A Middle Devonian radiolarian fauna from the Chotec Limestone (Eifelian) of the Prague Basin (Barrandian, Czech Republic)

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ABSTRACT

The occurrence of radiolarian faunas in the upper part of the Chotec Limestone is discussed in terms of faunal composition, systematics and geological implications. The most common entactinid species are treated systematically. The occurrence of radiolarians in large numbers in the rock succession began approximately 2 meters below the onset of the black shale sedimentation (Kacak Member). The abrupt sedimentological change, commonly viewed as an event therefore does not coincide with the faunal turnover, leading to a radiolarian dominance well before the onset of black shale deposition.

RÉSUMÉ

Une faune de radiolaires du Calcaire De Chotec (Devonien moyen, Eifelien supérieur) du bassin de Prague (Barrandien, République tchèque).

La présence de faunes de radiolaires dans la partie supérieure du Calcaire de Chotec est discutée en tenant compte de la composition faunique, de la systématique et des implications géologiques. Les espèces d'entactinés les plus communes sont traitées systématiquement. Les radiolaires sont présents en grand nombre dans la succession sédimentaire environ 2 mètres au-dessous des premiers schistes noirs (Kacak Formation). Le brusque changement de sédimentation ne correspond donc pas comme habituellement à un changement faunique, comme l'indique cette dominance des radiolaires bien avant le début de l'accumulation des schistes noirs.

KEY WORDS

Radiolarians, Middle Devonian, upper Eifelian, Barrandian, Chotec Limestone, Kacak event.

MOTS CLÉS Radiolaires, Dévonien moyen, Eifelien supérieur, Barrandien, Calcaire de Chotec, Kacak Formation.

INTRODUCTION

The Paleozoic area around Prague is a famous and classical region for many investigations in paleontology and biostratigraphy. The occurrence of radiolarians in certain rocks especially of Silurian age has been commonly mentioned (Rodic 1925; Prantl 1949) and some very detailed petrographic studies have been carried out (Rodic 1931). Although typical radiolarian rocks (radiolarian cherts, lydites) are not very common especially in the Devonian sequence it has been known for some decades, that some lithologies may bear radiolarian skeletons in significant amounts (Fabian 1933). The fact, that some of the sedimentary rocks in the Barrandian area bear well preserved radiolarians, is not well known, although in cases where preservation is good such occurrences might be of special importance for our knowledge of stratigraphy and development of radiolarian faunas during the Silurian and Devonian. The fauna that is figured and partly described in this paper has been considered in two earlier papers (Cejchan 1987; Budil 1995). The present paper intends to supply some addional information, observations and a systematic treatment of the common entactinid species in these faunas. The special lithologic framework in which these faunas occur may be worth noting in the context of the "bioevent character" of the Kacak sequence (and the "otomari-event", cf.Walliser 1984), immediately overlying the source rocks of our faunas.

LOCALITIES (cf. Figs 1, 2)

Radiolarian bearing rock samples come from two localities situated near Prague:

1. Railway cut in Praha 5-Hlupocepy. This exposure has been figured and described several times (e.g., in Budil 1995: 2-4; Chlupac 1960, 1993). It exposes a sucession from the higher part of the Chotec Limestone until the Roblin beds, overlying the Kacak Member. The Radiolarians have been extracted from a 15 cm thick bed of Chotec Limestone 50 cm below the base of the predominantly black siliceous Kacak sequence. Rare fin-



FIG. 1. — Distribution of the Kacak Member (in black) in the Barrandian area and geographic situation of the discussed localities.

dings of radiolarian faunas come from rocks 4 m below the Kacak sequence (Budil 1995).

2. Knezi hora hill near Karlstejn. This locality, although offering a good sequence through the uppermost Chotec Limestone and the base of the Kacak Member in its typical development, had not been studied in detail until quite recently (Budil 1995: 4-8). Radiolarians are even better preserved here than those from the Hlupocepy railway cut. Our sample comes from two limestone beds approx. 2 m resp. 1 m below the Kacak base (beds -10/-12 and -20).

