Festschrift zum 60. Geburtstag von Erik Flügel				Redaktion: Baba Senowbari-Daryan & Albert Daurer
Abh. Geol. B.-A.	ISSN 0378-0864 ISBN 3-900312-90-7	Band **50**	S. 219–255	Wien, 6. April 1994

Devonian Radiolarian Faunas of Conodont-Dated Localities in the Frankenwald (Northern Bavaria, Germany)

By WOLFGANG KIESSLING & HARALD TRAGELEHN*)

With 9 Text-Figures and 6 Plates

Deutschland
Devon
Radiolarien
Systematik
Stratigraphie
Paläoozeanographie

Contents

Zusammenfassung 219
Abstract 220
1. Introduction 220
1.1. Devonian Radiolarians 220
1.2. Regional Geology 221
2. Stratigraphy and Facies 221
3. Methods 222
3.1. Conodonts 222
3.2. Radiolarians 222
4. Results 222
4.1. Composition of the Insoluble Residue 222
4.2. Radiolarians 222
4.3. Locality descriptions 223
4.3.1. Geuserberg 223
4.3.2. Rodachsrangen 224
4.4. Quantitative Examinations of Radiolarian Faunas 226
4.5. Palaeoceanography 227
4.6. Evolution 227
4.7. Stratigraphy 229
5. Systematic Descriptions 229
Acknowledgements 241
Plates 1–6 242
References 254

Devonische Radiolarienfaunen aus conodontendatierten Lokalitäten im Frankenwald (Nordbayern, Deutschland)

Zusammenfassung

Aus insgesamt acht stratigraphischen Horizonten von Unter-, Mittel- und Oberdevonischen Kieselschiefern (Helle Kieselschieferserie) der Bayerischen Fazies des Frankenwaldes (Nordostbayern) konnten diverse und gut erhaltene Radiolarienfaunen gewonnen werden. Conodonten auf Spaltflächen von eingeschalteten tonigen Zwischenlagen erlaubten dabei eine exakte biostratigraphische Einstufung der Faunen innerhalb der Conodontenzonierung auf Zonen- oder sogar Subzonen-Niveau.

Der erstmalige Fund von sicher datierbaren Unterdevon-Radiolarien (Unter-Ems) erbrachte klare Argumente gegen einen vielfach diskutierten Faunenumbruch im Bereich der Unter-Mitteldevon-Grenze.

Gut erhaltene Faunen des höheren Oberdevons (Nehden- bis Dasberg-Stufe; Famenne) ermöglichten die Überprüfung bestehender Zonierungen (*Holoeciscus*-assemblage-Zonen) und deren Eichung im Rahmen der Conodontenstratigraphie.

*) Author's address: WOLFGANG KIESSLING, HARALD TRAGELEHN, Institut für Paläontologie, Universität Erlangen-Nürnberg, Loewenichstraße 28, D-91054 Erlangen.

Im Rahmen der systematischen Bearbeitung der Radiolarienfaunen wurden 86 Morphotypen beschrieben, davon 35 in offener Nomenklatur. Auf die Aufstellung neuer Taxa wurde weitgehend verzichtet. Lediglich vier deutlich abgrenzbare Arten (*Archocyrtium effingi* n.sp.; *Cyrtisphaeractenium*(?) *fluegeli* n.sp.; *Holoeciscus elongatus* n.sp.; *Tetrentactinia spinulosa* n.sp.) wurden benannt.

Abstract

Eight horizons of Early, Middle and Late Devonian cherts (Helle Kieselschieferserie) within the Bavarian Facies of the Frankenwald (North-East Bavaria) contained diverse and well-preserved radiolarian faunas. The exact stratigraphical position within the zone or even the subzone level of conodont biozonation was determined by conodonts obtained from interbedded shaly layers.

The first occurrence of certainly Early Devonian (lower Emsian) radiolarians provided clear arguments against theories of a severe faunal change at the Early-Middle Devonian boundary.

Well-preserved faunas of Late Devonian (Nehden to Dasberg stage, Famennian) age allowed existing zonations (*Holoeciscus*-assemblage zones) to be checked and calibrated within conodont stratigraphy. The systematic analysis led to the determination of 86 morphotypes; 35 of them are described in open nomenclature. Description of new taxa was limited to four clearly defined species (*Archocyrtium effingi* n.sp.; *Cyrtisphaeractenium*(?) *fluegeli* n.sp.; *Holoeciscus elongatus* n.sp.; *Tetrentactinia spinulosa* n.sp.).

1. Introduction

This paper deals with the systematics, evolution and stratigraphy of Devonian radiolarians in the Frankenwald.

Field work was mainly carried out in 1993 during stratigraphical studies of the Devonian strata of the Bavarian facies (TRAGELEHN in preparation). The discovery of different stratigraphical levels consisting of cherts and the positive test of their radiolarian content are the basis for this paper.

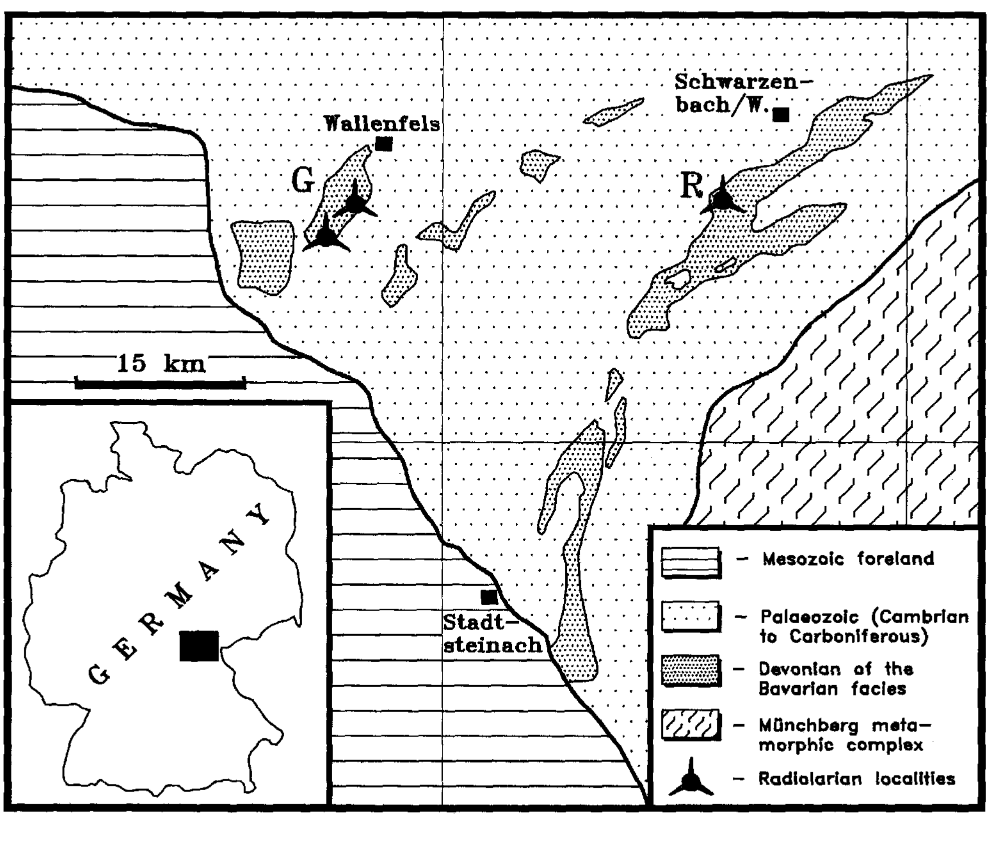
As the Late Devonian faunas are the best preserved, studies were concentrated on them, but older faunas were used for a review of the evolutionary tendencies.

1.1. Devonian Radiolarians

Devonian radiolarians were first described from Europe (RÜST, 1892) and Australia (HINDE, 1899), and later studied in many areas of the world. Important recent contributions on Devonian radiolarians have been published by FOREMAN (1963), NAZAROV (1975), HOLDSWORTH et al. (1978), NAZAROV et al. (1982), NAZAROV & ORMISTON (1983), CHENG (1986), ISHIGA et al. (1987, 1988), AITCHISON (1990, 1993b), WAKAMATSU et al. (1990), and LI & WANG (1991).

SCHMIDT-EFFING (1988) was the first to report the discovery of well-preserved radiolarians in the Devonian of the Frankenwald. He described a fauna of a probable Late Famennian age from the Steinachtal area and mentioned the occurrence of radiolarians in other localities without further descriptions. He was not able to determine the exact age, because his biostratigraphical correlation depended on a few *bispathodus*-conodont fragments from the acid residue of the radiolarian sample only.

Stratigraphic data of Devonian radiolarians are found in HOLDSWORTH & JONES (1980), CHENG (1986), AITCHISON (1993a), AITCHISON et al. (1992), ISHIGA et al. (1988) and WAKAMATSU et al. (1990). The zonations are mainly based on the first appearance datums of characteristic radiolarian taxa and are relatively rough (three assemblages for the Late Devonian). Frequently the faunas are not sufficiently dated by stratigraphically significant fossils (e.g. conodonts). In addition to the scarcity of age-diagnostic fossils in radiolarian-bearing rocks, reworking is a major problem in dating radiolarian faunas (HOLDSWORTH & MURCHEY, 1988; NOBLE, 1992). Our



Text-Fig. 1.
Position of radiolarian localities in the Devonian of the Bavarian facies in the western part of the Frankenwald.
G = Geuserberg massif; R = Rodachsrangen massif.

material could be dated exactly by the co-occurrence of conodonts, with a very detailed biostratigraphical record and no evidence of reworking. Therefore, the value and chronostratigraphic calibration of existing radiolarian biozones for the Late Devonian could be readily checked.

1.2. Regional Geology

The Palaeozoic of the 'Frankenwald' area – consisting of Middle Cambrian to Early Carboniferous strata – is part of the Saxothuringian Zone within the Variscan orogen.

Two facies are distinguished: The Thuringian facies is typical of the Saxothuringian Zone in fauna and lithology, whereas the Bavarian facies is closely linked to metamorphic areas ('Zwischengebirge' such as the Münchberg metamorphic complex) and characterized by special lithologies (e.g. WURM, 1961).

Palaeogeographical and tectonic settings of both facies are uncertain and have been intensively discussed for almost 90 years. The current, but still rather doubtful nappe-theory (SUESS, 1912; WURM, 1925; BEHR et al., 1982) considers the metamorphic 'Zwischengebirge' and the surrounding Bavarian facies to be the relic of a huge and complex nappe system, which derived from a root zone within the southernly situated Moldanubian.

Due to a couple of lithological and faunistic transitions, especially in the Devonian, other authors (e.g. GANDL, 1992; TRAGELEHN, 1993) consider the relative autochthony of the 'Bavarian' complex to be the more likely alternative.

The Devonian of the Bavarian facies is dominated by cherty shales and bedded cherts ('Helle Kieselschieferserie').

2. Stratigraphy and Facies

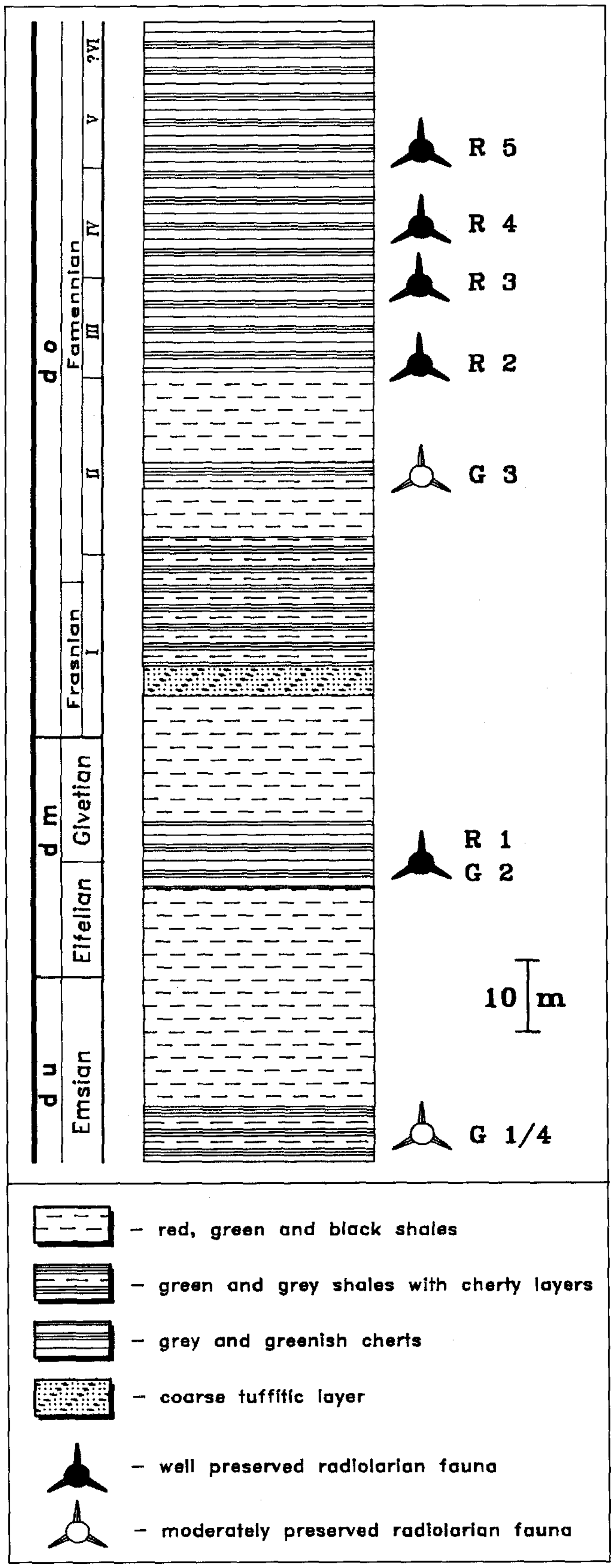
In our study, the 'Helle Kieselschieferserie' ranges from the Siegenian (*dehiscens*-zone or deeper) to the Late Famennian (*expansa*-zone). It is bordered by stratigraphic gaps at the top and bottom of the sequence.

The lithostratigraphy of the Bavarian facies in the Devonian comprises the following lithostratigraphical units (Text-Fig. 2):

9) Grey bedded cherts (Late Famennian).
8) Red cherty shales (Early Famennian).
7) Green cherty shales (Late Frasnian–Early Famennian).
6) Tuffs and laminated tuffites (Frasnian).
5) Black, scarcely cherty shales (Early Frasnian).
4) Grey laminated shales (Givetian).
3) Bedded cherts (Kieselschiefer) intercalated by green and black shales (Early Givetian).
2) Laminated olive green and grey shales (Eifelian).
1) Green and yellow-brown cherty shales (Emsian).

The idealised section has a thickness of about 200 m. Most of the conodont zones in the range charts used in this paper (KÖNIGSHOF & PIEC, 1991; WEDDIGE, 1977; ZIEGLER & KLAPPER, 1985) can be identified in the section. This indicates a continuous sedimentation without significant breaks.

The average sedimentation rate is calculated as 8 m/my. It was much higher in cherty intervals, reaching about 15 m/my within the Late Devonian. The depositional environment of the sequence was a deep marine basin with profound siliciclastic input, exposed to a few anoxic



Text-Fig. 2.
Composite section of the radiolarian-bearing Devonian of the Bavarian facies of North Bavaria.
The series comprises a time interval of ca. 390–355 Ma and consists mainly of intensively folded shales and cherts. The total thickness of the section is approximately 200 m. Owing to strong tectonics, the apparent thickness is in fact far greater.
Radiolarian-rich horizons in the cherts are indicated on the right. They are dated exactly by conodonts.

events. Bioturbation is very weak in most parts of the section and laminated shales predominate. Indications of turbiditic activity are scarce and only fine-grained distal portions are present.

Faunas described in this paper derive mainly from the westernmost outcrop of 'Helle Kieselschieferserie', where almost complete sections of this series were found. All cherty intervals contained radiolarian faunas. The stratigraphic position of these faunas could be dated exactly by conodonts. The range of uncertainty in dating is approximately one conodont subzone to one conodont zone (ca. 400 ky. to 1000 ky.).

3. Methods

3.1. Conodonts

While intensive tectonic fracturing has destroyed most of the sparse conodont elements in the cherts, there are still several adult conodonts in the small layers of interbedded shales, which can be prepared as negative molds. In spite of greater tectonic deformation of the softer shales, the microfractures within the conodonts, marked by siliceous material, usually do not cause any harm, as they are simply obliterated by preparation methods:

Conodonts are usually seen by direct observation in the field, mainly on shale surfaces. In the laboratory, relics of the original phosphatic conodont material are dissolved by hydrochloric acid. The negative form is still covered by siliceous microfractures or even oxidic crusts. These are removed with a fine brush or, occasionally, a preparation-needle. After final ultrasonic cleaning of the negative, the conodont cast is filled with latex or silicon. Afterwards the resulting 'positive' form can be photographed and determined in the usual manner.

The radiolarian-bearing localities described in this paper provided about 300 identifiable conodont specimens from 8 stratigraphical horizons. Furthermore, the determinations are supported by a large number of additional conodont samples collected in non radiolarian-bearing sections from the same profiles.

3.2. Radiolarians

Radiolarians are abundant and well-preserved in cherts or cherty shales only.

Samples of radiolarian-bearing rocks were exclusively taken from localities yielding age diagnostic conodonts in the shaly interlayers. 45 small radiolarian samples (some 100 g) were collected in the field. The radiolarian samples were crushed and processed with diluted HF in a method similar to that described by PESSAGNO & NEWPORT (1972). However, the concentration (8 %) and the etching times (3–4 hr) were less than those recommended by these authors. In order to obtain a sufficient amount of residue, etching was repeated several times. Most of the determinations were made by use of a Scanning Electron Microscope. Transmitted light observations were carried out, but offered only a few results, due to an obliteration of most of the internal structures.

Although the best preserved radiolarian faunas are commonly found in phosphatic nodules (CHENG, 1986) or carbonate concretions (AITCHISON, 1993b), where diagenetic overprint is low and a less aggressive HCl preparation can be used, we obtained some excellent faunas containing radiolarians with very fine preserved structures.

4. Results

Radiolarian faunas were recovered from eight localities in two different areas: the Geuserberg massif and the Rodachsrangen massif (Text-Fig. 1). The Geuserberg contained Late Silurian to Late Devonian faunas, while Middle to Late Devonian faunas were found in the Rodachsrangen. The best preserved faunas came from the Rodachsrangen. The Geuserberg is important, because of its rich Early and Middle Devonian radiolarians, which have rarely been studied in detail until now.

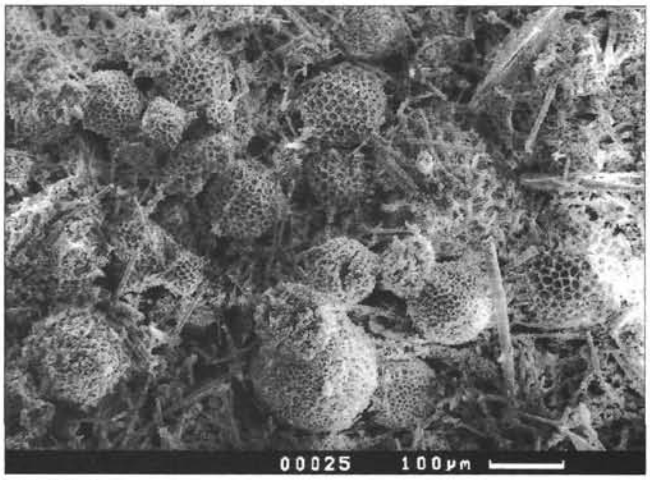
4.1. Composition of the Insoluble Residue

The HF-residue consists almost entirely of quartz. Clotted Qz-aggregates predominate in poorly preserved samples, whereas radiolarians make up most of the residues in better preserved samples. Additional faunal components are siliceous sponge spicules (monaxones, tetraxones and hexactins; Text-Fig. 3) and conodonts. As AITCHISON et al. (1992) noted, conodonts in cherts are common in the (recent) northern hemisphere, but uncommon in Australia.

In most of the residues, ore minerals including pyrite are the second most important components. Pyrite is often fresh and euhedral. Framboidal pyrite is present, but pyritization of radiolarians as observed in Early Carboniferous (BRAUN, 1990c) and younger cherts was never seen. Organic particles of remarkable size are especially abundant in black layers of Middle Devonian cherts.

4.2. Radiolarians

The faunas are generally dominated by simple spumellarians of the *Cenosphaera*(?)- and *Entactinia*-groups. This is mainly due to recrystallization, fracturing and dissolution (diagenetic and HF-treatment), favouring the selective preservation of the robust spherical radiolarians. But these forms also make up more than 50 % of well preserved faunas (see Text-Fig. 3).



Text-Fig. 3.
SEM photograph of an etched Late Devonian chert sample (R 4/2).
Spherical radiolarians as well as sponge spicules and isolated radiolarian spines play a significant role as rock-forming fossils.

The radiolarians are randomly distributed within the cherts, but layered recrystallization led to an enrichment of well-preserved forms in distinct laminae.

Typical small faunas of Late Devonian (Famennian) radiolarians in Central Europe contain the following species (BRAUN, 1990b; BRAUN et al., 1992; SCHMIDT-EFFING, 1988, this paper):

Archocyrtium sp. (small morphotypes)
Astroentactinia sp.
Entactinia herculea FOREMAN
Enactinosphaera(?) *palimbola* FOREMAN
Holoeciscus sp.
Palaeoscenidium cladophorum DEFLANDRE
Polyentactinia sp.

These taxa can, therefore, be considered as the main constituents of Famennian radiolarian faunas in the area studied. Data from the literature indicate they are the main consituents of assemblages in other areas as well, such as Australia and North America (CHENG, 1986; AITCHISON, 1990).

4.3. Locality Descriptions

The stratigraphic position of the localities and content of the most important radiolarians are summarized in Text-Figs. 2 and 4.

4.3.1. Geuserberg

Locality G1: Ackerwand at the southern slope of the Geuserberg massif (800 m SE of peak)
r 4461200 – h 5568750

The outcrop consists of massive black bedded cherts (Silurian lydites) underlying Early Devonian cherty shales with small chert interlayers. The locality was first described by ZITZMANN (1966) who considered it to be a continuous Silurian–Devonian transitional sequence. According to our conodont data, however, there is a gap between the Late Silurian (Ludlowian) and the Early Devonian (Early Emsian).

The radiolarian faunas of this locality will be described in detail in a separate paper (TRAGELEHN & KIESSLING, in prep.).

Radiolarians were found in two of four samples analyzed.

G 1/1 is of Late Silurian age based on graptolites (see ZITZMANN, 1966). It contains large spheres with short sturdy spines and some Palaeoscenidiidae.

G 1/4 is of Early Emsian age, owing to a conodont assemblage of *Polygnathus gronbergi* KLAPPER & JOHNSON group accompanied by *Ozarkodina steinhornensis steinhornensis* (ZIEGLER).

This sample contained a moderately well-preserved and diverse radiolarian fauna. Probable Early Devonian radiolarians are only reported by FURUTANI (1990) and WAKAMATSU et al. (1990). However, these faunas may also be of Late Silurian or Middle Devonian age, because no age diagnostic fossils were to be found.

