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a) KVAČEK, Z., DAŠKOVÁ, J., ZETTER, R. (2004): A re-examination of Cenozoic *Polypodium* in North America. - Review of Palaeobotany and Palynology, 128: 219–227.

b) DAŠKOVÁ, J. (2000): *Nyssa* - pollen *in situ* (Most Basin, Lower Miocene). - Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology, 30: 119–122. Brno.

c) DAŠKOVÁ, J. (v tisku): *In situ* pollen of *Alnus kefersteinii* (GOEPPERT) UNGER (Bechlejovice, Tertiary, Czech Republic). - Journal of the National Museum (Prague), Natural History Series.

d) KVAČEK, J., DAŠKOVÁ, J., PÁTOVÁ, R. (2006): A new schizaeaceous fern, *Schizaeopsis ekrtii* sp. nov., and its *in situ* spores from the Upper Cretaceous (Cenomanian) of the Czech Republic. - Review of Palaeobotany and Palynology, 140 (1–2): 51–60.

e) KVAČEK, J., DAŠKOVÁ, J. (2007): Revision of the type material in the genus *Nathorstia* Heer (Filicales). - Journal of the National Museum (Prague), Natural History Series, 176 (7): 117–123.

f) KVAČEK, J., FALCON-LANG, H., DAŠKOVÁ, J. (2005): A new Late Cretaceous ginkgoalean reproductive structure *Nehvizdyella* gen. nov. from the Czech Republic and its whole-plant reconstruction. - American Journal of Botany, 92 (12): 1958–1969.

g) LIBERTÍN, M., BEK, J., DAŠKOVÁ, J. (2005): Two new species of *Kladnostrobus* nov. gen. and their spores from the Pennsylvanian of the Kladno-Rakovník Basin (Bolsovian, Czech Republic). - Geobios, 38: 467–476.

h) BEK, J., DRÁBKOVÁ, J., DAŠKOVÁ, J., LIBERTÍN, M. (v tisku): The sub-arborescent lycopsid genus *Polysporia* Newberry and its spores from the Pennsylvanian (Bolsovian-Stephanian B) continental basins of the Czech Republic - Review of Palaeobotany and Palynology.

KVAČEK, Z., DAŠKOVÁ, J., ZETTER, R. (2004): A re-examination of Cenozoic *Polypodium* in North America. - Review of Palaeobotany and Palynology, 128: 219–227.

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A re-examination of Cenozoic *Polypodium* in North America

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Abstract

The sterile holotype of *Polypodium fertile* MacGinitie was re-examined together with other fertile type specimens from the Miocene Weaverville Formation at Redding Creek (California, western USA). In its leaf morphology, venation and in situ spores *Polypodium fertile* matches the extant *Polypodium vulgare* complex. The spores belong to the verrucose type I (*sensu* Lloyd). In view of discrepancies between the original description and the real morphology of the sterile frond of '*Polypodium*' *alternatum* Pabst from the Chuckanut Formation of northwestern Washington (Eocene), this fern must be excluded from the record of *Polypodium*.

Keywords: Cenozoic; Polypodiaceae; ferns incertae sedis; in situ spores; leaf fossil; North America

1. Introduction

Cenozoic ferns have been described since the very beginning of palaeobotanical research (e.g. Goeppert, 1836) – but not always sufficiently adequate to be identifiable to the natural system of families and genera. Only recently comparisons of venation and other morphological details as well as preparations of in situ spores have offered new data for critical re-evaluations of the fossil taxa described earlier (e.g. Barthel, 1976; Bozukov and Ivanov, 1995). A review of the fossil Polypodiaceae (van Uffelen, 1991) initiated a suite of studies focused on verifying the fossil record of this family based on megafossils. In Eurasia, the reliable fossil members of the Polypodiaceae s.s. have been reduced to only a few (van Uffelen, 1991; Kvaček, 2001; Butzmann and Fischer, 2001; Collinson, 2001). In the present account, a similar effort is attempted for some records in North America, namely *Polypodium fertile* MacGinitie (1937), California, Miocene, and *P. alternatum* Pabst (1968), NW Washington, Eocene. The megafossil remains of *Polypodium* from Sucker Creek, Oregon, Middle Miocene (Graham, 1999), have been lost although dispersed spores are available from this flora (P.F. Fields, pers. commun., April 2001). We are not aware of any other ferns identified with the Polypodiaceae s.s. from the North American Cenozoic (LaMotte, 1952, see Collinson, 2001). We refer to the previous publications (Collinson, 1996; Kvaček, 2001) for a more gen-