LITHOLOGY

The radiolarians come from the uppermost part of the Chotec Limestone (biomicritic limestones with intercalations of pelbiodetritic limestones) underlying the predominantly siliceous black sequence, the latter representing the so called Kacak event (Chlupac 1989). The limestone occurs in beds of thicknesses between 5 and 30 cm. It is dark grey in colour and bituminous. The cherts of the Kacak sequence, restricted to the area around Prague, have long been known to contain radiolarians (Fabian 1933; see



FIG. 2. — Lithologic succession of the sequences exposed at Praha-Hlubocepy railway cut and Karlstejn-Knezi hora hill. Note the different lithologic composition of the Kacak Member at the two localities. 1, massive biomicritric limestones; 2, thin bedded biomicritic limestones; 3, fine biodetrital limestones; 4, coarse biodetrital limestones; 5, lithoclastic breccia (not present in the sequence shown); 6, dark calcareous claystones and clay limestones; 7, thin bedded cherts; 8, calcareous siltstones and biodetritic limestones with silt.

Chlupac 1960: 176) for changes in terminology of the sequences). Radiolarian preservation seems to be more favorable in the limestone beds compared to the Kacak cherts.

AGE CONTROL

According to faunal data, the Kacak succession 2 m above the upper Chotec Limestone was initially considered to be basal Givetian (Chlupac 1960: 177), and later regarded uppermost Eifelian (Chlupac & Kukal 1986, 1988; Chlupac 1993). Kalvoda (1992) discussed the stratigraphic implications of conodonts in beds near the base of the Kacak sequence which in terms of the conodont chronology indicate an upper Tortodus kockelianus zone age (near the base of the Polygnathus ensensis zone). In terms of modern conodont chronologies (Sandberg & Ziegler 1996; Weddige 1996) this zone is well below the actual Eifelian/Givetian boundary. As our sample horizon is located a maximum of 2 m below the Kacak base our radiolarian fauna presumably also belongs to the upper Tortodus kockelianus zone. Budil (1995) discusses the considered interval (Chotec-Kacak boundary interval) in terms of the uppermost Eifelian. Because of the scarcity of well preserved conodonts and other faunas, the question of where the actual Eifelian/Givetian boundary is situated within the sequence has not been resolved. It is clear however, that on the basis of recent conodont zonation schemes (Sandberg & Ziegler 1996) the radiolarian faunas discussed herein stratigraphically belong to the upper Eifelian.

TECHNIQUES OF STUDY

The limestone samples were acid treated as in any processing for conodonts, in this case with acetic acid. Isolated radiolarians from the residue have been either picked and mounted on SEM stubs or embedded in Caedax for light microscopy. The latter technique serves well in the investigation of internal structures, which are of importance in generic and suprageneric taxonomy of spherical radiolarians.

SYSTEMATIC PALEONTOLOGY

The radiolarian fauna in general is dominated by Entactiniidae in terms of absolute numbers and species diversity. Ceratoikiscids and Palaeosceniids are rarer. All radiolarians are exceptionally well-preserved; in many of the entactinids the internal structures are present. Whereas in the Ceratoikiscids several clearly different morphotypes are distinguishable, the genus *Palaeoscenidium* is present only with one species. As the ceratoikiscids and palaeoscenids have been systematically treated in the paper of Cejchan (1987) no detailed taxonomic discussions of these will be made here. A more detailed taxonomic treatment is given for the most common species of entactinids.

Material figured and mentioned in the text (SEM stubs, light microscope slides) are housed at the collection of the Institute of Paleontology, University of Bonn. Coordinates given for specimens on numbered slides refer to the cross stage of a "Biolam M" microscope belonging to A. Braun.

Order ALBAILLELLARIA Deflandre, 1953 Family CERATOIKISCIDAE Holdsworth, 1969

Genus *Ceratoikiscum* Deflandre, 1953 *emend.* Holdsworth, 1969 (Fig. 3G, H)

Species of *Ceratoikiscum* are present in a remarkably good state of preservation. At least seven different species are present, but presently no further important additions can be made to the descriptions and figures in Cejachan (1987). As in other systems (Silurian, Lower Carboniferous) Ceratoikiscids are potentially useful for biostratigraphic zonations in the Lower and Middle Devonian. The Ceratoikiscids in this fauna show strong similarities to the species described in Foreman (1963) from the North American Famennian.