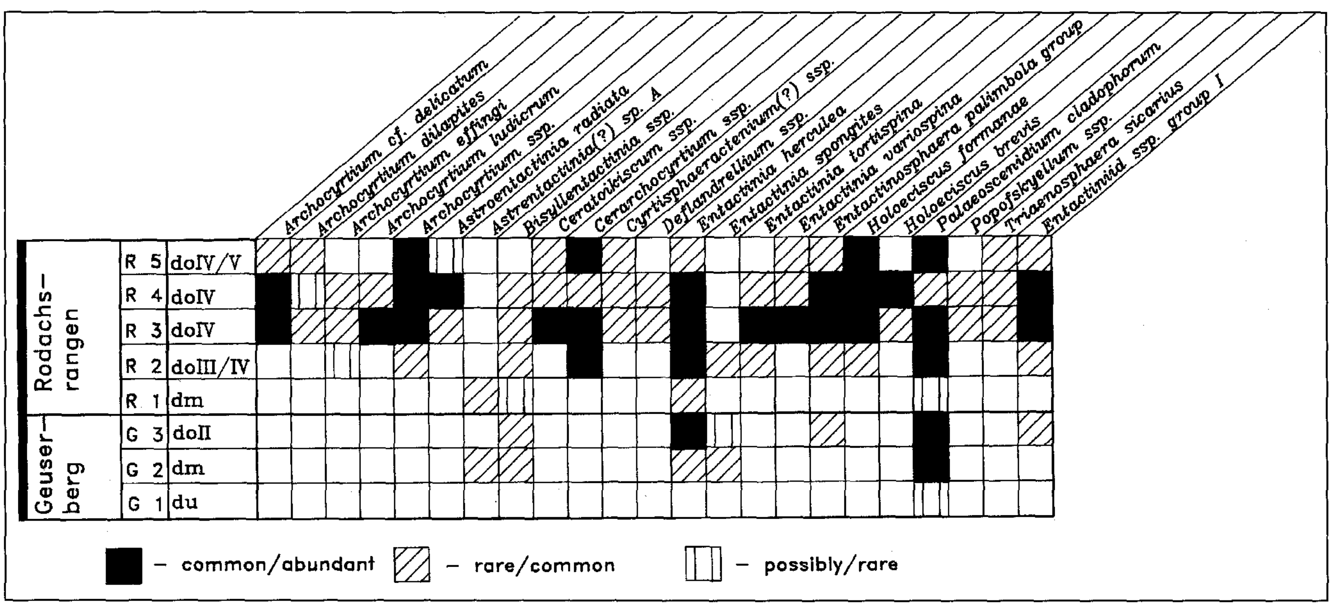
Large spherical "Palaeoactinommids" (sensu HOLDSWORTH, 1977) with short massive spines dominate the fauna. The number of spines varies from 4 to 12 (Pl. 6, Fig. 21–22). Nearly all forms bear three-bladed spines. Most of the spines are often arranged in a plane. Besides these particular morphotypes, forms with two massive polar spines, simple spheres and Palaeoscenidiidae (Pl. 6, Fig. 11) were found.

Locality G2: 'Höhe 626' near the top of the Geuserberg
r 4461350 – h 5569050
Eifelian/Givetian boundary

Thick bedded cherts are exposed at a forest road. A very thin layer of siliceous shales interlaying the radiolarian-bearing cherts provided a small fauna of 11 conodonts, including

Polygnathus cf. *pseudofoliatus* WITTEKINDT
Polygnathus linguiformis linguiformis HINDE, 'gamma' morph.
Belodella cf. *devonica* STAUFFER
Bryantodus pravus (BRYANT)

The specimen of *P.* cf. *pseudofoliatus* is poorly preserved. Its stratigraphical importance is therefore very restricted. *Po. l. linguiformis* 'gamma' is also of minor stratigraphical



Text-Fig. 4.
Stratigraphic position of radiolarian localities and distribution of the most important taxa with estimated abundances.
Most of the frequencies (except for the Early Devonian sample G 1) are controlled by preservation. The absence of species can, therefore, not be used for stratigraphical purposes.

significance, as it ranges from the Late Eifelian to the Earliest Frasnian.

Br. pravus is reported from the Eifelian and Early Givetian by BISCHOFF & ZIEGLER (1957), while *B. devonica* (generally ranging from the Early Devonian to the Early Late Devonian) is very common in the Frankenwald and has never been found higher than the middle Givetian (lower *'varcus'*-Zone).

Based on the poor conodont fauna, a Late Eifelian or Early Givetian age is probable, but has not been proved in this locality. The stratigraphical assignment is additionally supported by lithostratigraphic correlation with other locations of the Bavarian facies (e.g. locality R 1 of this paper) dated with conodonts. The data show that most of the Middle Devonian is developed in low siliceous shale facies. There is only a small sequence including very distinct parts of the late *kockelianus-* and early *ensensis-*conodont zone, where massive cherts predominate. Therefore, the assignment of the locality to this cherty interregnum is very likely.

Five of the ten samples analyzed contained radiolarian faunas (G 2/1, 3, 5–7). Species identified are *Astroentactinia*(?) sp. A, *Entactinia herculea* FOREMAN, *Entactinia spongites* FOREMAN, *Palaeoscenidium cladophorum* DEFLANDRE, *Polyentactinia*(?) *perampla* BRAUN, MAASS & SCHMIDT-EFFING, *Polyentactinia*(?) sp. C, and *Staurodruppa*(?) sp. None of these species is age diagnostic. *P. cladophorum* originates in the Eifelian according to NAZAROV & ORMISTON (1983) and persisted until the Early Carboniferous.

Locality G3: Eastern side of Geuserberg
r ^{44}62100 – h ^{55}68080
Early–middle *crepida*-zone
(Lower Nehden Stage, do$\text{II}\alpha$)

In this locality sparsely laminated, greenish to brownish siliceous shales predominate. The radiolarians were found in rare intercalations of cherty material.

A very rich and specific conodont fauna of 36 platform specimens, taken from 20 to 40 cm above the radiolarian sample, provides an exact stratigraphical classification:

Palmatolepis crepida SANNEMANN
Palmatolepis subperlobata BRANSON & MEHL
Palmatolepis quadrantinodosalobata SANNEMANN
Palmatolepis perlobata perlobata ULRICH & BASSLER
Palmatolepis minuta minuta BRANSON & MEHL
Palmatolepis cf. *triangularis* SANNEMANN.

This conodont association is typical of the Late Devonian lower/middle *'crepida'*-zone, characterized by the occurrence of the zone-fossil *P. crepida* in connection with a complete lack of *P. glabra*-forms, which are usually very common in the upper *'crepida'*-Zone. The specimen named *'P.* cf. *triangularis'* is very similar to transitional forms between *'P. triangularis'* and *'P. quadrantinodosalobata'*, as described by ZIEGLER (1962: Tab. 1) and therefore of less biostratigraphical importance.

Another conodont-sample, approximately 2 m higher in this section, provided a typically upper *'crepida'*-zone fauna.

Only one of the four samples examined bears a moderately preserved radiolarian fauna (G 3/2). *Palaeoscenidium cladophorum* DEFLANDRE, *Palaeoscenidium* sp., *Entactinia herculea*, *Entactinosphaera palimbola* FOREMAN group, ?*Archocyrtium* sp. and very large spherical morphotypes with two massive triradiate spines and a spongy shell (up to 530 μm in length) predominate.

4.3.2. Rodachsrangen

At the southern flank of the 'Rodachsrangen'-massif, along the narrow valley of 'Wilder Rodach-Bach', an almost complete profile from the Early Middle Devonian (*costatus*-Zone) to late Late Devonian (*expansa*-Zone) was reconstructed and dated by conodonts.

It provided the best preserved radiolarians described in this paper. They were mainly found in two stratigraphical sections, which are well-dated by conodonts:

Locality R1: Western margin of the area studied
r ^{44}71650 – h ^{55}68950
Eifelian/Givetian-boundary zone

Radiolarians occur in massive well-bedded cherts overlying dark greenish laminated shales with rich conodont faunas, including

Polygnathus cf. *angusticostatus* WITTEKINDT
Polygnathus costatus oblongus WEDDIGE
Polygnathus linguiformis HINDE ssp.

and several other species of less stratigraphical importance. The fauna belongs to the *kockelianus*-Zone, forming the uppermost part of the Eifelian.

Additionally, a few conodonts were found in small shaly interlayers within the radiolarian-bearing cherts:

Polygnathus ex gr. *xylus* (? *xylus ensensis*)
(ZIEGLER & KLAPPER)
Polygnathus ling. linguiformis HINDE, 'gamma' morph.
Polygnathus cf. *pseudofoliatus* WITTEKINDT.

Therefore, the beginning of chert-sedimentation starts in the uppermost *kockelianus*-zone or the lowermost part of Early Givetian *ensensis*-zone.

The chert sequence is overlain by grey laminated shales, still containing a few *ensensis*-zone conodonts. Hence, cherty sedimentation ended in the lower Givetian.

The radiolarians are poorly preserved, containing *Palaeoscenidium cladophorum* DEFLANDRE, *Entactinia herculea* FOREMAN, *Bisyllentactinia* sp., *Entactinosphaera* sp. and *Polyentactinia* sp.

Localities R2–5

After a long interval, characterized by the sedimentation of shales and cherty shales, thick bedded blue-grey to dark grey cherts occur again towards the end of the 'Nehden' stage in the uppermost part of the *marginifera*-zone. Cherty sedimentation then presumably prevailed until the end of the Late Devonian. However, a hiatus occurred in the Early Carboniferous, effected by erosion of the uppermost Devonian. Therefore, the Latest Devonian ('Wocklum') age could not be proved. The youngest strata documented belong to the *postera*-conodont-zone and can be correlated with the 'Dasberg'-stage. Synsedimentary folding complicates stratigraphic correlation and caused an apparent thickness (> 100 m) much more than the real thickness which is estimated to be 40 to 50 m (Text-Fig. 6).

Nearly all samples from this section provided well-preserved radiolarians with the best preserved ones being found in the middle portion.

The long list of radiolarians is not listed below in the locality descriptions but rather in the systematic descriptions (see also Text-Fig. 4).

Locality R2: Cliff at the valley road, central area
r ^{44}71900 – h ^{55}68750
Latest Nehden- to early Hemberg-stage

The outcrop consists of bedded cherts with very thin interlayers of cherty shales (Text-Fig. 5). There are no in-

Text-Fig. 5.
Outcrop photograph of loc. R 2 (road along 'Wilder Rodach-Bach' on the western flank of Rodachsrangen) showing the bedding style of Late Devonian cherts.
Thickness of beds varies from 2 to 15 cm (hammer for scale); the chert beds are separated by thin layers of shales.

dications of tectonic or synsedimentary folding in this section.

The samples yielded the following conodonts:

Palmatolepis marginifera marginifera (ZIEGLER)
Palmatolepis glabra distorta (BRANSON & MEHL)
Palmatolepis glabra lepta ZIEGLER & HUDDLE
Palmatolepis gracilis gracilis BRANSON & MEHL
Palmatolepis minuta minuta BRANSON & MEHL
Palmatolepis perlobata schindewolfii MÜLLER
Mehlina strigosa (BRANSON & MEHL).

Owing to the occurrence of *P. m. marginifera*, the possible age for this fauna ranges from the complete *marginifera*- and the lowermost part of the *trachytera*-zone. However, red shales about 3 to 5 m below contain an assemblage of the late *marginifera*-zone. This restricts the age of the locality to an interval, including the ?late/latest *marginifera*- and the early *trachytera*-zone (latest 'Nehden'- to earliest 'Hemberg'-stage).

Locality R3: Outcrop at a forest road;
eastern margin of the area studied
r ^{44}71950 – h ^{55}68770
Late Devonian (Hemberg-stage).

The samples were taken from an exposure resulting from the construction of a forest road several years ago. The outcrop is now nearly covered by plants.

As the conodont-bearing shales derive from rubble, it is not possible to fix the exact distance between conodont- and radiolarian-beds. The conodont-bearing bed is situated about 0.5 to 1.5 m higher, so that the age of the radiolarian samples may be slightly younger than the age of the conodont sample (but not more than one subzone).

The following forms could be determined from a sample consisting of 28 platform conodonts:

Palmatolepis glabra lepta ZIEGLER & HUDDLE
Palmatolepis rugosa ZIEGLER ssp. (aboral side)
Palmatolepis gracilis gracilis BRANSON & MEHL
Palmatolepis perlobata schindewolfii MÜLLER
Mehlina strigosa (BRANSON & MEHL)
Bispathodus stabilis (BRANSON & MEHL); morphotype 1
Branmehla bohlenana (HELMS).

Although the determination of the specific zone fossil is uncertain, the sample very likely belongs to the *trachytera*-zone ('Hemberg'-stage) for the following reasons:

a) *P. rugosa* ssp., which is preserved only in the aboral view, is very similar in shape to the zone-fossil *P. rugosa trachytera*;
b) the range of *P. glabra lepta* ends in the middle of the late *'trachytera'*-zone;
c) older forms, especially the *marginifera*- and *glabra*-group, which are very common in the profile until the beginning of the *trachytera*-zone, do not occur in this locality.
d) The first appearance of *Br. bohlenana* is reported from just below the beginning of *trachytera*-zone (nevertheless the stratigraphic value of spathognathid elements is generally very restricted and should be used cautiously!).

Locality R4: Small outcrop along upper forest road,
central area
r ^{44}71900 h – ^{55}68750

The outcrop is situated 30 m above locality R 2. Owing to synsedimentary slumping the relatively thick bedded cherts are isoclinally folded (Text-Fig. 6).

The conodont fauna contains

Pseudopolygnathus granulosus ZIEGLER
Scaphignathus subserratus (BRANSON & MEHL)
Polygnathus sp. (? *styriacus*)
Palmatolepis perlobata helmsi (ZIEGLER)
Palmatolepis perlobata schindewolfii MÜLLER
Palmatolepis gracilis gracilis BRANSON & MEHL
Palmatolepis gracilis sigmoidalis ZIEGLER
Palmatolepis minuta minuta BRANSON & MEHL
Palmatolepis minuta schleizia HELMS
Bispathodus stabilis (BRANSON & MEHL); morphotype 1
Branmehla inornata (BRANSON & MEHL)
Branmehla werneri (ZIEGLER)
Nothognathella sp.

The specimen of *Polygnathus* sp. (? *styriacus*) can not be definitely classified as *P. styriacus* due to poor preservation. Therefore, based on the range of *Pseudopolygnathus granulosus*, the sample belongs to an interval including the late *trachytera*- and early *postera*-zone.

Locality R5: Cliff, about 25 m above upper forest road
(R 4), central area
r ^{44}71860 – h ^{55}68770

The conodont fauna consists of

Pseudopolygnathus brevipennatus ZIEGLER
Pseudopolygnathus sp.
Palmatolepis perlobata helmsi (ZIEGLER)
Palmatolepis perlobata schindewolfii MÜLLER

Text-Fig. 6.
Outcrop photograph of loc. R 4 (forest road on the western flank of Rodachsrangen). Thick-bedded cherts with thin shaly interlayers form a narrow isoclinal fold. Axis near tip of hammer.

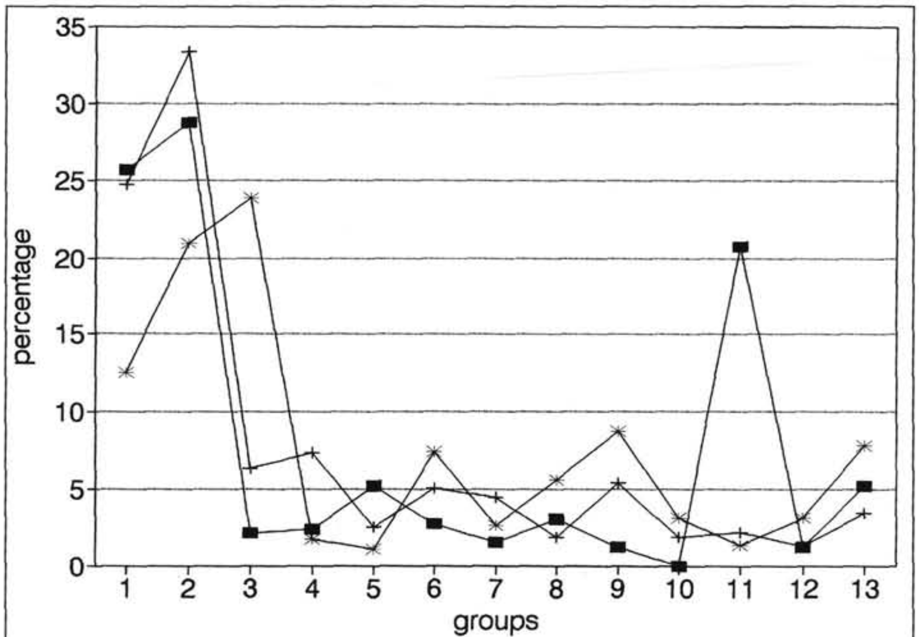
Palmatolepis gracilis gracilis BRANSON & MEHL
Palmatolepis gracilis sigmoidalis ZIEGLER
Bispathodus stabilis (BRANSON & MEHL); morphotype 1 and (?)2
Branmehla inornata (BRANSON & MEHL)
Branmehla werneri (ZIEGLER).

The occurrence of *P. perlobata helmsi* together with *Ps. brevipennatus* suggests the age of this sample lies within the early *expansa*-Zone ('Dasberg'-stage).

4.4. Quantitative Examinations of Radiolarian Faunas

In spite of the very strong influence of preparation and diagenesis (secondary factors) on the faunal composition, primary differences in our material can be recognized by using quantitative analysis. For quantification the radiolarians were clustered into thirteen artificial and natural groups, easily determinable at low magnifications (see Text-Fig. 7 for explanation). With the increasing intensity of secondary factors, massive spherical forms such as Entactiniidae should be enriched and smaller fragile forms such as *Palaeoscenidium* and Archocyrtiidae should be depleted in the residue. The quantitative analysis of three samples from Rodachsrangen shows that the relative abundance of the morphologic groups roughly follows an 'artificial' trend caused by secondary factors (Text-Fig. 7). However, there are important exceptions in two samples. In R 4/7 a strong relative enrichment of *E. palimbola* group (group 3) is identified, and in R 2/1 the Palaeosceniidae (group 11) are strongly enriched. Sample R 3/7 follows the 'normal' trend, though the radiolarians are better preserved than in sample R 2/1.

The changing relative abundances may be due either to evolution, or to bathymetric or oceanographic differences. Since Entactiniidae and Palaeosceniidae in particular, showed only minor evolutionary changes during the Late Devonian, evolution does not seem to be a reason for the changes in relative abundance. There is also no indication of significant changes in bathymetry in the Late Devonian Bavarian facies. The presence of *Holoeciscus* in all better preserved samples implies a continuously deep marine environment, because this species is ecologically similar to *Albaillella* (BRAUN, 1990b), which is a typical deep water indicator (HOLDSWORTH, 1966).



Text-Fig. 7.
Relative abundances of radiolarian groups in three Late Devonian samples of Rodachsrangen.
The groups are mainly artificial morphological assemblages but also taxonomic units. Discussion in text.
1 = large simple spheres (> 150 µm); 2 = small simple spheres (< 150 µm); 3 = *Entactinosphaera palimbola* group; 4 = spheres with two small polar spines; 5 = *Entactinia variospina* group; 6 = three- to four-spined spheres; 7 = spheres with four spines in a plane; 8 = six-spined spheres (*Entactinia* group); 9 = *Astroentactinia* group; 10 = *Polyentactinia* group; 11 = Palaeosceniidae; 12 = Archocyrtiidae; 13 = *Holoeciscus*.

Therefore, changing oceanographic conditions seem to be the most likely reason for the changing relative abundances (see below).

4.5. Palaeoceanography

Recent and Late Cenozoic radiolarians are widely used for oceanographic examinations. In the Mesozoic, palaeoceanographic data are rare and almost non-existent in Palaeozoic faunas. The Late Devonian radiolarian localities in a palaeogeographic map (Text-Fig. 8) show a worldwide distribution, restricted to tropical and subtropical latitudes. A similar observation was made for nearly all Palaeozoic faunas (HOLDSWORTH, 1977). The limitation to low latitudes may be one reason for the striking similarity of all Late Devonian radiolarian faunas described so far.

In contrast to HOLDSWORTH (1977), however, we argue that the diversity of Devonian radiolarian faunas is mainly a function of preservation (the number of identifiable species increases in better preserved samples) and evolution (increase of diversity throughout the Devonian) rather than a function basically determined by ocean proximity. An open ocean environment is not essential for a high radiolarian diversity; it can also prevail in small elongated basins (cf. JENKYNS & WINTERER, 1982). The small basin theory of JENKYNS & WINTERER for radiolarite development in the Mesozoic may be suggested for the Devonian. Some short term oceanographic fluctuations seem to be responsible for significant changes in faunal composition. Sample 3/1 is characterized by a striking abundance of Palaeosceniidae in spite of relatively strong recrystallisation (Text-Fig. 7). We conclude that the Palaeosceniidae reached a peak at this time (latest *marginifera*-zone) caused by favourable oceanographic conditions. The same conditions supporting the climax of Palaeosceniidae may also have caused the onset of radiation of early Archocyrtiidae, which are common in the same sample for the first time in their evolution (see below). As no data about the ecology of Devonian radiolarians have been reported yet, no suggestions can be made on the factors responsible for these observations. *Palaeoscenidium cladophorum* may be a valuable instrument for future palaeoceanographic studies, because

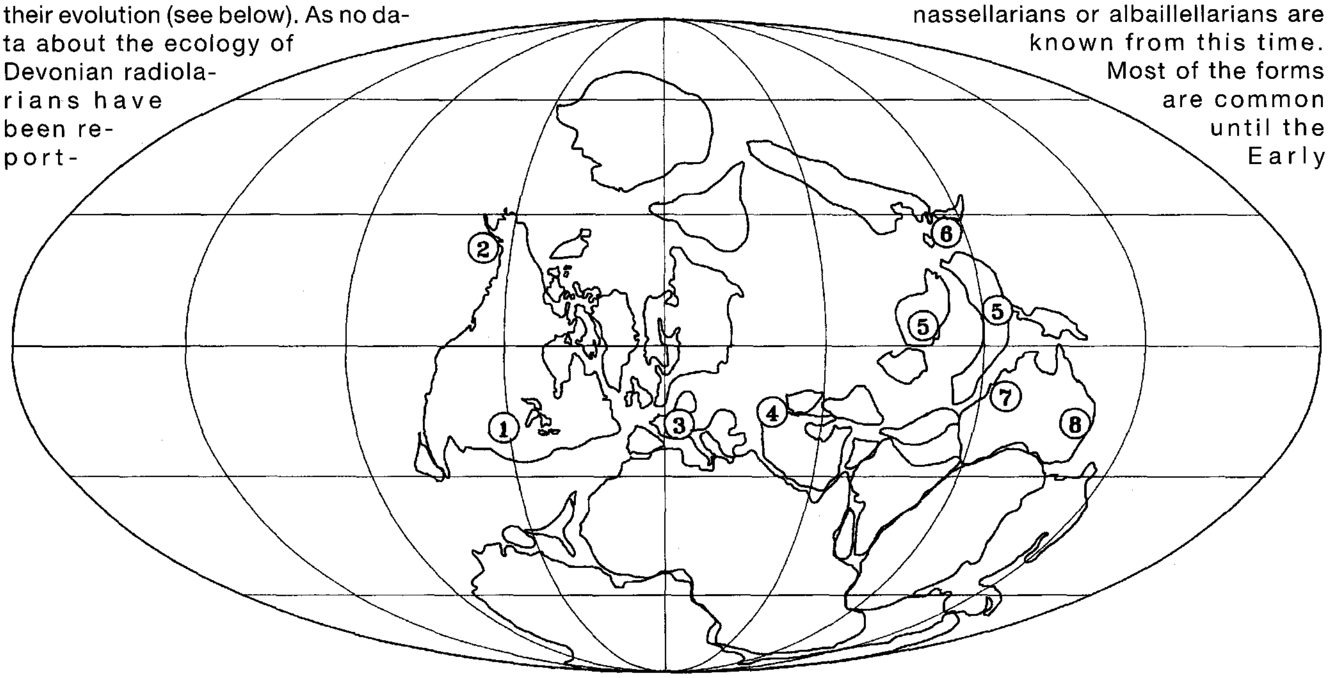
1) its frequency seems to be related to particular oceanographic conditions,
2) it is easy to determine,
3) it has a slow mode of evolution and
4) it appears in almost all Middle Devonian to Early Carboniferous samples.