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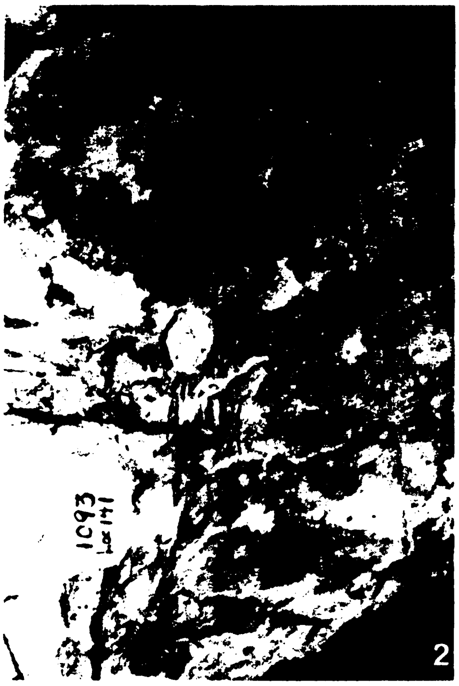
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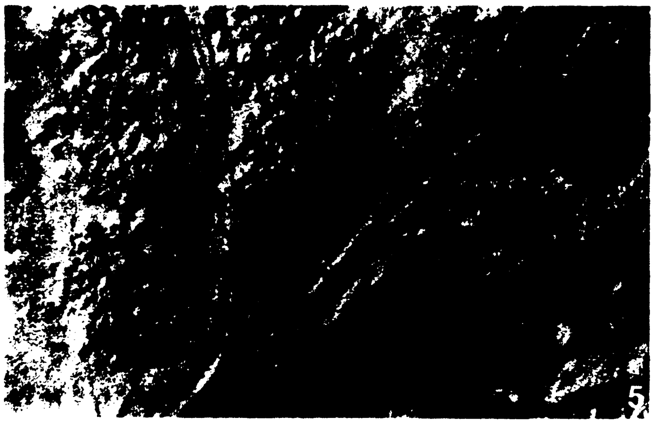
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eral review of the possibilities to evaluate properly fossils of this group of ferns.

2. Materials and methods

The holotype (No. 1015) and other specimens of *Polypodium fertile* MacGinitie housed in the collections of the University of California, Museum of Paleontology (UCMP), Berkeley, CA, have been available for the present study. Only one specimen (No. 1095) has yielded well-preserved spores in situ, while the other fertile specimens (Nos. 1093 and 1094) were too heavily oxidised having sori preserved only as impressions. The venation in the fertile specimens is poorly seen and difficult to reproduce. All available type materials occurred at a single locality (No. 141) in the Weaverville Formation at Redding Creek in California (MacGinitie, 1937). The leaf flora has not been revised since. It is assigned to the Miocene based on palynological data (Barnett, 1989; Graham, 1999).

A single specimen, the holotype of *Polypodium alternatum* Pabst, was also briefly inspected at the UCMP collections (No. 20538 A). The fossil frond is a black carbonised compression with the venation pattern observable only in very oblique light. Sori indicated by Pabst (1968) have not been observed on any pinna of the type specimen. Hence, no in situ spores could be prepared to verify the affinity. The type locality, Canyon Creek (locality PA-214), Chuckanut Formation, NW Washington, has been referred to the Eocene on palynological data (Johnson, 1984).

Other fossil and extant material of *Polypodium* and other Polypodiaceae s.s. (Charles University herbarium, Praha, National Museum, palaeontological collections, Praha, and herbarium, Průhonice, Graz University herbarium) has been documented elsewhere (Kvaček, 2001).

The remains of sori were removed mechanically from the specimen and carried to Europe in a drop of glycerin on a glass slide. One part of the sample was prepared at the Faculty of Science, Praha. The sori were given a brief treatment in Erdtman acetolysis solution, or only mechanically disintegrated, rinsed in water and mounted in glycerin. Another part was transferred to the Univeristy of Vienna and treated in a special way as described by Zetter (1989).

3. Systematic descriptions

Family: Polypodiaceae Berchtold et J. Presl
Subfamily: Polypodioideae emend. Nayar
Genus: *Polypodium* L. emend Ching (1978)

Polypodium fertile MacGinitie (Plates I–III)

Description (MacGinitie, 1937:131 emended with newly obtained characters): Fronds simply pinnate, incised nearly to rachis, more than 150 mm long, up to 120 mm wide, elongate; pinnae alternate, closely spaced, linear–attenuate, straight, up to 60 mm long and 8–10 mm wide, sinuses narrowly rounded; maximum width of pinna at base or slightly above; margin crenulate to sinuate–serrate; primary vein (costa) of pinna straight or slightly curved abmedially, at angle of 50–60° with rachis; pinna venation non-anastomosing, secondary veins (veinlets) 2 times (exceptionally 3 times) forked, arising at intervals of