Order ? SPUMELLARIDA Ehrenberg, 1875

Family ENTACTINIIDAE Riedel, 1967

Members of the Entactiniidae are the most com-

mon faunal constituents in the investigated faunas.

Genus Stigmosphaerostylus Rüst, 1892

For synonymy with *Entactinia* Foreman, 1963 and remarks see Aitchison & Stratford 1997.

TYPE SPECIES — *Stigmosphaerostylus notabilis* Rüst, 1982.

Stigmosphaerostylus herculeus (Foreman, 1963) (Fig. 4B)

DESCRIPTION

Spherical skeleton bearing six three-bladed spines, the length of which is approximately equal to the diameter of the skeletal sphere. Spines may be disposed at 90° angles to one another or placed slightly asymmetrical. No secondary spines have been observed, only small thornlike elevations are present at the corners of the lattice. About ten faily large, subcircular pores are present per half circumference. The specimen in slide K.h. -20 AC/3, r: 22, h: 13,5 shows a bar centered internal spicule, the spicular rays display a trifurcation before they reach the base of the spines. The specimen in slide K.h. -20/1, r: 22, h: 19 shows an excentric double spicule.

REMARKS

The specimens from our samples closely correspond in morphology to the paratype of *S. herculea* (Foreman, 1963) in Foreman (1963: pl. 1, figs 3C, D). Generic determination is based on characteristics of the internal structures of the skeleton.

Stigmosphaerostylus sp. aff. S. herculeaus (Foreman, 1963) (Fig. 4C, E, H)

aff. *Entactinia herculea* Foreman, 1963: pl. 1, fig. 3A-D (specimen in pl. 1, fig. 3B)

DESCRIPTION

Spherical skeleton with small, subangular pores (15 to 20 per half circumference) and six three-



FIG. 3. — SEM micrographs of radiolarians from the Upper part of the Chotec Limestone (upper Eifelian). Knezi hora hill near Karlstejn. Palaeosceniidae and Ceratoikiscidae. A-F, Palaeoscenidium cladophorum Deflandre, 1953. Specimens displaying different sizes and numbers of basal spinules. G, H, Ceratoikiscum sp. Scale bars: 100 µm.

bladed spines disposed approximately at right angles to one another. The length of the spines varies from one to one time and a half the diameter of the skeletal sphere. Small thorn-like byspines are present on the edges of the skeletal framework.

Remarks

This taxon summarizes the entactinid morphotypes characterized by a spine morphology similar to *S. herculeus* (Foreman, 1963) but uniformly having smaller and more numerous pores. The character of pore size and number was observed here to be not highly variable and transitional between morphotypes, whereas length and width of spines was found to be much more variable. We therefore do not include the species with small pores into *S. herculea* as has been done by Foreman (1963), but place it in a different, presumably closely related species.

Stigmosphaerostylus sp. aff. proceraspinus (Aitchison, 1993) (Fig. 4I)

DESCRIPTION

Spherical skeleton possessing a lattice-shell and six three-bladed spines, one of which is considerably longer than the others. The longer spine is slightly twisted along its axis. Lattice with rounded pores of irregular size (about 10 per half circumference). The specimen in slide Kh -20/1, r: 20.5, h: 26.5 displays a well preserved internal double spicule, the center of which is placed excentrically towards the large spine.

COMPARISON AND REMARKS

Generic assignment is based on characteristics of the internal skeleton. There are several externally very similar species characterized by an internal sphere and therefore referred to *Trilonche* Hinde, 1899 (ex *Entactinosphaera* Foreman, 1963) in the literature. In pore size and general shape our material is similar to some specimens of *S. proceraspinus* (Aitchison 1993: 113, pl. 6, fig. 1). Other specimens referred to the same taxon in Aitchison (1993, pl. 7, fig. 1) have much longer and more equally sized spines and are presumably not conspecific with our material. Considering the smaller pores in the lattice sphere of the type of *E. proceraspina* Aitchison, 1993, we leave the specific designation open, but place our material in close connection to *S. proceraspinus*.

> **Stigmosphaerostylus**? sp. aff. **S. hystricuosus** (Aitchison, 1993) (Fig. 4F, G)

Description

Small spherical skeleton possessing six long three-bladed spines. The length of the spines is more than three times the diameter of the skeletal sphere.