4.6. Evolution

Numerous papers discuss the evolutionary tendencies of Palaeozoic radiolarians (e.g. BRAUN, 1990a; BRAUN & SCHMIDT-EFFING, 1993; CHENG, 1986; NAZAROV & ORMISTON, 1985, 1986). Many of the phylogenetic tendencies elaborated by these authors seem to result from insufficient data rather than from real trends.

Since no sure Early Devonian radiolarians have been described up to now, the difference between Late Silurian and Middle Devonian faunas appeared to be great (NAZAROV & ORMISTON, 1985). The discovery of Early Devonian radiolarians in our material displays a more continuous evolution of radiolarians from Silurian to Late Devonian times. According to NAZAROV & ORMISTON (1985, 1986), the evolutionary trend from the Silurian to the Middle Devonian comprises spicule reduction, size reduction, thinning of the external shell and a change from cylindrical to three-bladed spines. However, our Early Devonian radiolarians are still large and have a massive shell, but the spines are almost always three-bladed (Pl. 6, Fig. 22–23). An outstanding feature of the Early Devonian fauna is the frequency of morphotypes with 8 or 10 massive triradiate spines.

In the Middle Devonian an increase in diversity can be seen in our faunas, but it is restricted to spumellarians. No nassellarians or albaillellarians are known from this time. Most of the forms are common until the Early



Text-Fig. 8.
Middle and Late Devonian radiolarian locations plotted on a Famennian palaeogeographical map of SCOTESE & MCKERROW (1990).
1 = Ohio (FOREMAN, 1963); 2 = Alaska (HOLDSWORTH et al., 1978); 3 = Germany (RÜST, 1892; SCHMIDT-EFFING, 1988; BRAUN, 1990b; BRAUN et al., 1992, present paper); 4 = Kazakhstan (NAZAROV, 1973, 1975); 5 = China (SHENG & WANG, 1982; WANG, 1991; LI & WANG, 1991); 6 = SW-Japan (WAKAMATSU et al., 1990); 7 = W-Australia (NAZAROV et al., 1982, NAZAROV & ORMISTON, 1983; AITCHISON, 1993b); 8 = E-Australia (HINDE, 1899; ISHIGA et al., 1988; AITCHISON, 1988, 1990, 1993a). All localities are situated between 30° north and south of the palaeo-equator.

Carboniferous with only minor morphological changes. Species with 8 or more massive radial spines are extinct.

Morphotypes belonging to *Astroentactinia* are characterized by large pores and a few spines (see systematic descriptions). There seems to be a gradual decrease in pore size and increase in spine numbers from the Middle to the Late Devonian. In our Middle Devonian material most of the radiolarians belong to two morphologic groups: Entactiniidae with spongy shells and Entactiniidae with large pores (*Polyentactinia* group). Morphotypes with regularly distributed pores of similar size, characterizing the Late Devonian to Early Carboniferous, are almost completely absent.

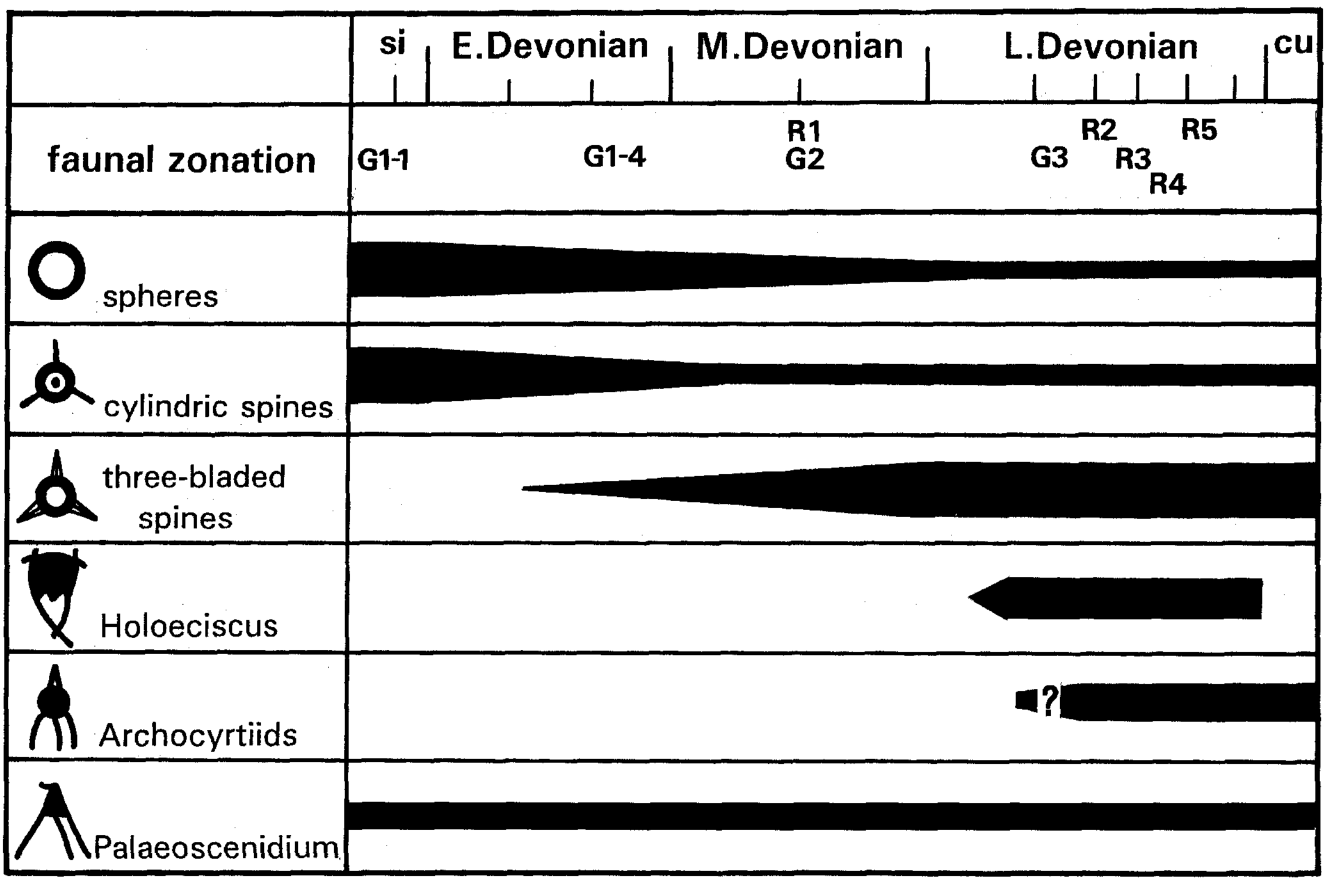
In the Late Devonian a radiation of albaillellarians and nassellarians can be recognized. The early cyrtoid nassellarians in particular are used to subdivide the Late Devonian (HOLDSWORTH & JONES, 1980; CHENG, 1986). The spumellarians (Entactiniidae) show a less intensive increase in diversity and comprise most of the morphotypes described from the Lower Carboniferous (see systematic descriptions). The biotic crisis at the Frasnian/Famennian boundary did not affect the radiolarians. Instead a rapid evolution is observed in the Famennian (NAZAROV & ORMISTON, 1985).

Since the Late Devonian is the pioneer age for cyrtoids, many ancestral forms of Early Carboniferous Albaillellaria and Nassellariida can be observed: *Huasha* (Pl. 1, Fig. 1–3) is a transitional form between the Ceratoikiscidae and true Albaillellidae, according to CHENG (1986) and BRAUN (1990). The early forms of *Cyrtisphaeractenium*, *Robotium* and *Deflandrellium* observed in our material are considerably smaller and have shorter spines than the same genera in the Early Carboniferous. *Archocyrtium* is also smaller in average and rarely bears a well-developed podome-wall, which is typical of Early Carboniferous specimens. Therefore, we suspect an evolutionary trend for early cyrtoid radiolarians towards larger sizes, longer cephalic spines and better developed podome-walls.

An interesting morphotype figured in Pl. 6, Fig. 23–24 may be a possible ancestor of Pylentomiidae. The shell is almost spherical but shows some characteristics of pylentomiids, such as a very small pylome-like opening and an arrangement of spines which might be interpreted as lying at apical and basal positions.

NAZAROV & ORMISTON (1985) presumed the *Tetrentactinia barysphaera* group to be a possible ancestral form of the Late Palaeozoic stauraxon spumellarians. But our morphotypes of that group (*T. teuchestes*) are restricted to the lower part of the middle Famennian and they obviously became extinct in the Late Famennian. Therefore, the NAZAROV & ORMISTON-hypothesis is considered to be incorrect.

The evolutionary trends derived from our material are summarized in Text-Fig. 9. *Palaeoscenidium* is present in all samples from the Silurian up to the Early Carboniferous. Uncertain Archocyrtiidae first arise in the early *crepida*-zone, but their first more frequent appearance (reappearance after HOLDSWORTH & JONES, 1980) is in the latest *marginifera*-zone. Peak abundances occur in the *trachytera*- and early *postera*-zones (R 3, R 4). *Holoeciscus* evolves in the Early Famennian (FOREMAN, 1963) with *H. auceps*. The first forms of the *H. formanae* group are not observed earlier than the latest *marginifera*-zone (R 2). Spumellarians with well developed three-bladed spines first appear in the Early Devonian (G 1/4) and become progressively important during



Text-Fig. 9.
Evolutionary tendencies and stratigraphic ranges of important Devonian radiolarians.
The compilation is based mainly on own data. See text for discussion.

the Middle Devonian. An opposite trend is recognized among spumellarians with cylindrical spines. Large simple spheres decrease in relative abundance during the Devonian, but this may be an effect of better preservation in Late Devonian samples.

4.7. Stratigraphy

Devonian radiolarians are still of minor value for stratigraphy. The evolutionary trends prograde slowly and continuously. In contrast to ORMISTON & NAZAROV (1988) and NOBLE (1992), we think that the only useful stratigraphic tools are the diversifying nassellarians and albaillellarians. The spheroidal morphotypes of NOBLE (1992) have a very restricted range in his material and are common in all of our Late Devonian and some of our Middle Devonian samples; hence, they do not have any stratigraphic value.

The biozonation scheme proposed by HOLDSWORTH & JONES (1980), with revisions by CHENG (1986), is frequently used to subdivide the Late Devonian using radiolarians. Nonetheless, the chronostratigraphic assignment is still poor. It is now possible to determine the limits of the Ho 2 assemblage with the aid of the dated conodont faunas.

The Famennian is subdivided into three zones: the *Holoeciscus*-1 assemblage (Ho 1), the *Holoeciscus*-2 assemblage (Ho 2) and the *Holoeciscus*-3 assemblage (Ho 3). Ho 1 is characterized by the presence of *Holoeciscus auceps* FOREMAN and predates the first occurrence of *H. formanae* CHENG, which marks the base of Ho 2. *H. formanae* is first observed in sample R 2. Therefore, according to the conodont data, the beginning of Ho 2 is at least as old as the latest *marginifera*-zone. *Popofskyellum* should also have its first appearance at the base of Ho 2. This genus, however, is first recognized in the R 3 outcrop. This may be a preservational effect, but it is also possible that *Popofskyellum* appears slightly later than *H. formanae* CHENG. According to HOLDSWORTH & JONES (1980) and CHENG (1986) the base of the Ho 3 is defined by the first appearance of *Pylentonema*. This genus is already seen in R 3. *Huasha* which also originates in the Ho 3 (P-1a assemblage of CHENG, 1986) has also been recovered from R 3. Therefore, the base of Ho 3 can be assigned to the *trachytera*-zone, although peak abundances of *Holoeciscus* are reached in the R 3 and R 4 exposures, which is an attribute of Ho 2 according to HOLDSWORTH & JONES (1980). The base of Ab 1 is placed in the Early Carboniferous by CHENG (1986). It is characterized by the first appearance of *Cyrtisphaeractenium*. However, morphotypes resembling this genus in number and arrangement of spines already occur in the R 4 and R 5 faunas. These very small forms may be precursors of *Cyrtisphaeractenium* or can be included in the genus if the classification scheme of CHENG is used (see systematic descriptions). Analogous remarks may be applied for *Robotium* and *Deflandrellium*, which are both thought to have made their earliest appearance in the Early Carboniferous, but already occur in our Late Devonian material.

Since *Holoeciscus* became extinct at the base of Ab 1, no fauna can be assigned to that assemblage, although spumellarians with long twisted spines typical of Ab 1 (HOLDSWORTH & JONES, 1980) occur in R 2 to R 4. The upper limit of Ho 3 must consequently be younger than the early *expansa*-zone of conodont stratigraphy.

The rapid evolution of the small Archocyrtiidae seen in our Late Devonian material should offer promising material for future stratigraphic work. Owing to their small size they may have been overlooked and hence ignored in current research.

5. Systematic Descriptions

Despite recent progress, the systematic analysis of Palaeozoic radiolarians is still rather underdeveloped. We used the taxonomic system of DEFLANDRE, CHENG, NAZAROV and others for the suprageneric classification. The morphotypes are assigned to three orders and seven well-defined families. However, many morphotypes do not fit into this system and still have to be described as incertae sedis.

We prefer the lumping method for determining species. This is especially useful in the family Entactiniidae, where more than 80 species have been described so far, despite their very few morphological properties. The systematics of Devonian nassellarians is also far from complete but many morphological characteristics make determinations easier.

The type material of the newly described species is deposited in the private collection of W.K.

The species occurrences are listed as sample numbers. Their frequency is indicated in brackets as follows: one specimen, rare (2–10), common (11–50) and abundant (> 50) after adding together all occurrences.

Class: Radiolaria
Subclass: Polycystinea EHRENBERG 1838
Order: Albaillellaria DEFLANDRE 1953, emend. HOLDSWORTH 1969
Family: Albaillellidae DEFLANDRE 1952, emend. HOLDSWORTH 1977
Subfamily: Lapidopiscinae CHENG 1986
Genus: *Huasha* CHENG 1986

Type species: *Huasha holdsworthi* CHENG.

Huasha magnifica CHENG
(Pl. 1, Fig. 1–3)

*1986 *Huasha magnifica* n.sp. – CHENG, p. 74, Pl. 1/2, Fig. 2–3, 6–9, 11, 15; Pl. 1/3, Fig. 1, 3; Pl. 5/2, Fig. 6, 8, 10 (Late Devonian–Lower Carboniferous; Oklahoma, USA).

Remarks: *H. magnifica* and other fragments of *Huasha* are the only taxa of Albaillellidae found in our material.

Occurrence: R 3/2 (rare).

Family: Ceratoikiscidae HOLDSWORTH 1969
Genus: *Ceratoikiscum* DEFLANDRE 1953

Type species: *Ceratoikiscum avimexpectans* DEFLANDRE.

Ceratoikiscum bujugum FOREMAN
(Pl. 1, Fig. 4)

*1963 *Ceratoikiscum bujugum* n.sp. – FOREMAN, p. 288–290, Pl. 8, Fig. 4; Pl. 9, Fig. 9 (Late Devonian; Ohio, USA).
1975 *Ceratoikiscum bujugum* FOREMAN – NAZAROV, p. 100–101, Pl. 13, Fig. 7; Pl. 14, Fig. 9 (Frasnian; S-Urals, Kazhakstan).
1993b *Ceratoikiscum bujugum* FOREMAN – AITCHISON, p. 108, Pl. 4, Fig. 13–14 (Frasnian; Canning Basin, W-Australia).

Occurrence: R 3/2 (rare).

Ceratoikiscum extraordinarium CHENG

(Pl. 1, Fig. 5–6)

*1986 *Ceratoikiscum extraordinarium* n.sp. – CHENG, p. 80–81, Pl. 8, Fig. 1–3, 5–7, 9, 12, 15–17 (Late Famennian–Tournaisian; Oklahoma, USA).

Remarks: Of this species only the well-developed caveal vans (CHENG, 1986) are preserved in our material. However, these are very characteristic and allow a confident species determination.

Occurrence: R 3/2, R 4/7 (rare).

Ceratoikiscum sp.

(Pl. 1, Fig. 7)

Remarks: The morphotype is similar to *C. delicatum* CHENG but has more massive rods.

Occurrence: R 3/2 (common).

Family: Holoeciscidae CHENG 1986
Genus: *Holoeciscus* FOREMAN 1963

Type species: *Holoeciscus auceps* FOREMAN.

Holoeciscus brevis CHENG

(Pl. 1, Fig. 10)

*1986 *Holoeciscus brevis* n.sp. – CHENG, p. 90–91, Pl. 1/17, Fig. 12, 19, 23 (Upper Famennian; Ouachita Mountains, Oklahoma, USA).

1988 *Holoeciscus brevis* CHENG – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 2–3; Pl. 3, Fig. 1–2, 8 (Famennian; Frankenwald, Bavaria, Germany).

?1992 *Holoeciscus brevis* CHENG – BRAUN et al., p. 168, Fig. 4 (Late Famennian; Vosges, France).

?1992 *Holoeciscus* cf. *brevis* CHENG – BRAUN et al., p. 168, Fig. 2/1–2 (Late Famennian; Vosges, France).

Remarks: The specimens figured by BRAUN et al. (1992) do not allow a certain species determination. Their morphotype in Fig. 4 resembles more the specimen figured in Pl. 1, Fig. 20.

Occurrence: R 3/6, 3/7, 4/7 (common).

Holoeciscus formanae CHENG

(Pl. 1, Fig. 8–9, 11–12)

*1986 *Holoeciscus formanae* n.sp. – CHENG, p. 91–92, Pl. 1/5, Fig. 4–6, 9–10, 14, 18 (Famennian–Tournaisian; Ouachita Mountains, Oklahoma, USA).

*1988 *Holoeciscus* sp. A – ISHIGA et al., Fig. 2c (middle Famennian; eastern Australia).

*1988 *Holoeciscus formanae* CHENG – AITCHISON, Fig. 2/1 (Late Devonian; Gwydir terrane, E-Australia).

1990b *Holoeciscus formanae* CHENG – BRAUN, p. 9–10, Pl. 1, Fig. 1–3 (Late Devonian, Hembergian; Main gravels, Germany).

*1990 *Holoeciscus formanae* CHENG – AITCHISON, Fig. 4 a–b (Late Famennian; Anaiwan terrane, E-Australia).

*1991 *Holoeciscus formanae* CHENG – WANG, Pl. 2, Fig. 8 (Famennian; Xinjiang, China).

*1992 *Holoeciscus formanae* CHENG – AITCHISON & FLOOD, Fig. 3/2 (Latest Devonian; eastern Australia).

Occurrence: R 2/1, 3/2, 3/6, 3/7, 4/2, 4/7, 5/2, 5/4 (abundant).

Holoeciscus elongatus n.sp.

(Pl. 1, Fig. 14–17)

Description: Lamellar shell (cavea) rectangular in lateral view, covering the upper and two thirds of the lower triangular rods. Subcircular basal aperture. Lamellar shell subcylindrical with elongated appearance, width to height ratio approximately 1:3. Three to four pairs of caveal ribs. Cavea with small ovate pores following the caveal ribs. Protruding ventral skeletal frame (stapia) spinose. Dorsal "wings" very weakly developed. Blade-like protruding spines on the ventral portion of the test, perpendicular to the skeletal plane.

Remarks: *H. elongatus* n.sp. differs from *H. auceps* FOREMAN in having a spinose, rather than spongy stapia. It differs from *H. formanae* CHENG in having very weakly developed dorsal "wings" and blade-like ventral spines rather than short spinules. Additionally it has three to four pairs of caveal ribs only, compared with five to six pairs on *H. formanae*. *H. elongatus* is further distinguished from *H. auceps* FOREMAN, *H. formanae* and *H. brevis* CHENG in having a lamellar shell covering much greater portions of both i.t. and b.t. spines (almost three-fourths versus one half to two-thirds).

Measurements (in μm, based on five specimens): Total height, 275–305 (mean 288); maximum width, 88–95 (mean 90); length of shell without stapia, 181–210 (mean 195).

Derivatio nominis: elongatus, -a, -um = elongated

Type locality: Rodachsrangen, R 3.

Stratum typicum: *trachytera*-zone (do IV).

Type material: Holotype, R 3/2-02; Paratype, R 4/2-34.

Occurrence: R 3/2, 3/3, 3/6, 4/2 (common).

Holoeciscus sp. A

(Pl. 1, Fig. 18)

cf. 1991 *Holoeciscus* sp. cf. *H. auceps* FOREMAN – WANG, Pl. 2, Fig. 12 (Famennian; Singiang, China).

Description: Shell covering half of the i.t. and b.t. spines. Stapia spongy to spinose. The morphotype is similar to *H. brevis* CHENG, but the stapia is more similar to *H. auceps* FOREMAN. It may, therefore, be a transitional form between these two species.

Occurrence: R 3/2, 4/7 (rare).

Holoeciscus sp.

(Pl. 1, Fig. 19–20)

Remarks: Abundant, poorly preserved specimens of *Holoeciscus* which are slightly different from known species could be found in our material.

Occurrence: All samples of R 2 to R 5 (abundant).

Order: Nassellariida EHRENBERG 1875
Family: Archocyrtiidae KOZUR & MOSTLER, emend. CHENG 1986

Remarks: According to CHENG (1986) the main distinctive feature on a generic level is the number and arrangement of spines. He developed a code notation for systematic studies on Archocyrtiidae with the general style X//Y//Z. The first number means the number of spines in an apical or subapical position, termed apical horns in this paper. Y indicates the number of spines merging from the lattice shell, called cephalic spines herein. Z is the number of spines merging from the podome which we name feet or basal spines. The basal opening of the Archocyrtiidae is called the podome, which is surrounded by an imperforate podome-wall in many morphotypes.

Genus: *Archocyrtium* DEFLANDRE 1972, emend. CHENG 1986

Type species: *Archocyrtium riedeli* DEFLANDRE.

Many of the described species may better be described as subspecies or modifications of few characteristic species. The differences are often minor and may only be a result of ecological or just random variation.