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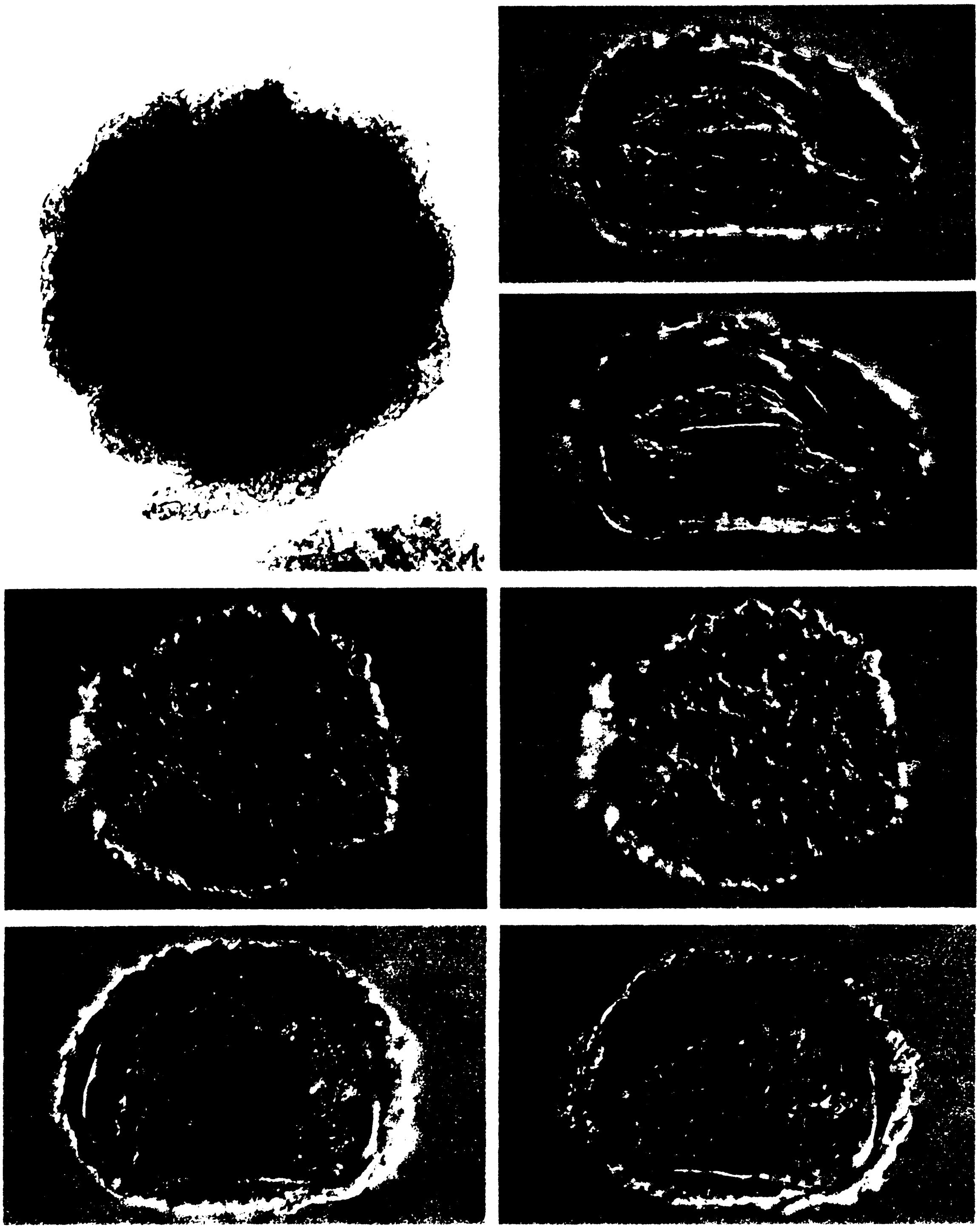
Plate I.

1–7. *Polypodium fertile* MacGinitie, Redding Creek, Weaverville Formation.
1. Holotype, UCMP 1015, re-figured from MacGinitie (1937, pl. 3, fig. 3). ×1.
2. Fertile frond, UCMP 1093. ×1.
3. Detailed venation from (1). ×2.5.
4. Isolated sporangium from UCMP 1095. ×100.
5. Position of sori, detail of (6). ×10.
6. Fertile specimen yielding in situ spores, UCMP 1095. ×1.
7. Enlarged fertile pinna from (6). ×3.



about 3 mm at an angle of 40–50° with expanded ends, not reaching the margin, the lowermost branch (tertiary vein) admedial, hardly reaching half way towards margin, in fertile specimens bearing sorus; sori superficial, roundish, about 2 mm across, closely spaced, without indusium, closer to costa than to margin; no paraphyses observed, sporangia without preserved details of stalk and annulus, about 0.2 mm across; spores monolete, ellipsoidal in polar view, reniform in equatorial view, mature specimens 50–66 μm long, 35–52 μm high, aperture monolete (1/4 to 1/2 of the length), bulged, slightly wrinkled, sculpture of surface irregularly rugulate (sometimes with spines) to verrucate, sculpture elements in distal area higher than in proximal area, spore wall thickness 4–5 μm, inner exospore 2 μm, outer exospore 3 μm.