Each spine bears a set of three spinules at one half of their length, each spinule being placed on one of the spine blades. A few specimens in light microscope slides possess remnants of more spinules (slide K.h. -20/2, r: 23.5, h: 26) which are not always disposed at the same level of the spines (slide K.h. -20 AC/3, r: 20.5, h: 17). The specimen in slide K.h. -20 AC/1, r: 26, h: 22 shows a distal bifurcation in some of the spinules. The skeletal lattice possesses fairly large, polygonal pores of irregular size (four to six per half circumference).

Comparison and remarks

Aitchison (1993) described several entactinid species possessing main spines with spinules from the Frasnian of Western Australia. Only in *S. hystricuosus* (Aitchison, 1993) however the size relations of the central shell and spines are comparable with our Bohemian material. In contrast to the type material of *S. hystricuosus*, only a few of our specimens possess more than a single tier of spinules on their main spines wheras *S. hystricuosus* is regularly characterized by several tiers of spinules. Concerning the externally similar material described as *Entactinia additiva* ? Foreman, 1963 by Nazarov *et al.* (1982), we refer to the remarks in Aitchison (1993: 113).

Genus *Trilonche* Hinde, 1899 *emend.* Foreman, 1963; Aitchison & Stratford, 1997

For synonymy with *Entactinosphaera* Foreman 1963 and further taxonomic discussions see Aitchison & Stratford (1997: 373).



Fig. 4. — SEM micrographs of radiolarians from the Upper part of the Chotec Limestone (upper Eifelian). Knezi hora hill near Karlstein. **A**, *Trilonche*? *echinata* (Hinde, 1899) *sensu* Foreman, 1963; **B**, *Stigmosphaerostylus herculeus* (Foreman, 1963); **C**, **E**, **H**, *Stigmosphaerostylus* sp. aff. *S. herculeus* (Foreman, 1963); **D**, *Trilonche* sp. aff. *T. riedeli* (Foreman, 1963); **F**, **G**, *Stigmosphaerostylus* sp. aff. *S. hystricuosus* (Aitchison, 1993); **I**, *Stigmosphaerostylus* sp. aff. *S. proceraspinus* (Aitchison, 1993); **I**, *Stigmosphaerostylus* sp. aff. *S. proceraspinus* (Aitchison, 1993); **S**, Stale bars: 100 µm.

TYPE SPECIES. — Trilonche vetusta Hinde, 1899.

Trilonche sp. aff. *T. riedeli* (Foreman, 1963) (Fig. 4D)

DESCRIPTION

Fairly large spherical skeleton possessing eight narrow three-bladed main spines and numerous small pores. The spines are narrow and only indistinctly three-bladed. Small acute thorn like by-spines are arising from the edges of the lattice sometimes giving rise to a delicate meshwork partly covering the pore bearing skeletal lattice. Light microscope slides (K. h. -20/1, r: 24, h: 21) show an internal sphere.

Remarks

The specific designation has been done on the basis of the characteristic spine morphology as well as on the basis of the overall morphology of the spherical skeleton. Pore size however in the type material in Foreman (1963, pl. 5, fig. 4 A-C) is larger and the number of spines in Foreman's material is smaller (only six compared to eight in our material). The specimen from the Frasnian of Western Australia figured as *Spongentactinella* sp. 1 GSWA F44073 in Aitchison (1993, pl. 7, fig. 5) is externally very similar to our material.

Trilonche ? echinata (Hinde, 1899) *sensu* Foreman 1963 (Fig. 4A)

DESCRIPTION

Medium sized spherical latticed skeleton possessing six three-bladed main spines besides long rod-like by-spines. The length of the main spines is exceeding the diameter of the central skeleton, the length of the by-spines approximately equals the skeletal diameter. Lattice shell with small, regularly sized, angular pores (about 20 per half circumference).

Remarks

The species designation is based on the morphology of the spines in the sense used by Foreman (1963). Generic assignment remains questionable as no internal structures could be found. The spine morphology in this taxon has in our material been found to be a constant character without great variability and transitions to other species. Similar material has been figured and described as *Entactinosphaera echinata* (Hinde) (now *T. echinata* by synonymy) by Aitchison (1993: 115, pl. 5, figs 6, 11, 14, pl. 7, fig. 3) from the Frasnian of Western Australia.