Archocyrtium cf. *angulosum* DEFLANDRE

(Pl. 1, Fig. 21)

cf.*1973 *Archocyrtium angulosum* n.sp. – DEFLANDRE, p. 150, Pl. 2, Fig. 3 (Visean; Hérault, France).
1988 *Archocyrtium* sp. cf. *A. coronaesimile* WON – AITCHISON, Fig. 2/6 (Early Carboniferous; E-Australia).
aff. 1992 *Archocyrtium angulosum* DEFLANDRE – NOBLE, Pl. 1, Fig. 12 (Latest Famennian–Early Carboniferous; Texas, USA).

Occurrence: R 3/6 (rare).

Archocyrtium cf. *delicatum* CHENG

(Pl. 1, Fig. 22–23; Pl. 2, Fig. 9–10)

cf.*1986 *Archocyrtium delicatum* n.sp. – CHENG, p. 123–124, Pl. 2/5, Fig. 20, 24; Pl. 6, Fig. 1, 12, 17 (Late Devonian; Oklahoma, USA).
non 1990b *Archocyrtium* cf. *delicatum* CHENG – BRAUN, p. 16–17, Pl. 1, Fig. 10.
1990 *Archocyrtium* sp. – AITCHISON, Fig. 5 I (Tournaisian; Anaiwan terrane, eastern Australia).

Remarks: According to CHENG (1990) the widely spaced pores without bars or pore cones are the distinctive features of this species. Therefore, our forms may belong to that species, although the apical horn is smaller than in *A. delicatum*.

Occurrence: R 3/2, 3/3, 3/6, 4/6, 4/7, 5/3 (abundant).

Archocyrtium diductum DEFLANDRE

(Pl. 2, Fig. 2)

*1973 *Archocyrtium diductum* n.sp. – DEFLANDRE, p. 150, Pl. 1, Fig. 4; Pl. 2, Fig. 4 (Early Carboniferous, Montagne Noire, France).
1987 *Archocyrtium diductum* DEFLANDRE – GOURMELON, p. 114–115, Pl. 18, Fig. 10–15 (Tournaisian; Montagne Noire, France).
1990c *Archocyrtium diductum* DEFLANDRE – BRAUN, p. 124–125, Pl. 16, Fig. 18; Pl. 17, Fig. 12 (Early Carboniferous; Rhenish Slate Mountains).

Occurrence: R 3/2 (rare).

Archocyrtium dilatipes DEFLANDRE

(Pl. 2, Fig. 1)

*1973 *Archocyrtium dilatipes* n.sp. – DEFLANDRE, p. 150, Pl. 1, Fig. 1–3; Pl. 2, Fig. 1–2 (Visean; Hérault, France).

Remarks: This species is very similar to *A. diductum* DEFL. but has a more massive apical horn and feet which are less divergent.

Occurrence: R 3/2, 4/2, 5/2 (rare).

Archocyrtium effingi n.sp

(Pl. 2, Fig. 14–15)

Description: Small sized *Archocyrtium* with an overall pyramidal shape. Short but massive apical horn. Cephalis subspherical with relatively large pores. Three short, straight, moderately divergent feet. Small podome-wall.

Remarks: *A. effingi* n.sp. is characterized by its angular pyramidal shape and small size. Compared with *A. angulosum* DEFLANDRE the apical horn is shorter and less robust and the podome-wall is smaller. From all other species of *Archocyrtium* it is distinguished by its angular shape and small size.

Measurements (in µm, based on two specimens): Total height, 103–119; length of apical horn, 26–29; width at base of feet (=maximum width), 67–74.

Derivatio nominis: In honour of SCHMIDT-EFFING who was the first to describe well preserved Late Devonian radiolarians from the Frankenwald.

Type locality: Rodachsrangen. Sample R 3/2, *trachytera*-zone (Hemberg-stage, do IV).

Type material: Holotype, R 3/2–45; paratype, R 4/2–81.

Occurrence: Same as for type material (common), possibly in R 2/1.

Archocyrtium eupectum BRAUN

(Pl. 2, Fig. 7)

*1989b *Archocyrtium eupectum* n.sp. – BRAUN, p. 90–91, Pl. 1, Fig. 11–13 (Tournaisian; Main gravels, Germany).
1990c *Archocyrtium eupectum* BRAUN – BRAUN, p. 125, Pl. 16, Fig. 7; Pl. 17, Fig. 13 (Early Carboniferous; Rhenish Slate Mountains, Germany).

Remarks: The characteristic straight margin of the podome-wall is well preserved in our material.

Occurrence: R 3/2 (rare).

Archocyrtium(?) *formosum* CHENG

(Pl. 2, Fig. 6)

*1986 *Archocyrtium formosum* n.sp. – CHENG, p. 124, Pl. 2/5, Fig. 13, 23 (Late Devonian–Early Carboniferous; Oklahoma, USA).

Remarks: Tiny spines on the cephalis make generic classification uncertain. However, all other characteristics are identical with *A. formosum*.

Occurrence: R 3/2, 3/7 (rare).

Archocyrtium sp.aff. *A. formosum* CHENG

(Pl. 2, Fig. 5)

Remarks: The cephalis is relatively larger than in *A. formosum*.

Occurrence: R 3/2 (one specimen).

Archocyrtium ludicrum DEFLANDRE group
(Pl. 2, Fig. 11–13)

*1973 *Archocyrtium ludicrum* n.sp. – DEFLANDRE, p. 150, Pl. 1, Fig. 5; Pl. 2, Fig. 5 (Visé; Hérault, France).
1988 *Archocyrtium* sp. cf. *A. ludicrum* DEFLANDRE – AITCHISON, Fig. 2/4 (Late Famennian- Early Tournaisian; eastern Australia).
1990 *Archocyrtium* sp. B – AITCHISON, Fig. 4 G (Late Famennian; eastern Australia).

Remarks: Some of our morphotypes have straighter and better developed basal spines than the type material of DEFLANDRE, and the cephalic pores are often better developed. However, the small size, the poorly developed podome-wall and the small apical horn are the distinctive features of that species group.

Occurrence: R 3/2, 3/3, 3/6, 3/7, 4/7 (common).

Archocyrtium cf. *riedeli* DEFLANDRE
(Pl. 2, Fig. 3)

cf.1960 *Archocyrtium riedeli* n.sp. – DEFLANDRE, Pl. 1, Fig. 17 (Tournaisian; France): no description!
1972a *Archocyrtium riedeli* DEFLANDRE – DEFLANDRE, Pl. 4, Fig. 4–5 (Tournaisian; France).
* 1972b *Archocyrtium riedeli* DEFLANDRE – DEFLANDRE, p. 15.
1990c *Archocyrtium* cf. *riedeli* DEFLANDRE – BRAUN, p. 128, Pl. 17, Fig. 10–11 (Tournaisian; Rhenish Slate Mountains and Frankenwald, Germany).

Remarks: Our forms can be compared with the paratype figured by DEFLANDRE (1972a). However, the apical horn is not as well developed and there are only three ridges visible on the horn.

Occurrence: R 3/2, 3/3 (rare).

Archocyrtium sp. aff. *A. typicum* CHENG
(Pl. 2, Fig. 8)

Remarks: This form is much smaller than *A. typicum*, but it has the same knife-edge-like apical horn.

Occurrence: R 3/2 (one specimen).

Archocyrtium wonae CHENG
(Pl. 2, Fig. 4)

aff.1973 *Archocyrtium clinoceros* n.sp. – DEFLANDRE, p. 151, Pl. 1, Fig. 7–8; Pl. 3, Fig. 3–4 (Visé; Hérault, France).
* 1986 *Archocyrtium wonae* n.sp. – CHENG, p. 128–129, Pl. 5, Fig. 8; Pl. 6, Fig. 4 (Late Famennian–Early Tournaisian; Oklahoma, USA).

Remarks: Our morphotype is considerably smaller than the type material of DEFLANDRE.

Occurrence: R 4/2 (rare).

Archocyrtium sp. A
(Pl. 2, Fig. 21)

cf.1986 *Archocyrtium* sp. – CHENG, Pl. 2/6, Fig. 3, 18 (Late Devonian; Oklahoma, USA).

Description: Small *Archocyrtium* with conspicuous feet which are very long and strongly divergent. Moderately developed apical horn.

Occurrence: R 3/3 (rare).

Archocyrtium sp. B
(Pl. 2, Fig. 19–20)

Description: This morphotype is characterized by its very small size, almost straight feet and large round pores in slightly elevated pore frames.

Occurrence: R 3/2, 4/2 (common).

Archocyrtium sp. C
(Pl. 2, Fig. 16)

Description: Small apical horn, large densely perforated cephalis, well developed triradiate feet with small podome-wall.

Occurrence: R 5/2 (one specimen).

Genus: *Cerarchocyrtium* DEFLANDRE 1973

Type species: *Cerarchocyrtium ambiguum* DEFLANDRE.

Cerarchocyrtium sp.aff. *Archocyrtium ludicrum* DEFLANDRE
(Pl. 2, Fig. 25)

Remarks: The only difference from *A. ludicrum* is the presence of a small spine on the cephalis, which is seen to be a distinctive feature on a generic level in recent classifications. This hints once more to the deficiency of the currently used systematics.

Occurrence: R 3/3 (rare).

Cerarchocyrtium sp.
(Pl. 2, Fig. 22–24)

Remarks: Only two species of *Cerarchocyrtium* are known from Late Devonian strata. We found four different morphotypes, all differing significantly from the described species. Most of the specimens are very small, rarely exceeding 100 μm in total height.

Occurrence: R 2/1, 3/2, 4/7, 5/3 (abundant).

Genus: *Cyrtisphaeractenium* DEFLANDRE 1972

Type species: *Cyrtisphaeractenium mendax* DEFLANDRE.

Our specimens differ from all species described in this genus by their small size, angular appearance and the short cephalic spines. However, the main characteristic feature is the number and distribution of spines, according to CHENG (1986). Therefore, our morphotypes are tentatively designated to the genus.

Cyrtisphaeractenium (?) *fluegeli* n.sp.
(Pl. 3, Fig. 1–6)

Description: Seven triradiate spines with the code notation 1//1/2//3 in CHENG's system. One subapical, three-bladed massive spine and three unequal cephalic spines. One cephalic spine on the upper hemisphere, three-bladed, nearly as massive as the subapical horn. The second cephalic spine more weakly developed, slightly curved. The location of this spine is strongly variable, ranging from an almost podominal (holotype) to a subapical position. A third cephalic spine is very tiny and only rarely observed. Three almost straight to curved feet. Feet slender or massive. Irregularly perforated cephalis, trapezoidal to subspherical in lateral view. Largest pores where spines are attached on cephalis. Most of the pores covered by microcrystalline quartz, often leaving only the largest pores open. All of the seven spines triradiate. Podome-wall only moderately developed and imperforate.

Remarks: The species is similar to *Cyrtisphaeractenium* sp. B of CHENG (1986), but has a shorter subapical horn and smaller cephalic spines. The species was defined quite broadly, because the position of the second cephalic spine seems to vary randomly, rather than being species-characteristic. The same is true for the shape of the basal spines.

Measurements (based on four specimens, in μm): Height of cephalis 30–47 (mean 35), length of subapical horn 28–33 (mean 30), length of basal spines 56–64 (mean 60), total height 105–128 (mean 115).

Derivatio nominis: In honour of our teacher ERIK FLÜGEL, director of the palaeontological institute of Erlangen.

Type locality: R 4, late *trachytera*- to early *postera*-zone (late do IV).

Type material: Holotype, R 4/2–74; Paratype R 4/7–69.

Occurrence: Late Devonian (middle *trachytera*- to early *postera*-zone, do IV) of the Frankenwald, Germany as far as is known. R 3/3, 4/2, 4/7 (common).

Cyrtisphaeractenium(?) sp. aff. *Archocyrtium validum* CHENG

(Pl. 3, Fig. 7)

aff. 1986 *Archocyrtium validum* n.sp. – CHENG, p. 127, Pl. 5, Fig. 14; Pl. 6, Fig. 13–14 (Late Famennian–Early Tournaisian; Oklahoma, USA).

1988 *Archocyrtium* cf. *validum* CHENG – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 4 (Famennian; Frankenwald, Germany).

Occurrence: R 5/4 (rare).

Cyrtisphaeractenium(?) sp. A

(Pl. 3, Fig. 8)

Description: Very small Archocyrtiid with short massive apical horn, three short, blunt spines on the cephalis and three divergent, curved feet. With a height of only 80 μm this species is the smallest complete radiolarian in our material.

Occurrence: R 4/2 (rare).

Genus: *Deflandrellium* CHENG 1986

Type species: *Deflandrellium georgesi* CHENG.

Deflandrellium sp. A

(Pl. 3, Fig. 9–10)

Description: Hemispherical cephalis with few irregularly distributed pores. Very small apical horn. Four long feet, slightly curved, only weakly triradiate.

Occurrence: R 3/3 (rare).

Deflandrellium sp. B

(Pl. 3, Fig. 19)

Description: Spherical cephalis with densely spaced pores. Tiny apical horn. Four long, moderately curved feet, only slightly divergent.

Occurrence: R 4/2 (rare).

Genus: *Robotium* CHENG 1986

Type species: *Robotium validum* CHENG.

Robotium sp. A

(Pl. 3, Fig. 13)

Description: Archocyrtiid with two diverging, unequal, triradiate subapical horns. Large pores developed where spines meet cephalis. Cephalis perforated, but pores often covered with microcrystalline quartz. Four diverging, triradiate feet. Small podome-wall.

Remarks: The number and arrangement of spines (code 2//0//4) makes the generic assignment indubitable. However, the morphotype is distinguished from all other species assigned to *Robotium* by their smaller size and much shorter subapical spines.
As *Robotium* is known only from Early Carboniferous strata up to now, the range of that genus has to be extended at least until the Middle Famennian. It is also possible that our morphotype belongs to a new genus ancestral to *Robotium*.

Occurrence: R 4/2 (rare).

Robotium sp. B

(Pl. 3, Fig. 11–12)

Description: Subtrapezoedral cephalis with two aligned, massive subapical horns and four relatively weakly developed, triradiate feet. Pores only evolved where apical horns join cephalis. Very small form.

Remarks: *Robotium* sp. A and B are different from all species described so far under this genus. The overall appearance is very similar to *Cerarchocyrtium singularium* CHENG, but this species has only three basal spines.

Occurrence: R 4/7 (rare).

Robotium sp. C

(Pl. 3, Fig. 14)

Description: Very small form with two diverging subapical horns and four diverging curved feet. For remarks see *Robotium* sp. A.

Occurrence: R 4/7 (rare).

Problematic Archocyrtiidae

According to CHENG (1986) the generic classification of the Archocyrtiidae is based on the number and the arrangement of spines. He was able to assign tentatively six genera to this family. In our material more possibilities of spine number and arrangements are realized, which could be designated to new genera, if his taxonomy is accepted. However, there are too few specimens, to erect new species and genera. Additionally the taxonomic framework erected by CHENG seems to be somewhat artificial. Especially the number of small cephalic spines is seen to have a low taxonomic value, as very similar morphotypes have to be designated to different genera, because of small additional cephalic spine/s (e.g. *Cerarchocyrtium* sp.aff. *A. ludicrum*). Therefore, we describe our morphotypes in open nomenclature.

Archocyrtiid sp. A

(Pl. 3, Fig. 15, 18)

Description: Four short subapical spines and three slightly curved basal spines on a small perforated subspherical cephalis. According to CHENG (1986) the code notation would be 4//0//3.

Occurrence: R 4/7 (rare).

Archocyrtiid sp. B

(Pl. 3, Fig. 16–17)

Description: Small Archocyrtiid with two unequal subapical spines, one cephalic spine and three slightly triradiate, divergent feet. Cephalis subspherical with relatively large irregularly distributed pores. Code notation: 2//1//3.

Occurrence: R 4/2 (rare).

Archocyrtiid sp. C

(Pl. 3, Fig. 21)

Description: Very small Archocyrtiid with three spines in a subapical position and three almost straight, strongly divergent feet. Code notation: 3//0//3.

Occurrence: R 4/2 (rare).

Family: Popofskyellidae DEFLANDRE 1964, emend. CHENG 1986
Genus: *Cyrtenactinia* FOREMAN 1963

Type species: *Cyrtentactinia primotica* FOREMAN.

Cyrtentactinia cf. *formosa* CHENG

(Pl. 3, Fig. 22)

cf.*1986 *Cyrtentactinia formosa* n.sp. – CHENG, p. 161, Pl. 2, Fig. 3, 5, 19, 23 (Late Famennian; Oklahoma, USA).

Remarks: A definite classification of this species is only hindered by poor preservation.

Occurrence: R 3/7 (rare).

Genus: *Popofskyellum* DEFLANDRE 1964, emend. CHENG 1986

Type species: *Popofskyellum pulchrum* DEFLANDRE.

Popofskyellum deflandrei CHENG

(Pl. 4, Fig. 1–2)

*1986 *Popofskyellum deflandrei* n.sp. – CHENG, p. 154, Pl. 3/3, Fig. 6–7, 11; Pl. 2, Fig. 7, 15 (Famennian–Tournaisian; Oklahoma and Arkansas, USA).

Occurrence: R 3/2, 3/7, 4/2 (rare).

Popofskyellum sp. cf. *Kantollum*(?) *blancoensis* CHENG

(Pl. 3, Fig. 23)

cf.*1986 *Kantollum*(?) *blancoensis* n.sp. – CHENG, p. 165, Pl. 3/3, Fig. 12 (Famennian–Early Carboniferous; Oklahoma, USA). Rem.: Pl. 2 and 3 are interchanged!

Remarks: As the form lacks externally visible strictures it is related to *Popofskyellum* rather than *Kantollum*.

Occurrence: R 3/2 (rare).

Popofskyellum cf. *annulatum* DEFLANDRE

(Pl. 3, Fig. 24–25)

cf.*1964 *Popofskyellum annulatum* n.sp. – DEFLANDRE, p. 3058, Fig. 11–12, 17 (Visean; Montagne Noire, France).
1988 *Cyrtentactinia*(?) sp. – AITCHISON, Fig. 2/5 (? Tournaisian; Gwydir terrane, eastern Australia).
1990 *Cyrtentactinia* sp. – AITCHISON, Fig. 4/D (Late Famennian; eastern Australia).
1992 *Cyrtentactinia* sp. – AITCHISON & FLOOD, Fig. 3/3 (Latest Devonian–Earliest Carboniferous; eastern Australia).

Remarks: The proximal portion is preserved only. The morphotype differs from *P. annulatum* in having longer, more robust spines and being slightly less conical. It differs from *P.* sp.aff. *Kantollum*(?) *blancoensis* in its larger size and more robust spines. The specimen of *Cyrtentactinia* sp. figured by AITCHISON (1990) and AITCHISON & FLOOD (1992) is identical but has very different measurements, according to the scale bars! The comparison of other identical specimens with known dimension led us to conclude that the scale bar in the 1992 publication is too long. Therefore, the measurements of *Cyrtentactinia* sp. of AITCHISON and AITCHISON & FLOOD may be considered as nearly identical with our *Popofskyellum* cf. *annulatum*.

Occurrence: R 3/2, 3/7 (common).

Popofskyellum sp. ff. *P. undulatum* DEFLANDRE

(Pl. 4, Fig. 3)

Remarks: Only the proximal portion is preserved. The morphotype differs from *P. undulatum* in having a more weakly developed lobulate shape and a slightly larger cephalis. It differs from *P.* sp.aff. *Kantollum*(?) *blancoensis* in its more conical shape.

Occurrence: R 3/6 (rare).

Family: Pylentomidae DEFLANDRE 1963, emend. HOLDSWORTH 1977, CHENG 1986
Genus: *Pylentonema* DEFLANDRE 1963

Type species: *Pylentonema antiqua* DEFLANDRE.

Pylentonema cf. *hindei* CHENG

(Pl. 3, Fig. 20)

cf.*1986 *Pylentonema hindei* n.sp. – CHENG, p. 117–118, Pl. 2, Fig. 16–17 (Late Famennian–Early Tournaisian; Oklahoma and Arkansas, USA).

1990 *Pylentonema* sp. – AITCHISON, Fig. 5/S (Tournaisian; Anaiwan terrane, eastern Australia).
1992 *Pylentonema* sp. – AITCHISON & FLOOD, Fig. 3/8 (Tournaisian; Anaiwan terrane, eastern Australia): scale bar too long!

Occurrence: R 3/2, 3/3, 4/2 (rare).

Order: Spumellarida EHRENBERG 1875
Family: Entactiniidae RIEDEL 1967

Remarks: We abstain from using a subfamily classification for the Entactiniidae, as this is not well confirmed in our opinion.

Genus: *Astroentactinia* NAZAROV 1975

Type species: *Astroentactinia stellata* NAZAROV.

Astroentactinia biaciculata NAZAROV
(Pl. 4, Fig. 6)

* 1975 *Astroentactinia biaciculata* n.sp. – NAZAROV, p. 84, Pl. 8, Fig. 8; Pl. 10, Fig. 6–7 (Frasnian; S-Urals, Kazakhstan).
1982 *Astroentactinia* sp. cf. *A. biaciculata* – NAZAROV et al., p. 170, Fig. 5/A (Frasnian; Canning-Basin, W-Australia).
non 1988 *Astroentactinia biaciculata* NAZAROV – BRAUN & SCHMIDT-EFFING, Fig. 18.
1988 *Astroentactinia biaciculata* NAZAROV – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 8; Pl. 2, Fig. 3 (Famennian; Frankenwald, Germany).
non 1989a *Astroentactinia biaciculata* NAZAROV – BRAUN, p. 370, Pl. 2, Fig. 2.
non 1990b *Astroentactinia biaciculata* NAZAROV – BRAUN, p. 13, Pl. 2, Fig. 8.

Occurrence: R 3/3, 4/1, 4/7 (common).

Astroentactinia multispinosa (WON)
(Pl. 4, Fig. 11)

* 1983 *Entactinia*? *multispinosa* n.sp. – WON, p. 145–146, Pl. 2, Fig. 15–16 (Early Carboniferous; Rhenish Slate Mountains, Germany).
non 1986 *Astroentactinia multispinosa* (WON) – GOURMELON, p. 185, Pl. 4, Fig. 2.
1990c *Astroentactinia multispinosa* (WON) – BRAUN, p. 103, Pl. 9, Fig. 1, aff. Fig. 2–3; Pl. 12, Fig. 1 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).

Occurrence: R 3/3 (rare).

Astroentactinia radiata BRAUN
(Pl. 4, Fig. 4)

1986 *Astroentactinia multispinosa* (WON) – GOURMELON, p. 185, Pl. 4, Fig. 2 (Early Carboniferous; High Pyreneans, France).
1988 *Astroentactinia biaciculata* NAZAROV – BRAUN & SCHMIDT-EFFING, Fig. 18 (Visean; Frankenwald, Germany).
1989b *Astroentactinia biaciculata* NAZAROV – BRAUN, p. 370, Pl. 2, Fig. 2. (Late Tournaisian; Main gravels, Germany).
* 1990c *Astroentactinia radiata* n.sp. – BRAUN, p. 103, Pl. 12, Fig. 2 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).
non 1993b *Astroentactinia radiata* n.sp. – AITCHISON, p. 118, Pl. 7, Fig. 13.

Remarks: According to BRAUN (1990c) the short-spined morphotypes should be named *A. radiata*, while the long-spined morphotypes are included under *A. biaciculata*.

Occurrence: R 3/6, R 4/6, R 4/7, R 5/2 (common).

