrothermal Si-bearing venting (Tarasov et al. 1999). Thus, localized F–F blooms of peculiar biosiliceous biota in not very deep epeiric sea might be at least partly ascribed to silicic exhalative volcanism in zones within a revived deep-seated fault zone (Maksimova 1979; Afanasjeva 2000; see Fig. 1D).

A biosiliceous acme is a worldwide phenomenon in the broad F–F transition, known primarily from Laurussian shelves (Racki 1999). However, recent taxonomic compilations by Vishnevskaya (1997) and Vishnevskaya and Kostyuchenko (2000) suggest a drop in radiolarian diversity in mid-Late Devonian time, as emphasized recently for the F–F epicontinental realm by Umeda (in press). Similar data for sponges were earlier presented by McKinney (1987). On the other hand, Afanasjeva (2000: 130, fig. 9; cf. also Kiessling and Tragelehn 1994) concluded that the F–F mass extinction is weakly recorded in radiolarian generic terms, and Late Devonian corresponds to the zooplankton diversity peak throughout Palaeozoic. Hence, biodiversity data, contrary to overall "biovolume" (= bioproductivity) trends, are still tentative. The Kowala basal Famennian radiolarian microfauna shows a crisis persistence of at least 12 (up to 16?) species known previously exclusively from the middle to late Frasnian (Afanasjeva 2000), mostly of the Timan-Petchora Province (see Table 1). Rapid turnovers are predicted rather for the post-crisis Famennian biotas, and this age indeed corresponds to accelerated radiolarian evolution (Nazarov and Ormiston 1985; Kiessling and Tragelehn 1994).

This ambiguity concerns also secular distribution of silica-replaced fossils (Kidder and Erwin 2001); in the region under study, their Famennian decrease in frequency is obviously linked solely with appearance of clay-rich basin deposits, hampering the diagenetic phenomena so common in Givetian–Frasnian pure limestone units (Karwowski et al. 1993). Thus, a detrimental effect of the F–F mass extinction on siliceous biota and silica cycling, supposed by Kidder and Erwin (2001), is disputable (see summary in Racki 1999), especially in the context of the chert-bearing F–F succession at Kowala (Racki et al. 2002).

Final remarks

High survival rates and regional blooms of possibly impoverished marine siliceous groups, along with coeval demise of calcareous biota, occurs at the Frasnian–Famennian (radiolarians, silicisponges) as well as at the end-Cretaceous (diatoms, radiolarians) mass extinctions (see Racki 1999 for the review). This phenomenon is interpreted as being controlled by major chemical and thermal changes stimulating biomineralisation processes. Drastic fluctuations in nutrient levels and productivity commonly accompanied major marine biotic crises (Martin 1998). Concentration of silicic acid in seawater adjusts the phenotypic expression of various spicule types genetically available in sponge species (shown experimentally by Maldonaldo et al. 1999).

As discussed by Racki and Cordey (2000), a cumulative stimulus of (1) higher rate of polygenic silica and other key nutrients, and (2) a disturbed greenhouse effect, episodically marked by more vigorous oceanic circulation, due to cooling pulses and a variety of volcanogenic upwellings and overturns, led to (3) moderate eutrophication pulses, and (4) culminated in more favourable conditions for siliceous over calcareous skeletal production, deposition and preservation. Such causal factors were likely to be more efficient in largely oligotrophic Palaeozoic epeiric seas (see Martin 1998), affected by variety of volcano-hydrothermal processes. High biosiliceous productivity appears to coincide with the ^{13}C positive anomalies, mostly when carbonate periplatform ooze input drastically reduced and fertility levels were higher (see summary in Racki and Cordey 2000). For example, an event coincidence of 20 Ma hiatus on carbonate platforms, the onset of biosiliceous deposition in the basins and the ^{13}C positive excursion is causally tied by Bartolini and Cecca (1999) to carbonate crisis due to eutrophication, which affected the Western Tethys during the Middle Jurassic. This scenario is applicable also for the F–F evolution of the Dyminy Reef and Chęciny-Zbrza basin, even if an increased off-shoal transport of fine-grained carbonates predominated in the crisis interval, recorded in intermittent calcareous-

biosiliceous deposition of the set H-3 (Racki et al. 2002). Comparison of major biotic turnovers shows that only spherical radiolarian lineages could have survived those biotic crises. The common taxa of Late Devonian assemblages from Poland and Russia (Afanasjeva 1997, 2000; Vishnevskaya et al. 1997) are entactiniids that diversified through the Famennian (Nazarov and Ormiston 1985). The successful stock is seen as shallow, warm-water dwellers, possibly with symbionts (Casey 1993). The F–F offshore assemblage from Poland is similar to shallow-water, inner shelf faunas with multi-layered entactiniids from East European domains. Nevertheless, this morphologically simplified scenario, and the demise of holoplanktic, cold- and deep-water biota due to expanding anoxia (e.g., Joachimski et al. 2001) is speculatively assumed for the F–F micropalaeontological record, in light of data stressing selective radiolarian preservation by Kiessling and Tragelehn (1994).

On the other hand, only rare Entactinosphaeridae persisted during the end-Permian ecosystem collapse, and minute spherical forms, like *Stylosphaera goruna* and species of *Amphisphaera*, survived the end-Cretaceous crisis (see Racki 1999). Vishnevskaya (1997) noted an acme of morphological diversity among radiolarians, with development of "abnormal" and "monstrous" specialized forms, just prior to the extinction events. Such evolutionary "experiments" are explained as attempts to accommodate to quickly changing habitats. Subsequent reduction to simple spherical and opportunistic species occurs when oceanic stability is disrupted during ecosystem collapse. Advantage of smaller forms with shorter life cycles, i.e. the Lilliput phenomenon (Urbanek 1993), probably conform to elevated ocean fertility in post-extinction settings (see Martin 1998). The highly productive opportunistic silica-secreting communities, being tolerant to hypoxic conditions, appear to thrive even in the harmful environments.

Acknowledgements

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