Order Incertae Sedis Family PALAEOSCENIIDAE Riedel, 1967 emend. Goodbody, 1986 Genus Palaeoscenidium Deflandre, 1953

Palaeoscenidium cladophorum Deflandre, 1953 (Fig. 3A-F)

Remarks

The figures show the skeleton of *P. cladophorum* in various orientations. Four distinct apical spines are present. The development of spinules on the basal spines is variable both in size and density. *P. cladophorum* is also common in Frasnian (Aitchison 1993), Famennian (Foreman 1963; Schmidt-Effing 1988; Kiessling & Tragelehn 1994) and Lower Carboniferous (Braun 1990) radiolarian faunas (up to the *Albaillella deflandrei* zone of the radiolarian zonation in Braun & Schmidt-Effing (1993).

RELEVANCE OF THE FAUNA IN THE EVOLUTIONARY CONTEXT

Radiolarians from the Upper Silurian and the Upper Devonian are different in various aspects. One of the main differences is the suprageneric composition of the spherical radiolarians, which belong to the Entactiniidae in the Upper Devonian (and are predominant at least in the Upper Paleozoic) and to other distinctly different groups in the Silurian (Inaniguttidae Nazarov & Ormiston, 1984, Rotasphaeracea Noble, 1994 and other groups not yet taxonomically separated). Looking at spherical radiolarians only, the impression arises, that there was a kind of "major turnover" somewhere during the Early or Middle

Devonian, leading to the disappearance of the Silurian Sphaerellaria and the predominance of the Entactinids. Based on these observations postulations of a sharp faunal change during Early or Middle Devonian have been made (Nazarov & Ormiston 1986). Recent findings of wellpreserved radiolarian faunas from this interval indicate however that this trend was more gradual than originally assumed (Furutani 1983; Kiessling & Tragelehn 1994). Descriptions of well-preserved faunas are of great importance for any further consideration of this time interval in radiolarian evolution. In terms of this question, the spherical radiolarians of the upper Eifelian fauna presently treated are "completely" modern with respect to Upper Devonian and Carboniferous to Permian faunas. There are no remnants of groups of higher taxonomic level characteristic for the Silurian as far as our investigations have proceeded. Thus, the major Silurian groups must have disappeared before the Late Eifelian and by that time the Entactinids must have gained their numeral predominance and modernity of their morphologic characters. This evolution probably took place during the Early Devonian, still devoid of any radiolarian fauna well enough preserved to make substanciated statements on the taxonomic constitution. Probably, future investigations will be successful in finding well preserved faunas in uppermost Silurian and Lower Devonian strata in the Barrandian area. The presence of uppermost Silurian (Pridolian) radiolarians in limestones of this area has been proven [Literature data and material donated by Dr. H. Jaeger, Berlin (†)], but other well preserved material needs to be found for further work and other lithologies in the Lower Devonian need to be investigated.

It is worth noting, that the seemingly sharp difference between Upper Silurian and Upper Devonian radiolarians exists only in the spherical radiolarians. According to the material collected up to now, Ceratoikiscids develop at a fairly constant rate from their first known occurrence in the Wenlockian, and the spicular Palaeosceniidae are seemingly only going through a decline because this group is present in Upper Silurian faunas with considerably greater taxonomic variety (Goodbody 1986; Amon *et al.* 1994).



FIG. 5. — Schematic representation of the observed differences between lithologic and faunal change near the Chotec Limestone-Kacak Member boundary.

GEOLOGIC SIGNIFICANCE (A. Braun)

Conspicuous change in sedimentary composition between the Chotec Limestone and the Kacak sequence is a feature similar to that of many sedimentary units assinged to this time interval in other areas (Weddige 1986: 281) and may indicate some form of transgressive changes (see House 1984; Haas 1994; Walliser 1994, 1995). Observations of the colours and composition of sediments attributed to this stratigraphic interval indicate that a transgressive deepening event is the most likely explanation for the observed geological phenomena (Walliser 1995, fig. 3). Transgression may have lead to reduction in sediment supply by drowning source areas of clastic sediments. Planctonic organisms penecontemporaneously began to dominate the communities because of the changes in water depth (and probably circulation). This may finally have resulted in the formation of "biosiliceous" deposits within condensed sediments, such as the cherts of the Kacak Member which developed in the area around Prague.