Astroentactinia digitosa BRAUN
(Pl. 4, Fig. 9)

*1990c *Astroentactinia digitosa* n.sp. – BRAUN, p. 101–102, Pl. 8, Fig. 10–12 (Early Carboniferous; Rhenish Slate Mountains, Germany).

Occurrence: R 3/2, 4/7 (rare).

Astroentactinia sp.aff. *A. paronae* (HINDE)
(Pl. 4, Fig. 5)

Remarks: According to NAZAROV (1975) and NAZAROV & ORMISTON (1983) the main distinctive feature of *A. paronae* (HINDE) is the presence of one larger spine and apart from this an appearance as *A. stellata* NAZAROV. Our morphotype has this single large spine but also larger pores and less numerous spines than *A. paronae*.

Occurrence: G 2/7 (rare).

Astroentactinia stellata NAZAROV
(Pl. 4, Fig. 7)

*1975 *Astroentactinia stellata* n.sp. – NAZAROV, p. 82–83, Pl. 8, Fig. 6 Pl. 10, Fig. 1–3 (Frasnian; S-Urals, Kazakhstan).
1983 *Astroentactinia stellata* NAZAROV – NAZAROV & ORMISTON, p. 459, Pl. 1, Fig. 8–9 (Frasnian; Canning Basin, W-Australia).
1990b *Astroentactinia biaciculata* NAZAROV – BRAUN, p. 13, Pl. 2, Fig. 8. (Late Devonian; Main gravels, Germany).
1992 *Astroentactinia* sp.aff. *A. radiata* BRAUN – BRAUN et al., p. 168–169, Fig. 2/7 (Famennian; Vosges, France).
1993b *Astroentactinia*? *stellata* NAZAROV – AITCHISON, p. 118, Pl. 6, Fig. 4 (Frasnian; Canning Basin, W-Australia).

Occurrence: R 3/3, ?3/6, 3/7 (common).

Astroentactinia(?) sp. A
(Pl. 4, Fig. 8, 10)

Description: Moderately large spherical shell with large irregular pores and few (8–12) equal tapering spines. The morphotype is distinguished from all other species assigned to *Astroentactinia* in having large pores and few moderately long spines. It is restricted to the Middle Devonian in our material.

Occurrence: G 2/5, 2/7, R 1/1 and an additional Middle Devonian sample from the Radspitze (common).

Genus: *Entactinia* FOREMAN 1963

Type species: *Entactinia herculea* FOREMAN.

Entactinia additiva FOREMAN [sensu NAZAROV & ORMISTON]
(Pl. 4, Fig. 13)

* 1963 *Entactinia*? *additiva* n.sp. – FOREMAN, p. 273–274, Pl. 1, Fig. 10; Pl. 3, Fig. 9 (Late Devonian; Ohio, USA).

1975 *Entactinia additiva* FOREMAN – NAZAROV, p. 49–50, Pl. 1, Fig. 7; Pl. 2, Fig. 6 (Famennian; S-Urals, Kazakhstan).
non 1982 *Entactinia additiva*? FOREMAN – NAZAROV et al., p. 164, Fig. 3/A-D.
1983 *Entactinia additiva* FOREMAN – NAZAROV & ORMISTON, p. 457, Pl. 1, Fig. 16 (Frasnian; W-Australia): new definition of species.
1988 *Entactinia*? *additiva* FOREMAN – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 7; Pl. 2, Fig. 2 (Famennian; Frankenwald, Bavaria).
1990 *Entactinia additiva*? FOREMAN – AITCHISON, Fig. 2 c (Late Devonian?; Gamilaroi terrane, E-Australia).

Occurrence: R 2/1, 3/2, 3/3, 3/6, 4/2, 4/7 (common).

Entactinia exilispina FOREMAN

(Pl. 4, Fig. 16)

*1963 *Entactinia exilispina* n.sp. – FOREMAN, p. 273, Pl. 1, Fig. 8 (Early Famennian; Ohio, USA).

Remarks: One of the biggest radiolarians in our material.

Occurrence: R 2/1 (one specimen).

Entactinia herculea FOREMAN

(Pl. 4, Fig. 12, 21–22)

*1963 *Entactinia herculea* n.sp. – FOREMAN, p. 271, Pl. 1, Fig. 3a–d (Late Devonian; Ohio, USA).
1988 *Entactinia*? *herculea* FOREMAN – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 9 (Famennian; Frankenwald, Germany).
1990b *Entactinia herculea* FOREMAN – BRAUN, p. 11, Pl. 2, Fig. 1–4 (Late Devonian, Hembergian; Main gravels, Germany).
1992 *Entactinia herculea* FOREMAN – BRAUN et al., p. 169–170, Fig. 2/8 (Famennian; Vosges, France).

Remarks: This species rarely shows by-spines described by FOREMAN (1963) as typical (see Pl. 4, Fig. 12). The Early Carboniferous species *Entactinia vulgaris* WON is morphologically very similar to the Late Devonian *E. herculea* FOREMAN (see remarks in BRAUN, 1990b). It is distinguished herein from *E. vulgaris* by its relatively longer and more massive spines and more irregularly distributed, slightly smaller pores. The more unequal pores are also used to separate it from *Entactinosphaera grandis* NAZAROV, because the internal morphology could mostly not be observed.

Occurrence: G 2/5, 2/7, 3/2 and all samples from Rodachsrangen (abundant).

Entactinia(?) *pantotolma* BRAUN

(Pl. 4, Fig. 14)

*1989b *Entactinia*? *pantotolma* n.sp. – BRAUN, p. 88–89, Pl. 2, Fig. 6–7 (Early Carboniferous; Main gravels, Germany).

Remarks: Though our morphotype is smaller than the type material of BRAUN.

Occurrence: R 3/3, 5/2 (rare).

Entactinia spongites FOREMAN

(Pl. 4, Fig. 15)

*1963 *Entactinia spongites* n.sp. – FOREMAN, p. 272–273, Pl. 1, Fig. 7 (Early Famennian; Ohio, USA).
1982 ?*Spongentactinia spongites* (FOREMAN) – NAZAROV et al., p. 168, Fig. 4/G (Frasnian; Canning-Basin, W-Australia).

Occurrence: G 2/7, ? 3/2, R 2/1 (common).

Entactinia tortispina (ORMISTON & LANE) group

(Pl. 4, Fig. 17–18)

*1976 *Polyentactinia tortispina* n.sp. – ORMISTON & LANE, p. 166–167, Pl. 2, Fig. 1–5 (Early Carboniferous; Oklahoma, USA).
1983 *Entactinia tortispina* (ORMISTON & LANE) – WON, p. 143–144, Pl. 4, Fig. 18–20 (Early Carboniferous; Rhenish Slate Mountains, Germany).
1983 *Entactinia ormistoni* n.sp. – WON, p. 142–143, Pl. 4, Fig. 17 (Early Carboniferous; Rhenish Slate Mountains, Germany).
1983 *Entactinia parva* n.sp. – WON, p. 143, Pl. 4, Fig. 15–16 (Early Carboniferous; Rhenish Slate Mountains, Germany).
1986 *Entactinia tortispina* (ORMISTON & LANE) – GOURMELON, p. 182–183, Pl. 4, Fig. 3 (Early Carboniferous; High Pyreneans, France).
1987 *Entactinia tortispina* (ORMISTON & LANE) – GOURMELON, p. 47–49, Pl. 3, Fig. 1–5 (Tournaisian; France).
1988 *Entactinia tortispina* (ORMISTON & LANE) – BRAUN & SCHMIDT-EFFING, Fig. 20 (Visean; Frankenwald, Germany.
1989 *Entactinia tortispina* (ORMISTON & LANE) – BRAUN, p. 87, Pl. 2, Fig. 8–12 (Early Carboniferous; Main gravels, Germany).
1990a *Entactinia tortispina* (ORMISTON & LANE) – BRAUN, Pl. 1, Fig. 6 (Early Carboniferous; Germany).
1990c *Entactinia tortispina* (ORMISTON & LANE) – BRAUN, p. 108–109, Pl. 8, Fig. 1–5; Pl. 12, Fig. 7 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).

Remarks: This species group is highly variable in number and arrangement of spines as well as in the morphology of the central sphere. The main characteristics are the long and twisted spines. The number of spines ranges from 4 to 8, but only 4- to 6-spined forms have been observed in our material. For discussion see BRAUN (1990c).

Occurrence: R 2/1, 3/2, 3/3, 3/6, 3/7, 4/7 (common).

Entactinia variospina (WON) group

(Pl. 4, Fig. 23–24)

? 1892 *Xiphosphaera macrostyla* n.sp. – RÜST, p. 141, Pl. 9, Fig. 10 (Late Devonian; Harz, Germany).
* 1983 *Palaeoxyphostylus variospina* n.sp. – WON, p. 156–157, Pl. 8, Fig. 1–4, 6–22 (Early Carboniferous; Rhenish Slate Mountains, Germany).
non 1986 *Entactinia variospina* (WON) – GOURMELON, p. 183, Pl. 4, Fig. 1.
1988 *Staurodruppa* sp.aff. *S. prolata* FOREMAN – AITCHISON, Fig. 4 I (Early Carboniferous; Anaiwan terrane, E-Australia).
1989a *Entactinia variospina* (WON) – BRAUN, p. 368, Pl. 2, Fig. 3–4; Pl. 4, Fig. 5 (Early Carboniferous; Germany).
1990a *Entactinia variospina* (WON) – BRAUN, Pl. 1, Fig. 4 (Early Carboniferous; Germany).
1990c *Entactinia variospina* (WON) – BRAUN, p. 109–110, Pl. 7, Fig. 4–6 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).
cf. 1991 *Entactinia* cf. *variospina* (WON) – LI & WANG, Pl. 2, Fig. 16–17 (Frasnian; Guangxi, China).
1992 *Palaeoxyphostylus variospina* WON – NOBLE, Pl. 1, Fig. 8 (Late Devonian–Early Carboniferous; Texas, USA).

Remarks: After WON (1983) the species may have 2–6 spines and the number is only ecologically determined. The presence of two massive polar spines with or without smaller equatorial spines is characteristic for that species. We agree with the concept of low taxonomic significance of spine numbers. However, it seems to be useful to distinguish some subspecies even for environmental analysis in the future. Especially, morphotypes with a triradiate symmetry, which are similar to the younger Triactoma, may belong to an other taxon. Additionally forms with the same morphology, but four small spines in the equatorial plane, are described as *Entactinosphaera aitpaiensis* NAZAROV (see below). Note also that in other groups and systematics, spine number is still used not only for species but also for generic or family discrimination (see especially Archocyrtiidae).

Occurrence: R 3/2, 3/3, 3/7, 4/2, 5/4 (abundant).

Entactinia vulgaris WON

(Pl. 4, Fig. 19–20)

* 1983 *Entactinia vulgaris* n.sp. – WON, p. 144, Pl. 4, Fig. 1–3 (Early Carboniferous; Rhenish Slate Mountains, Germany).
?1986 *Entactinia vulgaris* WON – GOURMELON, p. 184, Pl. 2, Fig. 4 (Lower Carboniferous; High Pyreneans, France).
1989 *Entactinia vulgaris* WON – GIESE & SCHMIDT-EFFING, p. 74, Pl. 2, Fig. 4, 9 (Lower Carboniferous; Hessen, Germany).
1989b *Entactinia vulgaris* WON – BRAUN, Pl. 2, Fig. 1–5 (Early Carboniferous; Main gravels, Germany).
1990c *Entactinia vulgaris vulgaris* WON – BRAUN, p. 110–111, Pl. 7, Fig. 7–10 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).
1991 *Entactinia oumuhaensis* WANG – WANG, Pl. 2, Fig. 14 (Famennian; Singiang, China).

Remarks: The forms are slightly larger than in the type material of WON (1983). However, as no by-spines were ever observed and the main spines being considerably shorter, an assignment to *Entactinia herculea* FOREMAN is not possible. A separation of two subspecies as defined by BRAUN (1989b) is not useful in our material, because there are continuous transitions from morphotypes having 10 pores per half a circumference to forms having up to 16 pores.

Occurrence: R 3/3, 3/6 (common).

Genus: *Entactinosphaera* FOREMAN 1963

Type species: *Entactinosphaera esostrongyla* FOREMAN.

Entactinosphaera (?) *aitpaiensis* NAZAROV

(Pl. 4, Fig. 25)

*1973 *Entactinosphaera aitpaiensis* n.sp. – NAZAROV, p. 697, Pl. 1, Fig. 4–5 (Frasnian; S-Urals, Kazakhstan).
1975 *Entactinosphaera aitpaiensis* NAZAROV – NAZAROV, p. 63, Pl. 6, Fig. 2–4 (Frasnian; S-Urals, Kazakhstan).
1975 *Entactinosphaera egindyensis* n.sp. – NAZAROV, p. 61–63, Pl. 6, Fig. 1, 5 (Frasnian; S-Urals, Kazakhstan).
1992 *Entactinosphaera*(?) *aitpaiensis* NAZAROV – BRAUN et al., p. 171, Fig. 2/12, 14 (Famennian; Vosges, France).

Remarks: The only visible difference to *Entactinia variospina* (WON) are the four short spines in the equatorial plane. Both species occur in the same samples and may just be ecological variations. As noted above the definition of *E. variospina* should, therefore, be modified.

Occurrence: R 3/2, 3/3 (rare).

Entactinosphaera fredericki FOREMAN

(Pl. 4, Fig. 26–27)

*1963 *Entactinosphaera fredericki* n.sp. – FOREMAN, p. 275, Pl. 5, Fig. 5a–c; Pl. 6, Fig. 8 (Early Famennian; Ohio, USA).

Remarks: In our material, the inner shell is preserved only, which is similar to the intermediate shell of *E. riedeli* FOREMAN, but is distinguished from the latter by the lack of pore rosettes around main spines and its smaller size.

Occurrence: R 3/6, 4/7 (rare).

Entactinosphaera palimbola FOREMAN group

(Pl. 5, Fig. 2, 4–5)

* 1963 *Entactinosphaera palimbola* n.sp. – FOREMAN, p. 277, Pl. 2, Fig. 7a–e; Pl. 3, Fig. 3a–d (Late Devonian; Ohio, USA).
1983 *Belowea* sp.aff. *Entactinosphaera palimbola* FOREMAN – WON, p. 131–132, Pl. 5, Fig. 7–11; Pl. 13, Fig. 1–2 (Early Carboniferous; Rhenish Slate Mountains, Germany).
1988 *Entactinosphaera*? *palimbola* FOREMAN – SCHMIDT-EFFING, p. 34, Pl. 1, Fig. 5–6 (Famennian; Frankenwald, Germany).
1990b *Entactinosphaera*? *palimbola* FOREMAN – BRAUN, p. 12, Pl. 2, Fig. 5–6 (Late Devonian, Hembergian; Main gravels, Germany).
aff. 1990c *Entactinosphaera palimbola* FOREMAN – BRAUN, p. 112–113, Pl. 7, Fig. 11–12 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).
1991 *Entactinia* sp. cf. *E. cometes* FOREMAN – WANG, Pl. 2, Fig. 16 (Famennian; Singiang, China).
pars 1991 *Entactinosphaera palimbola* FOREMAN – LI & WANG, p. 400, Pl. 1, Fig. 12–14, non Fig. 11 (Frasnian; Guangxi, China).
1991 *Entactinosphaera assidera* NAZAROV – LI & WANG, p. 399, Pl. 1, Fig. 17 (Frasnian; Guangxi, China).
non 1993b *Entactinosphaera palimbola* FOREMAN – AITCHISON, p. 116, Pl. 5, Fig. 5.

Remarks: The generic assignment of this species is difficult to confirm. WON (1983) states that the meshwork of the outer shell is characteristic for the genus Belowea, whereas the number of inner shells is only of minor importance and the number of spines is not even species-characteristic. It should be noted, however, that there is a great variability even in the outer shell ornamentation, ranging from ragged edges (FOREMAN, 1963) to a dense polygonal framework. Until new systematic work permits a better defined taxonomy we leave the species in the genus *Entactinosphaera* and accept the variability of the species as defined in the description of FOREMAN (1963).

Occurrence: G 3/2, all samples of R 2 to R 5 (abundant).

Entactinosphaera (?) sp. aff. *E. palimbola* FOREMAN

(Pl. 5, Fig. 3)

1990c *Entactinosphaera palimbola* FOREMAN – BRAUN, p. 112–113, Pl. 7, Fig. 11–12 (Early Carboniferous; Rhenish Slate Mountains, Germany).
pars 1992 Spumellaria of morphotype 3 – NOBLE, Pl. 1, Fig. 6–7, non Fig. 5 (Latest Famennian–Earliest Carboniferous; Marathon Basin, Texas, USA).
1993 *Entactinosphaera palimbola* FOREMAN – BRAUN & SCHMIDT-EFFING, Pl. 1, Fig. 7 (Tournaisian; Germany).

Remarks: This morphotype differs from *E. palimbola* FOREMAN in being smaller and having much larger pores. It differs from *Entactinia cometes* FOREMAN in its smaller size and less spiny surface.

Occurrence: R 3/7, 5/4 (common).

Entactinosphaera riedeli **FOREMAN**
(Pl. 5, Fig. 1)

*1963 *Entactinosphaera riedeli* n.sp. – FOREMAN, p. 275–276, Pl. 5, Fig. 4a–c; Pl. 6, Fig. 9 (Early Famennian; Ohio, USA).

Occurrence: R 4/7 (rare).

cf. *Entactinosphaera symphypora* **FOREMAN**
(Pl. 5, Fig. 7)

cf.*1963 *Entactinosphaera symphypora* n.sp. – FOREMAN, p. 277, Pl. 2, Fig. 5a–c; Pl. 3, Fig. 4 (Early Famennian; Ohio).

Remarks: Though our morphotype is much larger (175 versus 110 μm) than the type material of FOREMAN, the very small pores, the thorny surface and the moderately developed main spines indicate a very close relationship.

Occurrence: R 5/4 (rare).

Genus: *Polyentactinia* FOREMAN 1963

Type species: *Polyentactinia craticulata* FOREMAN.

Polyentactinia aranea **GOURMELON**
(Pl. 5, Fig. 10)

1986 *Polyentactinia* sp. A – GOURMELON, p. 185–186, Pl. 4, Fig. 5 (Early Carboniferous; Pyreneans, France).
*1987 *Polyentactinia aranea* n.sp. – GOURMELON, p. 77–78, Pl. 10, Fig. 7–9 (Tournaisian; Montagne Noire, France).
1990c *Polyentactinia aranea* GOURMELON – BRAUN, p. 130–131, Pl. 14, Fig. 4–5, 10; Pl. 15, Fig. 13–15 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).

Occurrence: R 3/2, 4/6 (common).

Polyentactinia craticulata **FOREMAN**
(Pl. 5, Fig. 11)

1963 *Polyentactinia craticulata* n.sp. – FOREMAN, p. 281, Pl. 5, Fig. 3a–b; Pl. 9, Fig. 5a–b.

Occurrence: R 4/7 (one specimen).

Polyentactinia fenestrata **(HINDE)**
(Pl. 5, Fig. 8–9)

*1899 *Heliosphaera fenestrata* n.sp. – HINDE, p. 49–50, Pl. 8, Fig. 27 (Middle–Late Devonian; SE-Australia).

Occurrence: R 3/6, 3/7 (common).

Polyentactinia*(?) *perampla **BRAUN, MAASS & SCHMIDT-EFFING**
(Pl. 5, Fig. 15)

cf.1982 *Polyentactinia*? sp. – NAZAROV et al., p. 170, Fig. 4 h (Frasnian; Canning Basin, W-Australia).
1988 *"Palaeoactinomma"* sp. (sensu HOLDSWORTH 1977) – SCHMIDT-EFFING, p. 35, Pl. 1, Fig. 10, Pl. 2, Fig. 4 (Famennian; Frankenwald, Germany).
1990b *Polyentactinia*? sp. – BRAUN, p. 15, Pl. 1, Fig. 8–9 (Late Devonian, Hembergian; Main gravels, Germany).
* 1992 *Polyentactinia*? *perampla* n.sp. – BRAUN, MAASS & SCHMIDT-EFFING (Famennian; Vosges, France).

Remarks: Our specimens vary considerably in size and pore morphology. There are specimens very similar to the type material of BRAUN et al. but often the shell is significantly larger and contains more pores than the holotype (see Pl. 5, Fig. 15). However, the observation of abundant transitions led us to include these morphotypes under *P.* (?) *perampla*.

Occurrence: G 2/5, 2/7, R 3/2, 3/3, 3/6, 3/7, 4/6 (common).

***Polyentactinia*(?) sp. A**
(Pl. 5, Fig. 12)

Description: Small sphere with an angular meshwork. Pores variable in size and shape. Four(?) similar main spines, longer than diameter of shell. Lattice shell with thorny surface.

Occurrence: R 3/7 (rare).

***Polyentactinia*(?) sp. B**
(Pl. 5, Fig. 13)

Description: Large sphere with an angular meshwork. Pores variable in size and shape. One robust three-bladed spine and abundant short secondary spines on shell surface.

Occurrence: R 3/2, 3/7 (rare).

***Polyentactinia*(?) sp. C**
(Pl. 5, Fig. 14)

Description: Large sphere with an angular meshwork. Pores large, variable in size and shape. Two short polar spines. This form is restricted to the Middle Devonian. It is comparable with *Astroentactinia*(?) sp. A, which is also restricted to Middle Devonian strata.

Occurrence: G 2/5, 2/7 (rare).

Genus: *Tetrentactinia* FOREMAN 1963

Type species: *Tetrentactinia barysphaera* FOREMAN.

Remarks: The outer shape of this genus varies considerably. The generic assignment depends on the structure of the internal spicule, which is only rarely visible.

Tetrentactinia spinulosa **n.sp.**
(Pl. 5, Fig. 16–17)

Description: Four long tetrahedrally arranged needle-like spines with many spinules. Spinules arising centrally are thick and branching, forming a small irregular to subspherical spongy shell. Externally located spinules at several levels, short and pointed, sometimes branching. External spinule concentrated at the middle part of the main spines.

Remarks: This species is similar to *Tetrentactinia quadrispinosa* FOREMAN, but differs in its external spinules and its longer main spines.

Measurements (based on two specimens, in μm): Diameter of shell: 67–74; diameter of main spines 9–14, Length of main spines 135–170.

Derivatio nominis: spinulosus, -a, -um = spiny.

Type material: Holotype, R 3/2–52; Paratype, R 3/2a–8.

Stratum typicum: Rodachsrangen. Sample R 3/2, *trachytera*-zone (Hemberg-stage, do IV).

Occurrence: Same as for type material (rare).

Tetrentactinia teuchestes FOREMAN

(Pl. 5, Fig. 18–19)

*1963 *Tetrentactinia teuchestes* n.sp. – FOREMAN, p. 283, Pl. 7, Fig. 8a–b (Early Famennian; Ohio, USA).

Remarks: Although there is no internal lattice shell observed and the number of spongy spines is less than 20 (16–18?), the determination seems to be justified, because of the characteristic spongy surface and short spongy spines. *T. teuchestes* is closely related to *T. barysphaera* FOREMAN and *T. somphosphaera* FOREMAN, all of them being possible ancestors of stauraxon radiolarians evolving in the Early Carboniferous (NAZAROV & ORMISTON, 1985, see above for discussion).

Occurrence: R 2/1.

Genus: *Triaenosphaera* DEFLANDRE 1973

Type species: *Triaenosphaera sicarius* DEFLANDRE.

Triaenosphaera sicarius DEFLANDRE

(Pl. 5, Fig. 21–22)

1960 *Triaenosphaera sicarius* n.sp. – DEFLANDRE, Pl. 1, Fig. 10 (Visean; Montagne Noire, France).
*1973 *Triaenosphaera sicarius* n.sp. – DEFLANDRE, p. 1150, Pl. 2, Fig. 3–4 (Visean; Hérault, France).
1978 *Triaenosphaera sicarius* DEFLANDRE – HOLDSWORTH et al., p. 781, Fig. 2a–c (Late Devonian; Alaska, USA).
1986 *Triaenosphaera sicarius* DEFLANDRE – GOURMELON, p. 186–187, Pl. 2, Fig. 1 (Lower Carboniferous; High Pyreneans, France).
1988 *Triaenosphaera sicarius* DEFLANDRE – SCHMIDT-EFFING, p. 35, Pl. 3, Fig. 5 (Famennian; Frankenwald, Bavaria).
1990c *Triaenosphaera sicarius* DEFLANDRE – BRAUN, p. 114–115, Pl. 11, Fig. 8–9 (Early Carboniferous; Rhenish Slate Mountains).

Occurrence: R 3/3, 3/6, 4/6, 5/2 (common).

Triaenosphaera hebes WON

(Pl. 5, Fig. 25)

*1983 *Triaenosphaera hebes* n.sp. – WON, p. 167, Pl. 3, Fig. 12–13 (Early Carboniferous; Rhenish Slate Mountains).
1990c *Triaenosphaera hebes* WON – BRAUN, p. 114–115, Pl. 11, Fig. 8–9 (Early Carboniferous; Rhenish Slate Mountains).

Occurrence: R 3/2 (rare).

Triaenosphaera sp. A

(Pl. 5, Fig. 20)

Remarks: The relation of spine size to sphere diameter is similar as in *T.* (?) *bareillensis* GOURMELON. However, our form is much smaller than this species.

Occurrence: R 5/2 (rare).

Problematic Entactiniidae

In our material abundant entactinids with four to five main spines could be observed. As such forms are not described yet and inner structure could not be examined, they are reported herein in open nomenclature. Some forms resemble *Pylentonema* but lack any indication for cyrtoid nassellarians.

Entactiniid sp. group I

(Pl. 5, Fig. 23–24)

Description: Moderately large spheres with large pores and five massive spines tracing the shape of a pyramid. Four slightly unequal spines nearly in one plane and one spine perpendicular to that plane.

Occurrence: G 3/2, most of the R 2 to 5 samples (common).

Entactiniid sp. group II

(Pl. 6, Fig. 1–2)

Description: Moderately large spheres with large pores and five irregularly distributed, massive, three-bladed spines.

Occurrence: Nearly all samples of R 2 to 5 (abundant).

Entactiniid sp. group III

(Pl. 6, Fig. 3)

Description: Moderately large spheres with large pores and four main spines in a plane forming a right-angle cross.

Remarks: This morphotype is sometimes difficult to determine with certainty, since many six spined specimens may have a four-rayed appearance, if spines are broken near base. Note that forms with four very long spines can be included under *Entactinia tortispina* in current classifications.

Occurrence: Nearly all samples of R 2 to 5 (common).

Spumellarida incertae sedis

The following spumellarians have been assigned to families of the HAECKEL system by different authors. But they are treated as Spumellarida incertae sedis, since HAECKEL's classification system was produced for modern radiolarians which are proved to have only few relation to Palaeozoic ones.

Genus: *Staurodruppa* HINDE 1899

Type species: *Staurodruppa praelonga* HINDE.

Staurodruppa(?) sp.

(Pl. 6, Fig. 13–14)

Remarks: The morphotype has very robust three bladed spines and a spongy meshwork arranged in concentric (?) layers. It is common in and restricted to the Middle Devonian.

Occurrence: G 2/5, 2/7, R 1/4 (common).

Genus: *Stauroplegma* HINDE 1890

Type species: *Stauroplegma brevispina* HINDE.

Stauroplegma sp. A
(Pl. 6, Fig. 16)

Description: Irregular reticular to spongy cortical shell with four very massive spines in a plane forming a regular cross. The very massive spines combined with a relatively small shell distinguish the form from *S. pulcherium* SHENG & WANG and *S. robustospina* SHENG & WANG, which are else comparable.

Occurrence: R 4/7 (rare).

Genus: *Staurostylus* HAECKEL 1882

Type species: *Staurostylus graecius* HAECKEL.

Staurostylus sp. A
(Pl. 6, Fig. 12)

Description: Moderately large widely perforated sphere with short massive radial main spines in a plane, the opposite pair of spines larger than the other.

Spineless Spheres

Palaeozoic simple spineless spheres are described in detail in older literature only (HINDE, 1899; RÜST, 1892) and are designated to *Cenosphaera* sp. which is common in recent oceans. However, most of the Palaeozoic spumellarians, previously thought to be related to modern genera, now are shown to belong to specific Palaeozoic taxa. This conclusion was only possible due to examinations of the internal structure of radiolarians and the realization of their taxonomic importance. As internal structures could rarely be observed in our material we had to describe unknown morphotypes in open nomenclature, since the application of the classical Haeckelian system has been proved to be inadequate for Palaeozoic radiolarians.

Spineless sphere sp. A
(Pl. 6, Fig. 20)

cf.1978 Spumellaria family and genus indet. – HOLDSWORTH et al., Fig. 2l, o (Late Devonian; Alaska, USA): Figs. 2 and 3 are mixed up!

Description: Large spineless sphere (210 µm in diameter) with very small pores. There is no evidence for broken spines.

Occurrence: Almost all samples (abundant).

Spineless sphere sp. B
(Pl. 6, Fig. 19)

Description: Sphere of intermediate size (170 µm diameter) with relatively large pores in hexagonal pore frames.

Occurrence: Almost all samples (abundant).

Spheres with two polar spines
(Pl. 6, Fig. 18)

Description: Small spheres with relatively large pores and thin, long excentrical spines are very common in the Late Devonian samples. The forms do not resemble any known species, but are similar to the morphotypes figured by AITCHISON (1990, Fig. 3C–F) from the Silurian.

Occurrence: R 4/1, R 4/2 (common).

Spheres with 8 or 10 triradiate spines
(Pl. 6, Fig. 21–22)

Remarks: These morphotypes are restricted to the Early Devonian and will be described in detail (TRAGELEHN & KIESSLING, in preparation).

Occurrence: G 1/4 (common).

Order: incertae sedis
Genus: *Bisyllentactinia* NAZAROV 1975

Type species: *Bisyllentactinia rudicula* NAZAROV.

Stauroplegma(?) *xiphophorus* (RÜST)
(Pl. 6, Fig. 15)

*1892 *Staurostylus xiphophorus* n.sp. – RÜST, p. 143, Pl. 11, Fig. 1 (Carboniferous; southern Urals, Russia).

Occurrence: Geuserberg, sample 30/33 of possibly Frasnian age (rare).

Bisyllentactinia arrhinia (FOREMAN)
(Pl. 6, Fig. 4, 8)

*1963 *Haplentactinia arrhinia* n.sp. – FOREMAN, p. 270, Pl. 1, Fig. 1, Pl. 3, Fig. 1 (Late Devonian; Ohio, USA).

1975 *Bisyllentactinia* cf. *arrhinia* (FOREMAN) – NAZAROV, p. 94–95, Pl. 13, Fig. 3; Pl. 14, Fig. 2–3 (Frasnian; S-Urals, Russia).

Remarks: In our material only the first group of spinules along the main spines are preserved. Included are also forms with not exactly isometric axes (see NAZAROV, 1975).

Occurrence: R 3/6, 3/7, R 4/6 (common).

Family: Palaeoscenidiidae RIEDEL 1967, emend. HOLDSWORTH 1977, FURUTANI 1983, GOODBODY 1986
Genus: *Palaeoscenidium* DEFLANDRE 1953

Type species: *Palaeoscenidium cladophorum* DEFLANDRE.

Palaeoscenidium cladophorum DEFLANDRE
(Pl. 6, Fig. 5–7, 9–10)

*1953 *Palaeoscenidium cladophorum* n.sp. – DEFLANDRE, p. 408, Fig. 308 (Visean; Montagne Noire, France).

1960 *Palaeoscenidium cladophorum* DEFLANDRE – DEFLANDRE, Pl. 1, Fig. 21 (Visean; Montagne Noire, France).

1960 *Palaeoscenidium bicorne* n.sp. – DEFLANDRE, Pl. 1, Fig. 20 (Visean; Montagne Noire).

1963 *Palaeoscenidium cladophorum* DEFLANDRE – FOREMAN, p. 302, Pl. 8, Fig. 10; Pl. 9, Fig. 6 (Early Late Devonian; Ohio, USA).

1975 *Palaeoscenidium cladophorum* DEFLANDRE – NAZAROV, p. 45, Pl. 1, Fig. 8–9 (Frasnian; S-Urals, Kazakhstan).

1982 *Palaeoscenidium cladophorum* DEFLANDRE – NAZAROV et al., p. 172, Fig. 5/D–F (Frasnian; Canning Basin, W-Australia).

1988 *Palaeoscenidium cladophorum* DEFLANDRE – SCHMIDT-EFFING, p. 35, Pl. 1, Fig. 11–12 (Famennian; Frankenwald, Bavaria).
1988 *Palaeoscenidium cladophorum* DEFLANDRE – ISHIGA et al., Fig. 2/j (? Frasnian; eastern Australia).
1990b *Palaeoscenidium cladophorum* DEFLANDRE – BRAUN, p. 17–18, Pl. 1, Fig. 4–5 (Late Devonian, Hembergian; Main gravels, Germany).
1990c *Palaeoscenidium cladophorum* DEFLANDRE – BRAUN, p. 135, Pl. 6, Fig. 13–14; Pl. 10, Fig. 4–7 (Early Carboniferous; Rhenish Slate Mountains and Frankenwald, Germany).
1990 ? *Palaeoscenidium cladophorum* DEFLANDRE – AITCHISON, Fig. 2 e; Fig. 3 m; Fig. i–j (Late Devonian? and Late Famennian; Gamilaroi, Djungati and Anaiwan terrane, E-Australia).
1991 *Palaeoscenidium cladophorum* DEFLANDRE – WANG, Pl. 2, Fig. 15 (Famennian; Singiang, China).
1991 *Palaeoscenidium cladophorum* DEFLANDRE – LI & WANG, Pl. 2, Fig. 18–19 (Frasnian; Guangxi, China).
1992 *Palaeoscenidium cladophorum* DEFLANDRE – AITCHISON & FLOOD, Fig. 3/7, (Latest Devonian–Early Carboniferous; eastern Australia).
1992 Unidentified radiolarian – NOBLE, Pl. 2, Fig. 12 (Early Carboniferous; Texas, USA).
1992 *Palaeoscenidium* sp. – BRAUN et al., p. 171–172, Fig. 2/6 (Famennian; Vosges, France).
1993b *Palaeoscenidium cladophorum* DEFLANDRE – AITCHISON, p. 121–122, Pl. 1, Fig. 15–17, 19; Pl. 2, Fig. 17, 20 (Frasnian; Canning Basin, W-Australia).

Remarks: As the original description of DEFLANDRE (1953) is only related to the genus, FOREMAN (1963) was the first to describe the species characteristics. The variation of the species is not known and it is uncertain whether morphotypes with only two apical spines (*P. bicorne* DEFLANDRE, nomen nudum) or basal spines without spinules which are common in our material, should be included under that species. We encompassed all these variations under the species *P. cladophorum*, because random or ecologically caused irregularities seem to be more probable. Most of the species described by AITCHISON (1993) should be included under *P. cladophorum* as well.

Occurrence: All samples with the exception of G 1 (abundant).

Pylentonemiid(?) sp. A

(Pl. 6, Fig. 23–24)

Description: Spherical, strongly perforated radiolarian with four spines. One spine in an oblique "apical" position and three "basal" curved spines surrounding a very narrow pylome(?). Even if it is not sure that the form is a nassellariid at all, it seems to be a precursor of *Pylentonema*, which may also be true for *Pylentonema insueta* NAZAROV (1975) described from the Ordovician.

Occurrence: R 3/7 (one specimen).

Acknowledgements

We express our thanks to Dr. M. JOACHMISKI for supporting us with a CAD file of the palaeogeographic map.

We are grateful to Priv.-Doz. Dr. T. STEIGER and a second anonymous reviewer for valuable comments on the paper.

Plate 1

Late Devonian Allbaillellaria and Archocyrtiidae of Rodachsrangen

Figs. 1–3: ***Huasha magnifica* CHENG.**
Lateral views on skeletal plane. Caveal ribs only partly preserved.
All specimens from sample R 3/2.
Scale bar = 50 μm.

Fig. 4: ***Ceratoikiscium bujugum* FOREMAN.**
One of the six extratriangular spines is broken.
Sample R 3/2.
Scale bar = 100 μm.

Figs. 5–6: **Caveal vans of *Ceratoikiscium extraordinarium* CHENG.**
The very typical shape of these vans allows a definite species determination even of small fragments.
Sample R 3/2.
Scale bar = 50 μm.

Fig. 7: ***Ceratoikiscium* sp. with affinity to *C. delicatum* CHENG.**
Sample R 3/2.
Scale bar = 105 μm.

Fig. 8: ***Holoeciscus formanae* CHENG.**
Very well preserved specimen.
Sample R 4/2.
Scale bar = 95 μm.

Fig. 9: ***Holoeciscus formanae* CHENG.**
Posterior view showing ventral-most pair of caveal rib (arrows).
Sample R 3/2.
Scale bar = 100 μm.

Fig. 10: ***Holoeciscus brevis* CHENG.**
With unusually long stapia spines.
Sample R 4/7.
Scale bar = 100 μm.

Fig. 11: ***Holoeciscus formanae* CHENG.**
Note pore in stapia.
Sample R 3/2.
Scale bar = 100 μm.

Fig. 12: ***Holoeciscus* cf. *formanae* CHENG.**
With very long spines on stapia.
Sample R 3/2.
Scale bar = 100 μm.

Fig. 13: **Transitional form between *Holoeciscus formanae* CHENG and *H. elongatus* n.sp.**
Sample R 4/7.
Scale bar = 100 μm.

Figs. 14–17: ***Holoeciscus elongatus* n.sp.**
Figs. 14–15: holotype.
Figs. 16–17: paratype.
Samples R 4/2 and R 3/2, respectively.
Scale bar = 100 μm.

Fig. 18: ***Holoeciscus* sp. A.**
Note rather spongy stapia and narrow spacing of aperture spines.
Sample 4/7.
Scale bar = 100 μm.

Figs. 19–20: ***Holoeciscus* ssp.**
Samples R 4/2 and R 5/3, respectively.
Scale bar = 100 μm.

Fig. 21: ***Archocyrtium* cf. *angulosum* DEFLANDRE.**
Sample R 3/6.
Scale bar = 50 μm.

Figs. 22–23: ***Archocyrtium* cf. *delicatum* CHENG.**
Samples R 5/3 and R 4/7, respectively.
Scale bar = 50 μm.

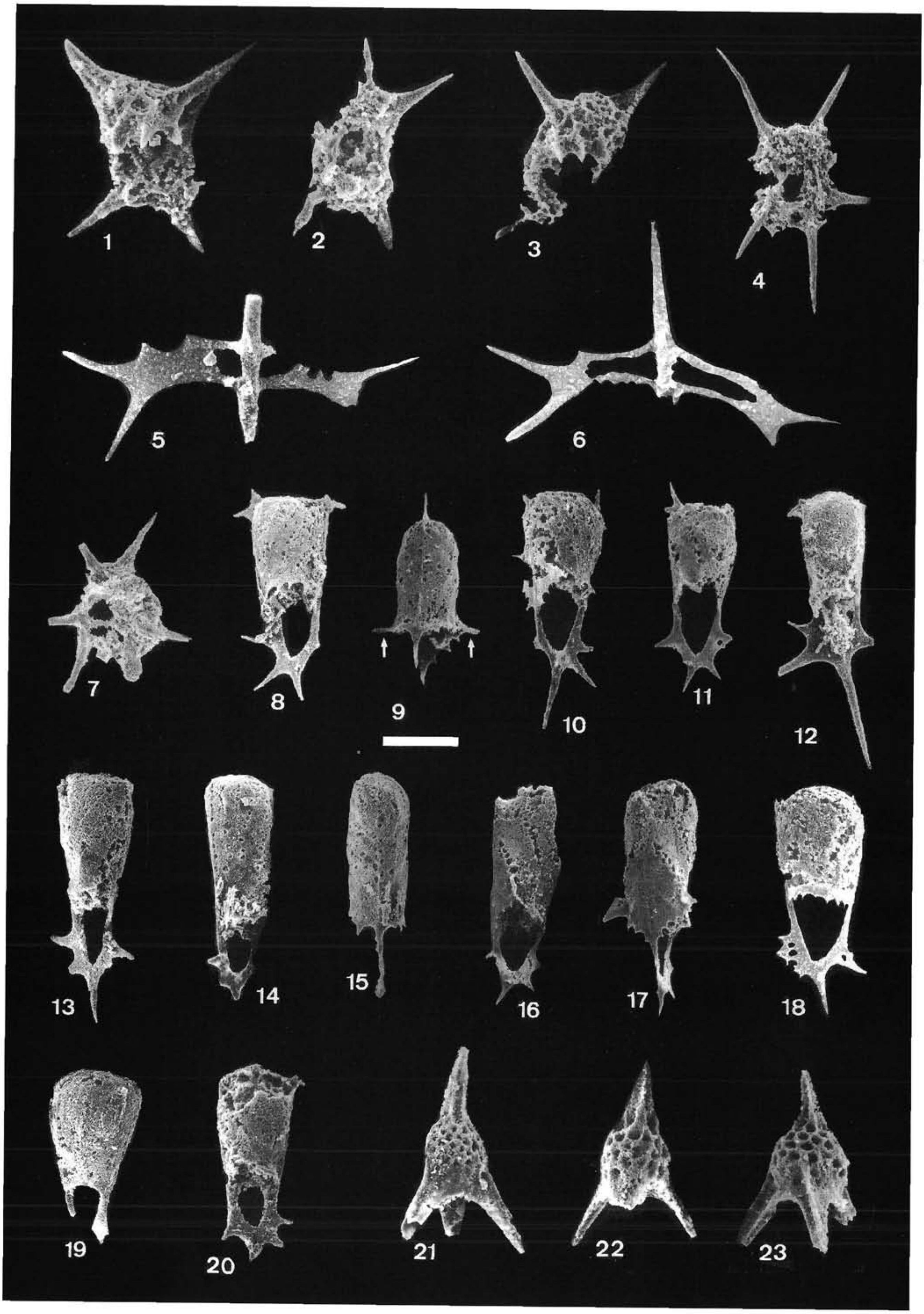

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Plate 2

Late Devonian Archocyrtiidae of Rodachsrangen

Fig. 1: ***Archocyrtium dilatipes* DEFLANDRE.**
Note massive subparallel feet, apical horn and general angular appearance.
Sample R 5/2.
Scale bar = 50 μm.

Fig. 2: ***Archocyrtium diductum* DEFLANDRE.**
Sample R 3/2.
Scale bar = 50 μm.

Fig. 3: ***Archocyrtium* cf. *riedeli* DEFLANDRE.**
Sample R 4/2.
Scale bar = 50 μm.

Fig. 4: ***Archocyrtium wonae* CHENG.**
Sample R 4/2.
Scale bar = 50 μm.

Fig. 5: ***Archocyrtium* sp.aff. *A. formosum* CHENG.**
Sample R 3/2.
Scale bar = 25 μm.

Fig. 6: ***Archocyrtium(?) formosum* CHENG.**
Note tiny spines on cephalis.
Sample R 3/7.
Scale bar = 35 μm.

Fig. 7: ***Archocyrtium eupectum* BRAUN.**
Note straight basal margin of podome-wall.
Sample R 3/2.
Scale bar = 55 μm.

Fig. 8: ***Archocyrtium* sp.aff. *A. typicum* CHENG.**
Sample R 3/2.
Scale bar = 50 μm.

Figs. 9–10: ***Archocyrtium* cf. *delicatum* CHENG.**
Samples R 4/6 and R 3/2, respectively.
Scale bar = 50 μm and 35 μm.

Figs. 11–13: ***Archocyrtium ludicrum* DEFLANDRE group.**
Samples R 4/7, R 3/3 and R 3/3, respectively.
Scale bar = 50 μm.

Figs. 14–15: ***Archocyrtium effingi* n.sp.**
Fig. 14: Paratype.
Fig. 15: Holotype.
Samples R 4/2 and R 3/2, respectively.
Scale bar = 50 μm.

Fig. 16: ***Archocyrtium* sp. C.**
Sample R 5/2.
Scale bar = 50 μm.

Figs. 17–18: ***Archocyrtium* ssp.**
Samples R 4/2 and R 3/6, respectively.
Scale bar = 50 μm.

Figs. 19–20: ***Archocyrtium* sp. B.**
Samples R 3/2 and R 4/2, respectively.
Scale bar = 50 μm.

Fig. 21: ***Archocyrtium* sp. A.**
Sample R 3/3.
Scale bar = 50 μm.

Figs. 22–24: ***Cerarchocyrtium* ssp.**
Samples R 5/3, R 3/2 and R 3/3, respectively.
Scale bar = 50 μm for Figs. 22–23, 45 μm for Fig. 24.

Fig. 25: ***Cerarchocyrtium* sp.aff. *Archocyrtium ludicrum* DEFLANDRE.**
Sample R 3/3.
Scale bar = 45 μm.