Furthermore the above mentioned change in sedimentary composition is interpreted in terms of a short termed, abrupt event ("Kacak event"; Chlupac 1989: 483). The abrupt change in sedimentological composition from the Chotec Limestone to the Kacak chert sequence seems to imply a similarly abrupt change in environmental factors and it is general opinion, that most "bio-events" coincide with lithological changes ("most of the global bio-events are connected with a litho-event, i. e. a strong facies change"; Walliser 1995: 4). Looking at the predominant lithology it may seem to be obvious in our example to assume a sudden bloom of radiolarians following a "normal" Chotec Limestone organism assemblage (trilobites, tentaculites, conodonts etc.) which led to a similarly sharp lithological boundary between limestone and radiolarian-dominated cherts in sections near Prague (Hlupocepy railway cut, Barrandov), and to some extent in other sections as well.

The Barrandian localities treated in this paper may, because of their particular sedimentary facies contribute to this discussion because the sediments present here (limestones) allow for a good preservation of the organisms under consideration (calcareous hard parts as well as radiolarian skeletons).

The following observations can be made:

The abrupt change in sediment type is, in terms of paleoecology, not paralleled by an abrupt change in fossil content. Predominance and preservation of Radiolaria began at least as early as deposition of the uppermost 2 m unit of the Chotec Limestones. In the uppermost part of the Chotec Limestone, typical "Chotec-Limestone"organisms become rarer and less well-preserved as mentioned by several authors. Some last remains of the typical "Chotec Limestone fauna" however have been described from the last few decimetres of the Chotec limestone formation (Budil 1995). Only after such a general shift in organism population did the abrupt change in sedimentological realm occur.

There were biological changes within the considered interval of uppermost Chotec limestones and lower Kacak Member. In biological terms however, gradual "extinctions" and entrances in organism ecology occur well before the clearly visible changes in sediment facies and can be observed over at least 2 m of sediment thickness. Disregarding the highly hypothetical question as to how much time may be represented by these 2 meters, it is obvious in non-turbiditic sediments of sedimentary basins like the Barrandian, that the time interval neccessary for their deposition cannot be called an abrupt event in terms of days, months or even a few years

Higher up in the sequence (at the Kacak base) such ecological shifts were paralleled by changes in the predominant composition of the sediments, and it is quite probable, that such compositional changes were in our case also later diagenetically enhanced to give the sharp contrast as seen in todays outcrops.

Thus, the Kacak event, being presumably due to changes in water depth and sediment supply leaving traces in many other areas, can be shown to have occurred ecologically more gradually than implied when only considering the sedimentological boundaries. These observations exclude catastrophic pictures arising when reading the terminology sometimes used in event discussions, and contribute to the picture of many of such events as "mild" ones in the terminology of Walliser (1995).

It is not our aim to cast doubt on the general existence of relatively short-termed processes known to be present during the Phanerozoic (Walliser 1995), that changed sedimentological characters as well as the living conditions of organisms and causing ecological stresses as a possible reason for larger scale extinctions, organism displacements etc. And in view of the published considerations on possible causes and natures of "events" (Walliser 1995), it would surely be not justified to restrict our view of events to asteroid impacts and to discuss any proposed event (sedimentologically or organism-based) in the light of such extraterrestrial causes, which are the exception rather than the rule (Walliser 1995). Thus, we do not reject the existence of the Kacak "events" as long as the use of the term event does not imply a short term catastrophical happening. Many such processes as far as we know today seem to be closely connected to changes in sea level (Johnson et al. 1985; Ross & Ross 1985; Walliser 1995), whatever their causes might have been, and it is clear, that such changes could well have lasted even a few million years. At least in some cases however such changes do not coincide with lithological boundaries. This, based on the present observations, can be shown to be true in the case of the Kacak event. The latter as far as it is represented by the typical (cherty) sediments was only the culmination of a transgressive deepening, leaving its faunal traces well before the actual Kacak sequence.

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