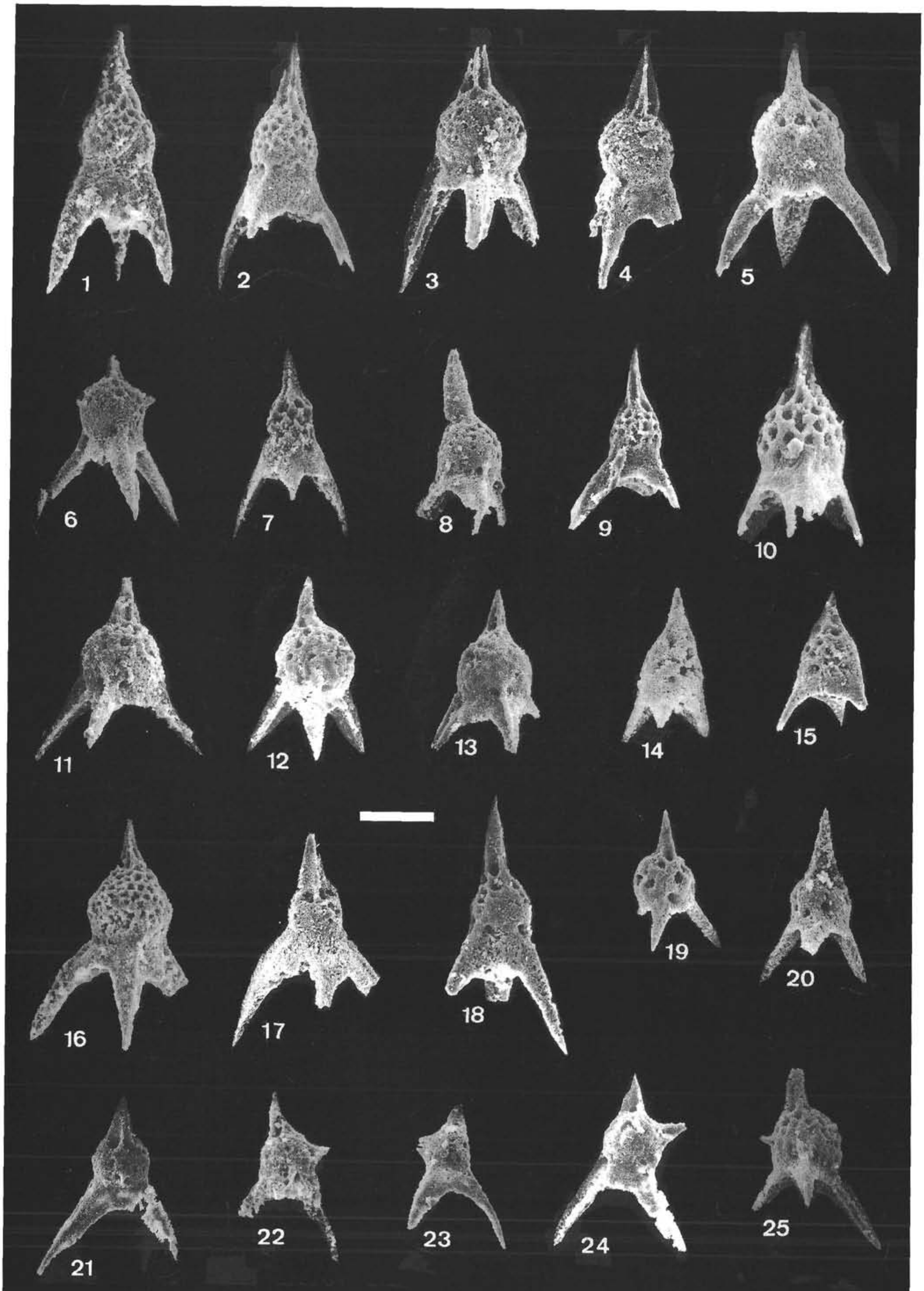

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Plate 3

Late Devonian Archocyrtiidae, Pylentomidae and Popofskyellidae from Rodachsrangen

Figs. 1–6: ***Cyrtisphaeractenium(?) fluegeli* n.sp.**
Figs. 1–2: holotype; Figs. 3,6: paratypes.
Fig. 1: Stereo- image of lateral view.
Fig. 2: Oblique apical view of the same specimen showing perforated cephalis, normally covered by microgranular quartz.
Fig. 3: Lateral view of paratype.
Fig. 4: 'Abnormal' morphotype with angular outline and massive feet.
Fig. 5: Same specimen in an oblique apical view.
Fig. 6: Oblique lateral view of second paratype. Arrows indicate second cephalic spine whose position is very variable, ranging from almost podominal (Figs. 1–3) to subapical (Figs. 4).
Samples R 4/2, R 4/7, R 3/3 and R 3/3, respectively.
Scale bar = 45 μm for Fig. 1 and 50 μm for Figs. 2–6.

Fig. 7: ***Cyrtisphaeractenium(?)* sp.aff. *Archocyrtium validum*.**
Sample R 5/4.
Scale bar = 50 μm.

Fig. 8: ***Cyrtisphaeractenium(?)* sp. A.**
Very small Archocyrtiid.
Sample R 4/2.
Scale bar = 25 μm!

Figs. 9–10: ***Deflandrellium* sp. A.**
Fig. 9: Lateral view.
Fig. 10: Oblique basal view.
Sample R 3/3.
Scale bar = 50 μm.

Figs. 11–12: ***Robotium* sp. B.**
Fig. 11: Lateral view.
Fig. 12: Antapical view.
Sample R 4/7.
Scale bar = 50 μm for Fig. 11 and 33 μm for Fig. 12.

Fig. 13: ***Robotium* sp. A.**
Sample R 4/2.
Scale bar = 50 μm.

Fig. 14: ***Robotium* sp. C.**
Sample R 4/7.
Scale bar = 50 μm.

Figs. 15,18: **Archocyrtiid sp. A.**
Fig. 15: Lateral view.
Fig. 18: Oblique apical view with four subapical spines arranged at right angles.
Sample R 4/7.
Scale bar = 50 μm.

Figs. 16–17: **Archocyrtiid sp. B.**
Fig. 16: Oblique antapical view.
Fig. 17: Lateral view.
Sample R 4/2.
Scale bar = 52 μm.

Fig. 19: ***Deflandrellium* sp. B.**
Note pylentomiid appearance.
Sample 4/2.
Scale bar = 33 μm.

Fig. 20: ***Pylentonema* cf. *hindei* CHENG.**
Sample R 3/3.
Scale bar = 50 μm.

Fig. 21: **Archocyrtiid sp. C.**
Sample R 4/2.
Scale bar = 33 μm.

Fig. 22: **Poorly preserved *Cyrtentactinia* cf. *formosa* CHENG.**
Sample R 3/7.
Scale bar = 50 μm.

Fig. 23: ***Popofskyellum* sp. cf. *Kantollum(?) blancoensis* CHENG.**
Sample R 3/2.
Scale bar = 50 μm.

Figs. 24–25: **Proximal portions of *Popofskyellum* cf. *annulatum* DEFLANDRE.**
Samples R 3/7 and R 3/2.
Scale bar = 50 μm.

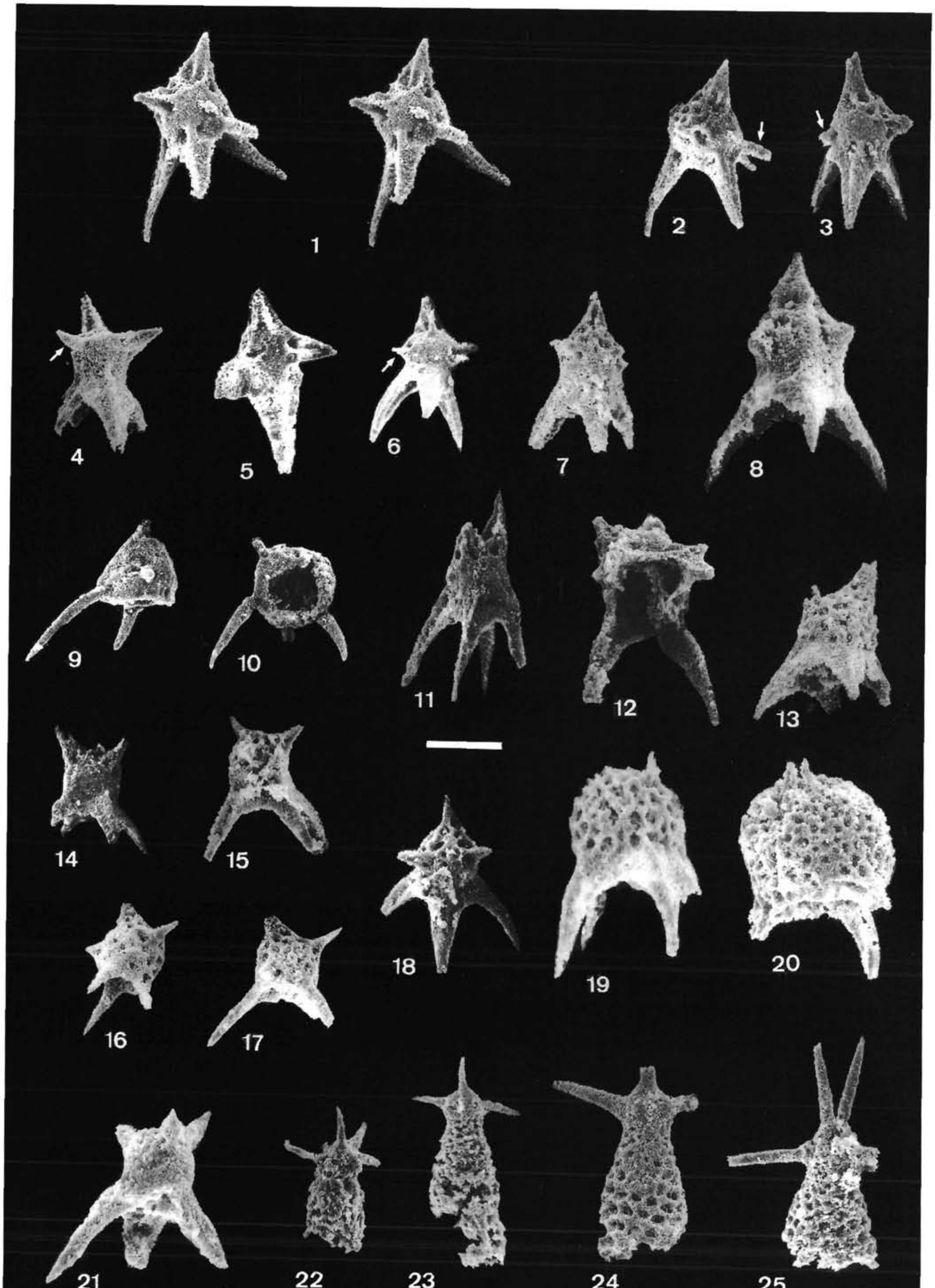

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Plate 4

Late Devonian Popofskyellidae and Middle and Late Devonian Entactiniidae

Figs. 1–2: ***Popofskyellum deflandrei*** **CHENG.**
Fig. 2 showing well developed lateral rod.
Samples R 3/7 and R 4/2, respectively.
Scale bar = 50 μm.

Fig. 3: ***Popofskyellum*** **sp.aff.** ***P. undulatum*** **DEFLANDRE.**
Sample R 3/2.
Scale bar = 50 μm.

Fig. 4: ***Astroentactinia radiata*** **BRAUN.**
Sample R 3/6.
Scale bar = 50 μm.

Fig. 5: ***Astroentactinia*** **sp.aff.** ***A. paronae*** **(HINDE).**
Sample G 2/7.
Scale bar = 100 μm.

Fig. 6: ***Astroentactinia biaciculata*** **NAZAROV.**
Sample R 3/3.
Scale bar = 50 μm.

Fig. 7: ***Astroentactinia stellata*** **NAZAROV.**
Sample R 3/3.
Scale bar = 100 μm.

Figs. 8,10: **Different specimens of** ***Astroentactinia*(?) sp. A.**
Sample G 2/7.
Scale bar = 100 μm.

Fig. 9: ***Astroentactinia digitosa*** **BRAUN.**
Sample R 4/7.
Scale bar = 100 μm.

Fig. 11: ***Astroentactinia multispinosa*** **WON.**
Sample R 3/3.
Scale bar = 100 μm.

Fig. 12: **Rare specimen of** ***Entactinia herculea*** **FOREMAN with well preserved by-spines.**
Sample R 3/3.
Scale bar = 55 μm.

Fig. 13: ***Entactinia additiva*** **FOREMAN sensu NAZAROV & ORMISTON.**
Sample 3/3.
Scale bar = 100 μm.

Fig. 14: ***Entactinia*(?)** ***pantotolma*** **BRAUN.**
Sample R 3/3.
Scale bar = 55 μm.

Fig. 15: ***Entactinia spongites*** **FOREMAN.**
Sample G 2/7.
Scale bar = 100 μm.

Fig. 16: ***Entactinia exilispina*** **FOREMAN.**
Note big size and thick spongy layer.
Sample R 2/1.
Scale bar = 135 μm!

Figs. 17–18: ***Entactinia tortispina*** **(ORMISTON & LANE) group.**
Two very different morphotypes are figured.
Samples R 3/7 and R 3/2, respectively.
Scale bar = 100 μm.

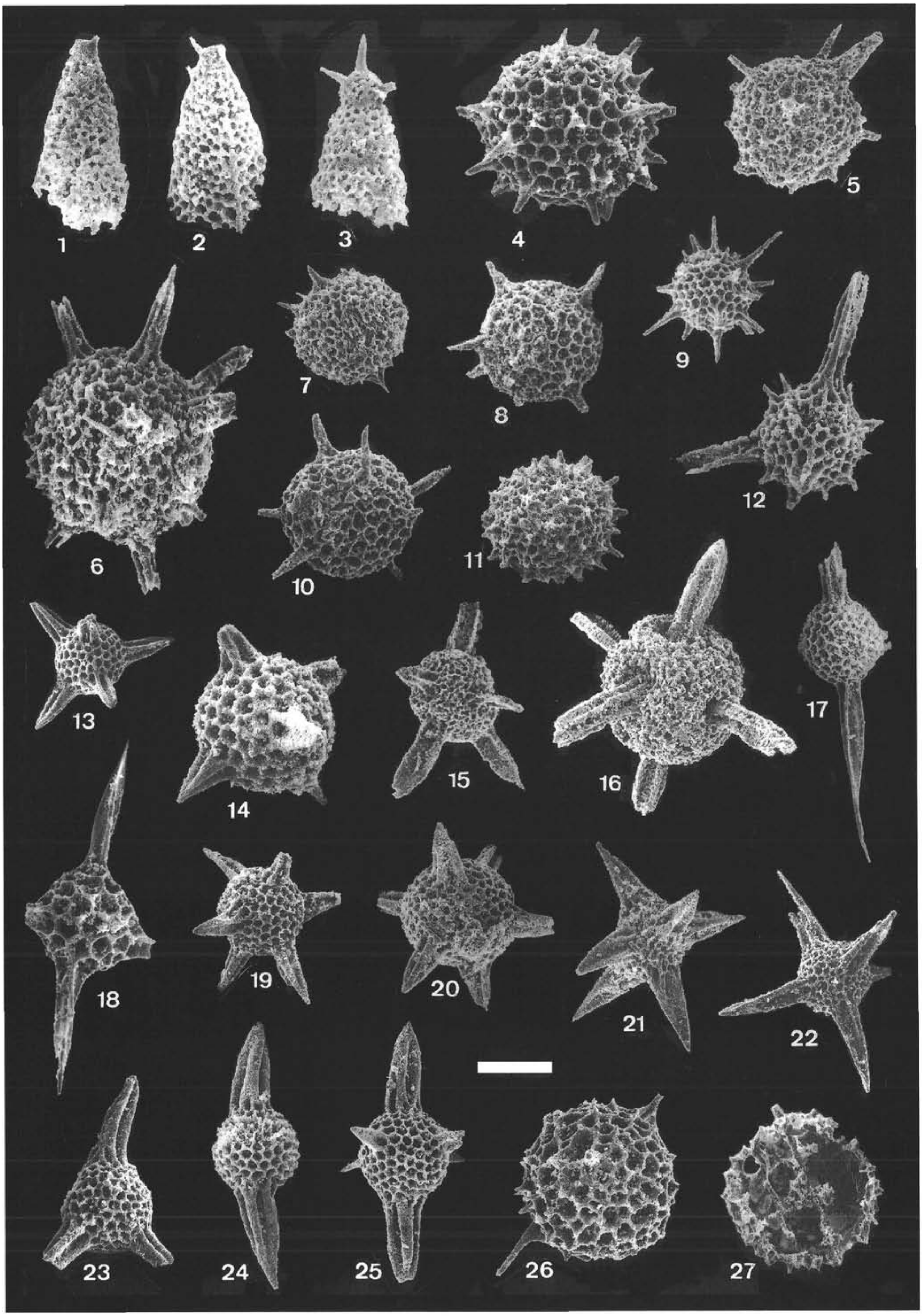
Figs. 19–20: ***Entactinia vulgaris*** **WON.**
The two morphotypes figured can be designated to the subspecies *E. v. vulgaris* WON and *E. v. microporata* BRAUN. But continuous transitions do not support this distinction.
Samples R 3/6 and R 3/2, respectively.
Scale bar = 100 μm.

Figs. 21–22: ***Entactinia herculea*** **FOREMAN.**
Samples R 4/6 and R 3/7, respectively.
Scale bar = 100 μm.

Figs. 23–24: ***Entactinia variospina*** **(WON) group.**
The two morphotypes figured show the possible morphological variation of that species group.
Samples R 3/3 and R 3/8, respectively.
Scale bar = 100 μm.

Fig. 25: ***Entactinosphaera*(?)** ***aitpaiensis*** **NAZAROV.**
Note similarity to *E. variospina* in Fig. 24.
Sample R 3/3.
Scale bar = 100 μm.

Figs. 26–27: ***Entactinosphaera fredericki*** **FOREMAN.**
Fig. 26: Complete specimen of inner sphere.
Fig. 27: Broken specimen of inner sphere exposing the well developed internal spicule.
Samples R 3/6 and R 4/7, respectively.
Scale bar = 100 μm.



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27

Plate 5

Middle and Late Devonian Entactiniidae

Fig. 1: ***Entactinosphaera riedeli*** **FOREMAN.**
Broken specimen showing intermediate and inner sphere and internal spines. Note rosettes of larger pores surrounding each of the main spines.
Sample R 4/7.
Scale bar = 100 μm.

Figs. 2,4–5: ***Entactinosphaera palimbola*** **FOREMAN group.**
Different specimens showing the whole range of morphological variation. Note the characteristic ragged edges of pores in Figs. 2 and 4.
Fig. 2: Morphotype with slender main spine and small by-spines.
Fig. 4: Specimen with relatively short but very robust main spines, three preserved secondary spines and plenty of by-spines.
Fig. 5: Form with a twisted main spine.
Samples R 3/7, R 4/6 and R 3/7, respectively.
Scale bar = 100 μm.

Fig. 3: ***Entactinosphaera*(?) sp.aff. *E. palimbola*** **FOREMAN.**
Note relatively small size and large pores.
Sample R 5/4.
Scale bar = 100 μm.

Fig. 6: ***Entactinosphaera*** **sp.**
With four short robust spines in a plane.
Sample R 4/7.
Scale bar = 50 μm.

Fig. 7: Cf. ***Entactinosphaera symphypora*** **FOREMAN.**
Sample R 5/4.
Scale bar = 100 μm.

Figs. 8–9: ***Polyentactinia fenestrata*** **(HINDE).**
Note weak attachment of larger spines on shell surface.
Samples R 3/6 and R 3/7, respectively.
Scale bar = 100 μm.

Fig. 10: ***Polyentactinia aranea*** **GOURMELON.**
Sample R 3/2.
Scale bar = 100 μm.

Fig. 11: ***Polyentactinia craticulata*** **FOREMAN.**
Sample R 4/7.
Scale bar = 100 μm.

Fig. 12: ***Polyentactinia*(?) sp. A.**
Sample R 3/7.
Scale bar = 100 μm.

Fig. 13: ***Polyentactinia*(?) sp. B.**
Sample R 3/2.
Scale bar = 100 μm.

Fig. 14: ***Polyentactinia*(?) sp. C.**
Sample G 2/7.
Scale bar = 100 μm.

Fig. 15: ***Polyentactinia*(?) *perampla*** **BRAUN, MAASS & SCHMIDT-EFFING.**
Sample R 3/7.
Scale bar = 100 μm.

Figs. 16–17: ***Tetrentactinia spinulosa*** **n.sp.**
Fig. 16: Holotype.
Fig. 17: Paratype.
Sample R 3/2.
Scale bar = 100 μm.

Figs. 18–19: ***Tetrentactinia teuchestes*** **FOREMAN.**
Note size variation.
Sample R 2/1.
Scale bar = 100 μm.

Fig. 20: ***Triaenosphaera*** **sp. A.**
Sample R 5/2.
Scale bar = 50 μm.

Figs. 21–22: ***Triaenosphaera sicarius*** **DEFLANDRE.**
Samples R 3/6 and R 4/6, respectively.
Scale bar = 100 μm.

Figs. 23–24: **Entactiniid sp. group I.**
Samples R 4/7 and R 3/2, respectively.
Scale bar = 100 μm.

Fig. 25: ***Triaenosphaera hebes*** **WON.**
Sample R 3/2.
Scale bar = 100 μm.

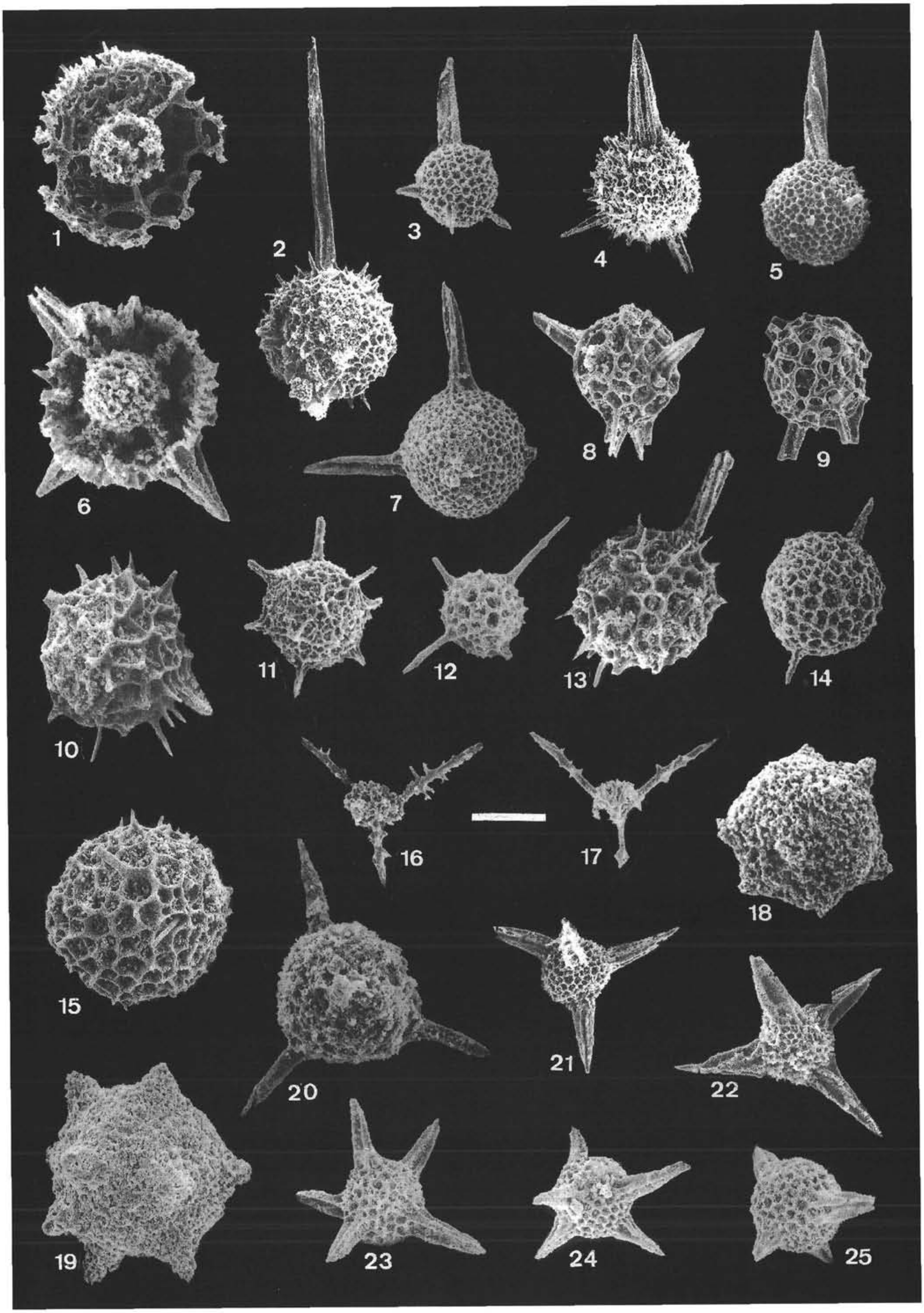

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Plate 6

Entactiniidae and radiolarians of uncertain affinity

Figs. 1–2: **Entactiniid ssp. group II.**
Samples R 3/2 and R 3/7, respectively.
Scale bar = 100 μm.

Fig. 3: **Entactiniid ssp. group III.**
Sample R 3/2.
Scale bar = 100 μm.

Figs. 4,8: ***Bisyllentactinia arrhinia* (FOREMAN).**
Only the first group of spinules is preserved.
Samples 4/6 and R 3/7.
Scale bar = 50 μm.

Figs. 5–7,9–10: ***Palaeoscenidium cladophorum* DEFLANDRE.**
Note strong variability of species.
Samples R 2/1, R 5/2, G 2/5, G 2/7, R 3/6, respectively.
Scale bar = 100 μm for Figs. 5, 6 and 9, 50 μm for Figs. 7 and 10.

Fig. 11: ***Palaeoscenidium* sp. of Early Devonian sample G 1/4.**
Scale bar = 50 μm.

Fig. 12: ***Staurostylus* sp. A.**
Note opposite pair of spines being considerably smaller than the other.
Sample R 4/7.
Scale bar = 50 μm.

Figs. 13–14: ***Staurodruppa*(?) sp.**
Samples G 2/7 and G 2/5, respectively.
Scale bar = 100 μm.

Fig. 15: ***Stauroplegma*(?) *xiphophorus* (RÜST).**
Undated Devonian sample 30/33 (?Adorf stage).
Scale bar = 100 μm.

Fig. 16: ***Stauroplegma* sp. A.**
Sample R 4/7.
Scale bar = 100 μm.

Fig. 17: ***Ceratoikiscum(?)* sp.**
Note very small size.
Sample R 5/2.
Scale bar = 50 μm.

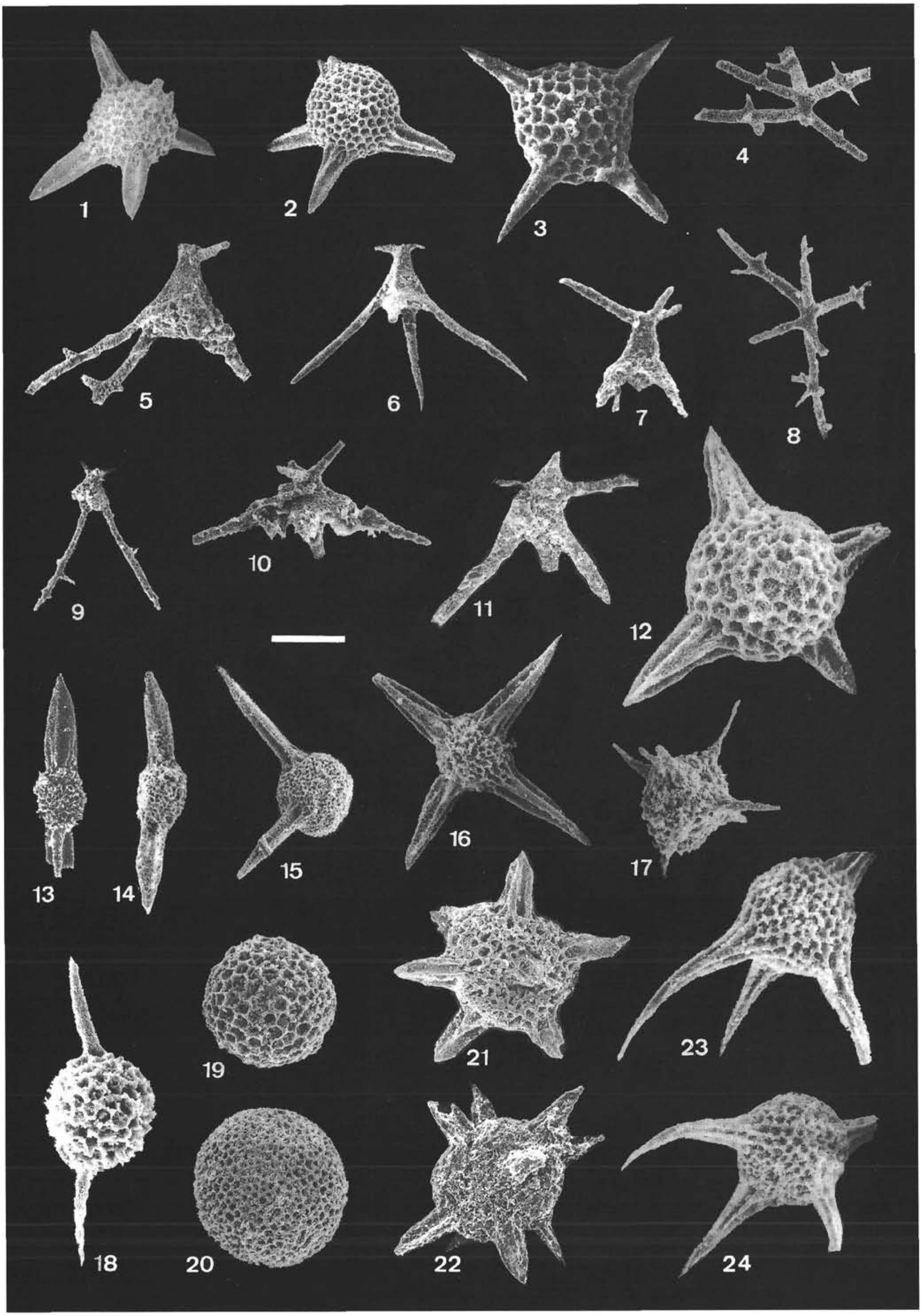
Fig. 18: **Problematic spheroidal radiolarian with two polar spines.**
Sample R 4/2.
Scale bar = 50 μm.

Fig. 19: **Spineless sphere sp. B.**
Sample G 2/3.
Scale bar = 100 μm.

Fig. 20: **Spineless sphere sp. A.**
Sample R 3/7.
Scale bar = 100 μm.

Figs. 21–22: **Early Devonian spheroidal radiolarians with robust three-bladed spines.**
Fig. 21: Sphere with 8 spines.
Fig. 22: Sphere with 10 spines.
Sample G 1/4.
Scale bar = 100 μm.

Figs. 23–24: **Pylentommiid(?) sp. A.**
Fig. 23: Lateral view with massive 'subapical' spine.
Fig. 24: 'Antapical' view.
Note larger pore (pylome?) on Fig. 24.
Sample R 3/7.
Scale bar = 45 μm for Fig. 23 and 50 μm for Fig. 24.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

References

AITCHISON, J.C. (1988): Late Paleozoic radiolarian ages from Gwydir terrane, New England orogen, eastern Australia. – Geology, **16**, 793–795, Boulder.

AITCHISON, J.C. (1990): Significance of Devonian–Carboniferous radiolarians from accretionary terranes of the New England orogen, Eastern Australia. – Marine Micropaleont., **15**, 365–378, Amsterdam.

AITCHISON, J.C. (1993a): Albaillellaria from the New England orogen, Eastern NSW, Australia. – Marine Micropaleont., **21**, 353–367, 1 Pl., Amsterdam.

AITCHISON, J.C. (1993b): Devonian (Frasnian) radiolarians from the Gogo Formation, Canning Basin, Western Australia. – Palaeontographica, **228**, 105–128, 7 Pl., Stuttgart.

AITCHISON, J.C. & FLOOD, P.G. (1992): Implications of radiolarian research for analysis of subduction complex terranes in the New England Orogen, NSW, Australia. – Palaeogeogr., Palaeoclimatol., Palaeoecol., **96**, 89–102, Amsterdam.

AITCHISON, J.C., FLOOD, P.G. & SPILLER, F.C.P. (1992): Tectonic setting and paleoenvironment of terranes in the southern New England orogen, eastern Australia as constrained by radiolarian biostratigraphy. – Paleogeogr., Palaeoclimatol., Palaeoecol., **94**, 31–54, Amsterdam.

BEHR, H.J., ENGEL, W. & FRANKE, W. (1982): Variscan Wildflysch and nappe tectonics in the Saxothuringian Zone (Northeast Bavaria, West Germany). – Amer. J. Sci., **282**, 1438–1470, New Haven.

BENDER, P., BRAUN, A. & KÖNIGSHOF, P. (1991): Radiolarien und Conodonten aus unterkarbonischen Kieselkalken und Kieselschiefern des nördlichen Rheinischen Schiefergebirges. – Geologica et Palaeontologica, **25**, 87– 97, 2 Pl., Marburg.

BISCHOFF, G. & ZIEGLER, W. (1957): Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. – Abh. Hess. L.A. Bodenforsch., **22**, 1–136, 21 Pl., Wiesbaden.

BRAUN, A. (1989a): Unterkarbonische Radiolarien aus Kieselschiefergeröllen des Mains bei Frankfurt am Main. – Jber. Mitt. oberrhein. geol. Ver., N.F. **71**, 357–380, Stuttgart.

BRAUN, A. (1989b): Neue unterkarbonische Radiolarien-Taxa aus Kieselschiefergeröllen des unteren Maintales bei Frankfurt a.M. – Geologica et Palaeontologica, **23**, 83–99, 2 Pl., Marburg.

BRAUN, A. (1989c): Eine Radiolarien-Fauna aus dem Ober-Viseum des Dinant-Beckens. – Geologica et Palaeontologica, **23**, 101–111, 3 Pl. Marburg.

BRAUN, A. (1990a): Evolutionary tendencies and biostratigraphic potential of selected radiolarian taxa from the Early Carboniferous of Germany. – Marine Micropaleont., **15**, 351–364, 2 Pl., Amsterdam.

BRAUN, A. (1990b): Oberdevonische Radiolarien aus Kieselschiefer-Geröllen des unteren Maintales bei Frankfurt a.M. – Geol. Jb. Hessen, **118**, 5–27, 2 Pl., Wiesbaden.

BRAUN, A. (1990c): Radiolarien aus dem Unter-Karbon Deutschlands. – Cour. Forsch. Inst. Senckenberg, **133**, 1–143, 17 Pl., Frankfurt.

BRAUN, A. & AMON, E.O. (1991): Fluoritisierte Radiolarien aus Kieselkalk-Bänken der Mittel-Viseums (Unterkarbon) des Rheinischen Schiefergebirges (Deutschland). – Paläont. Zeitschr., **65**/1–2, 25–33, Stuttgart.

BRAUN, A., MAASS, R. & SCHMIDT-EFFING, R. (1992): Oberdevonische Radiolarien aus dem Breuschtal (Nord-Vogesen, Elsaß) und ihr regionaler und stratigraphischer Zusammenhang. – N. Jahrb. Geol. Paläont. Abh., **185**, 161–178, Stuttgart.

BRAUN, A. & SCHMIDT-EFFING (1988): Radiolarienfaunen aus dem tiefen Visé (Unterkarbon) des Frankenwaldes (Bayern). – N. Jb. Geol. Paläont. Mh., **1988**/11, 645–660, Stuttgart.

BRAUN, A. & SCHMIDT-EFFING, R. (1993): Biozonation, diagenesis and evolution of radiolarians in the Lower Carboniferous of Germany. – Marine Micropaleont., **21**, 369–383, 3 Pl., Amsterdam.

CHENG, Y.-N. (1986): Taxonomic Studies on Upper Paleozoic Radiolaria. – National Museum Natural Sci. (Spec. Publ.), **1**, 1–311, 41 Pl., Taichung, Taiwan.

DEFLANDRE, G. (1953): Radiolaires fossiles. – In: GRASSÉ, P.P.: Traité de Zoologie, vol. 1, pt. 2, 398–436, Paris (Masson et Cie.).

DEFLANDRE, G. (1960): A propos du dévelopment des recherches sur les Radiolaires fossiles. – Rev. Micropaléont., **2**, 212–218, 1 Pl., Paris.

DEFLANDRE, G. (1963): *Pylentonema*, nouveau genre de Radiolaire du Viséen: Sphaerellaire ou Nassellaire? – Comptes Rend. Acad. Sciences, **257**, 3981–3984, Paris.

DEFLANDRE, G. (1964): La famille des Popofskyellidae fam. nov. et le genre *Popofskyellum* DEFL., Radiolaires viséens de la Montagne Noire. – Comptes Rend. Acad. Sci., **259**, 3055–3058, Paris.

DEFLANDRE, G. (1972a): Le système trabeculaire interne chez les Pylentonémidés et les Popofskyellidés, Radiolaires du Paléozoique. Phylogenèse des Nasselaires. – Comptes Rend. Acad. Sci., **274**, 3535–3540, 4 Pl., Paris.

DEFLANDRE, G. (1972b): Remarques complementaires sur la morphologie et la nomenclature de quelques genres de Radiolaires du Paléozoique. – Comptes Rend. Acad. Sci., **275**, 13–16, Paris.

DEFLANDRE, G. (1973): Sur quelques nouvelles espèces d'*Archocyrtium*, Radiolaires Pylentonemidae du Viséen de Cabrières. – Comptes Rend. Acad. Sci., **277**, 149–156, 4 Pl., Paris.

FOREMAN, H.P. (1963): Upper Devonian Radiolaria from the Huron Member of the Ohio Shale. – Micropaleont., **9**, 267–304, 9 Pl., New York.

FURUTANI, H. (1990): Middle Paleozoic Radiolarians from Fukuji Area, Gifu Prefecture, Central Japan. – J. Earth Sci. Nagoya Univ., **37**, 1–56, 14 Pl., Nagoya.

GANDL, J. (1992): Zur Faziesentwicklung im jüngeren Paläozoikum NE-Bayerns. – Zentralblatt Geol. Paläont., Teil 1, **1992**, 21–43, Stuttgart.

GIESE, M. & SCHMIDT-EFFING, R. (1989): Eine Radiolarienfauna aus dem Unter-Karbon von Amönau bei Wetter (Rheinisches Schiefergebirge/Hessen). – Geologica et Palaeontologica, **23**, 71–81, 2 Pl., Marburg.

GOURMELON, F. (1986): Etude des Radiolaires d'un Nodule Phosphaté du Caronifère inférieur de Bareilles, Hautes Pyrenées, France. – Geobios, **19**, 179–197, 4 Pl., Lyon.

GOURMELON, F. (1987): Les Radiolaires Tournaisiens des Nodules Phosphatés de la Montagne Noire et des Pyrenées Centrales. – Biostratigraphie du Paléozoique, **6**, 1–172, 22 Pl., Brest.

GOURMELON, F. (1988): Découverte de Radiolaires dans un niveau à nodules phosphatés du Carbonifère de la région de Bèchar (Sahara algérien). – Géologie Méditerranéenne, **XIII**, 185–195, 1 Pl., Aix-en-Provence.

HINDE, G.J. (1899): On the Radiolaria in the Devonian rocks of New South Wales. – Quarterly Journ. Geol. Soc. London, **55**, 38–64, 2 Pl., London.

HOLDSWORTH, B.K. (1966): A preliminary study of the paleontology and paleoenvironment of some Namurian limestone "bullions". – Mercian Geologist, **1**, 315–377, 3 Pl., Nottingham.

HOLDSWORTH, B.K. (1977): Paleozoic Radiolaria: Stratigraphic Distribution in Atlantic Borderlands. – In: SWAIN, F.M. (ed.): Stratigraphic micropaleontology of Atlantic Basin and Borderlands, Developments in Paleont. and Stratigr., **6**, 167–184, 2 Pl., Amsterdam (Elsevier).

HOLDSWORTH, B.K. & JONES, D.L. (1980): Preliminary radiolarian zonation for Late Devonian through Permian time. – Geology, **8**, 281–285, Boulder.

HOLDSWORTH, B.K., JONES, D.L. & ALLISON, C. (1978): Upper Devonian Radiolaria separated from chert of the Ford Lake Shale, Alaska. – Journ. Res. U.S. Geol. Survey, **6**, 775–788, Washington.

HOLDSWORTH, B.K. & MURCHEY, B.L. (1988): Paleozoic radiolarian biostratigraphy of the northern Brooks Range, Alaska. – In: GRYC, G. (ed.): Geology and exploration of the national petroleum reserve in US, Geol. Surv. Prof. Pap., **1399**, 777–792, 2 Pl., Washington.

ISHIGA, H., LEITCH, E.C., NAKA, T., WATANABE, T. & IWASAKI, M. (1987): Late Devonian Paleoscenidiidae from the Hastings Block, New England Fold Belt, N.S.W., Australia. – Earth Sciences (Chikyu Kagaku), **71**, 297–302, 2 Pl., Chikyu Kagaku.

ISHIGA, H., LEITCH, E.C., WATANABE, T., NAKA, T. & IWASAKI, M. (1988): Radiolarian and conodont biostratigraphy of siliceous rocks from the New England Fold Belt. – Aust. Journ. Earth Sciences, **35**, 73–80, Sydney.

JENKYNS & WINTERER (1982): Palaeooceanography of Mesozoic ribbon radiolarites. – Earth and Planetary Science Letters, **60**, 351–372, Amsterdam.

KÖNIGSHOF, P. & PIEC, M. (1991): Stratigraphische Reichweiten *oberdevonischer Conodonten – eine Übersichtstabelle.* – Jahrb. Geol. B.-A., **134**, 735–736, 1 Pl., Wien.

LI, Y.-X. & WANG Y.-J. (1991): Upper Devonian (Frasnian) radiolarian fauna from the Luozigou basin, Wangqing county, Jilin. – Acta Micropalaeont. Sinica, **8**, 395–404, 2 Pl., Nanjing.

NAZAROV, B.B. (1975): Radiolaria of the Lower–Middle Paleozoic of Kazakhstan. – Trudy geol. Inst. Akad. Nauk SSR, **275**, 1–202, 21 Pl., Moscow.

NAZAROV, B.B., COCKBAIN, A.E. & PLAYFORD, P.E. (1982): Late Devonian Radiolaria from the Gogo Formation, Canning Basin, Western Australia. – Alcheringa, **6**, 161–173, Sydney.

NAZAROV, B.B. & ORMISTON, A.R. (1983): Upper Devonian (Frasnian) radiolarian fauna from the Gogo Formation, Western Australia. – Micropaleont., **29**, 454–466, 2 Pl., New York.

NAZAROV, B.B. & ORMISTON, A.R. (1985): Evolution of Radiolaria in the Paleozoic and its correlation with the development of other marine fossil groups. – Senckenbergiana lethaea, **66**, 203–215, Frankfurt.

NAZAROV, B.B. & ORMISTON, A.R. (1986): Trends in the development of Paleozoic Radiolaria. – Marine Micropaleont., **11**, 3–32, 7 Pl., Amsterdam.

NAZAROV, B.B. & ORMISTON, A.R. (1988): The Biostratigraphic Potential of Paleozoic Radiolaria. – First International Conference on Paleozoic Radiolaria (EURORAD V), Abstracts, Geol. et Pal. **22**, 200, Marburg.

NOBLE, P. (1992): Biostratigraphy of the Caballos Novaculite-Tesnus Formation boundary, Marathon Basin, Texas. – Palaeogeogr., Palaeoclimatol., Palaeoecol., **96**, 141–153, 2 Pl., Amsterdam.

ORMISTON, A.R. & LANE, H.R. (1976): *A unique radiolarian fauna* from the Sycamore Limestone (Mississippian) and its biostratigraphic significance. – Palaeontographica, Abt. A, **154**, 158–180, 6 Pl., Stuttgart.

PESSAGNO, E.A.jr. & NEWPORT, R.L. (1972): A technique for extracting Radiolaria from radiolarian cherts. – Micropaleont., **18**, 231–234, New York.

RÜST, D. (1892): Beiträge zur Kenntnis der fossilen Radiolarien aus Gesteinen der Trias und der palaeozoischen Schichten. – Palaeontogaphica, Abt. A, **38**, 107–192, 25 Pl., Stuttgart.

SCHMIDT-EFFING, R. (1988): Eine Radiolarien-Fauna des Famenne (Ober-Devon) aus dem Frankenwald. – Geol. et Palaeont., **22**, 33–41, 3 Pl., Marburg.

SCOTESE, C.R. & MCKERROW, W.S. (1990): Revised world maps and introduction. – In: MCKERROW, W.S. & SCOTESE, C.R. (eds.): Palaeozoic palaeogeography and biogeography, Geol. Soc. London, Memoir, **12**, 1–21, London.

SUESS, F.E. (1912): Vorläufige Mitteilung über die Münchberger Deckscholle. – Sitzber. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. IIa, **121**/10, 253, Wien.

TRAGELEHN, H. (1993): „Bayerisches" contra „Thüringisches" Devon des Frankenwaldes – Fazies-Übergänge oder Fazies-Analogien? – 63th meeting Paläontologische Gesellschaft, abstracts, p. 21, Prague.

WAKAMATSU, G.K., SUGIYMA, K. & FURUTANI, H. (1990): Silurian and Devonian radiolarians from the Kurosegawa Tectonic Zone, southwest Japan. – J. Earth Sciences, Nagoya Univ., **37**, 159–194, 13 Pl., Nagoya.

WANG, Y.-J. (1991): On progress in the study of Paleozoic radiolarians in China. – Acta Micropalaeont. Sinica, **8**, 237–252, 4 Pl., Nanjing.

WEDDIGE, K. (1977): Die Conodonten der Eifel-Stufe im Typusgebiet und in benachbarten Faziesgebieten. – Senckenbergiana Laethea, **58**, 271–419, 6 Pl., Frankfurt.

WON, M.-Z. (1983): Radiolarien aus dem Unterkarbon des Rheinischen Schiefergebirges (Deutschland). – Palaeontographica, Abt. A, **182**, 116–175, 14 Pl., Stuttgart.

WURM, A. (1925): Geologie von Bayern, 1 (Nordbayern, Fichtelgebirge und Frankenwald). – Handb. Geol. u. Bodensch. Deutschlands, II. Abt., **2**, 1–374, Berlin.

WURM, A. (1961): Geologie von Bayern, 1 (Frankenwald, Münchberger Gneismasse, Fichtelgebirge, nördlicher Oberpfälzer Wald). – 555 pp., Berlin.

ZIEGLER, W. (1962): Taxonomie und Phylogenie Oberdevonischer *Conodonten und ihre stratigraphische Bedeutung.* – Abh. Hess. L.A. Bodenforsch., **38**, 1–166, 11 Tab., 14 Pl., Wiesbaden.

ZIEGLER, W. & KLAPPER, G. (1985): *Stages of the Devonian System.* – Episodes, **8**, 104–109, Ottawa.

ZITZMANN, A. (1966): Stratigraphisch-fazielle Untersuchungen zwischen Thüringer und Bayerischer Fazies des Frankenwaldes. – Geol. Jahrb., **84**, 261–280, Hannover.

ZITZMANN, A. (1968a): Das Paläozoikum im Grenzbereich Bayerischer und Thüringischer Faziesreihe des Frankenwaldes. – Geol. Jahrb., **86**, 579–654, 4 Pl., Hannover.

ZITZMANN, A. (1968b): Zur Kieselschieferserie des Frankenwaldes. Neuaufschlüsse auf Bl. 5735 Schwarzenbach am Wald. – Geol. Bl. NO-Bayern, **18**/3, 188–193, 1 Pl., Erlangen.