Discussion: Although the holotype is sterile, its association with other fertile fronds of the same morphology indicates that this population of *Polypodium fertile* from Redding Creek is probably homogenous. The expanded endings of veinlets, which do not reach the margin, admedial basal veinlet, arrangement of sori and character of spores demonstrate its affinity to *Polypodium* sensu stricto (Ching, 1978). Similar dispersed spores were described from the same locality as *Polypodiidites* sp. 2 (Barnett, 1989).

MacGinitie (1937), based only on the frond morphology, believed extant *Polypodium glycyrrhiza* D.C. Eaton to be the nearest living relative but he admitted also a great resemblance to the populations of the *P. vulgare* L. complex from Atlantic North America (now e.g. diploid *P. appalachianum* Haufler et Windham or tetraploid *P. virginianum* L.) and even *Polypodium hispidulum* Bart. (Mexico) and *P. plesiosorum* Kunze (SW USA and Mexico), now mostly excluded from *Polypodium* s.s. In the new light shed by the morphology and size of spores, *P. fertile* is most similar to those species of the *P. vulgare* complex with bigger and prominently verrucate spores. Lloyd (1981) differentiated three types of *Polypodium* spores based on exospore surface. The spores of *P. fertile* belong to his type I – verrucose type. Spores of the tetraploid *P. hesperium* Maxon (British Columbia to Baja California), *P. saximontanum* Windham (Rockies from Colorado to Wyoming) and *P. virginianum* L. (Atlantic USA) are most similar to the fossil. *P. fauriei* Christ (Japan) and *P. glycyrrhiza* (western North America from British Columbia to California) also have verrucate sculpture (Tryon and Lugardon, 1991), but verrucae are smaller than in the mentioned species as well as in *P. vulgare* L. Differences between fossil *Polypodium fertile* and *Polypodium radonii* Z. Kvaček (2001) from the Oligocene of Central Europe are not great. Spores of *P. fertile* are approximately the same size as those of *P. radonii* (about 62×48 μm) but verrucae in *P. fertile* are slightly more robust and higher. The sizes of laesura also differ being straight in both, but longer in *P. fertile* than in *P. radonii*. Both species match the *Polypodium vulgare* complex in the spores.

Excluded species – fam. inc.

‘*Polypodium*’ *alternatum* Pabst (Plate IV)

Description (Pabst, 1968:47 corrected): Incomplete frond more than 60 mm long and up to 30 mm wide, probably parallel-sided, deeply incised with about 1–1.5-mm-wide lamina at rachis; rachis straight, grooved; pinnae linear to narrowly elongate, narrowly rounded at apex, up to 15 mm long and 6 mm wide at base, alternate, slightly decurrent at lower side, sinuses asymmetrically rounded, margin entire; midrib vein (costa) of

Plate II.

1–7. *Polypodium fertile* MacGinitie, Redding Creek, Weaverville Formation.
1. Sporangium separated from UCMP 1095. ×400.
2,3. Two different focussing levels of in situ spore in polar view, UCMP 1095. ×1000.
4,5. Two different focussing levels of in situ spore in oblique view, UCMP 1095. ×1000.
6,7. Two different focussing levels of in situ spore in lateral view, UCMP 1095. ×1000.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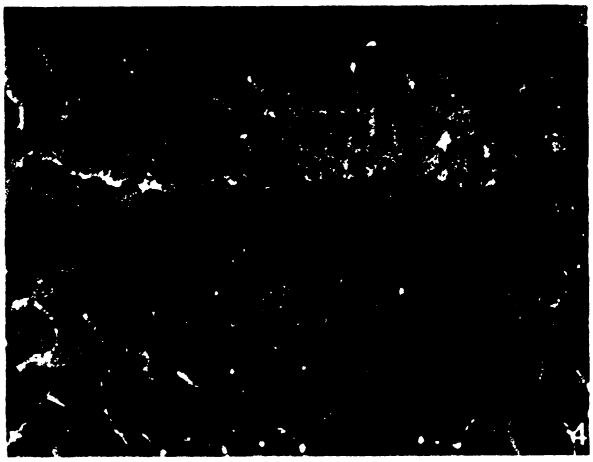
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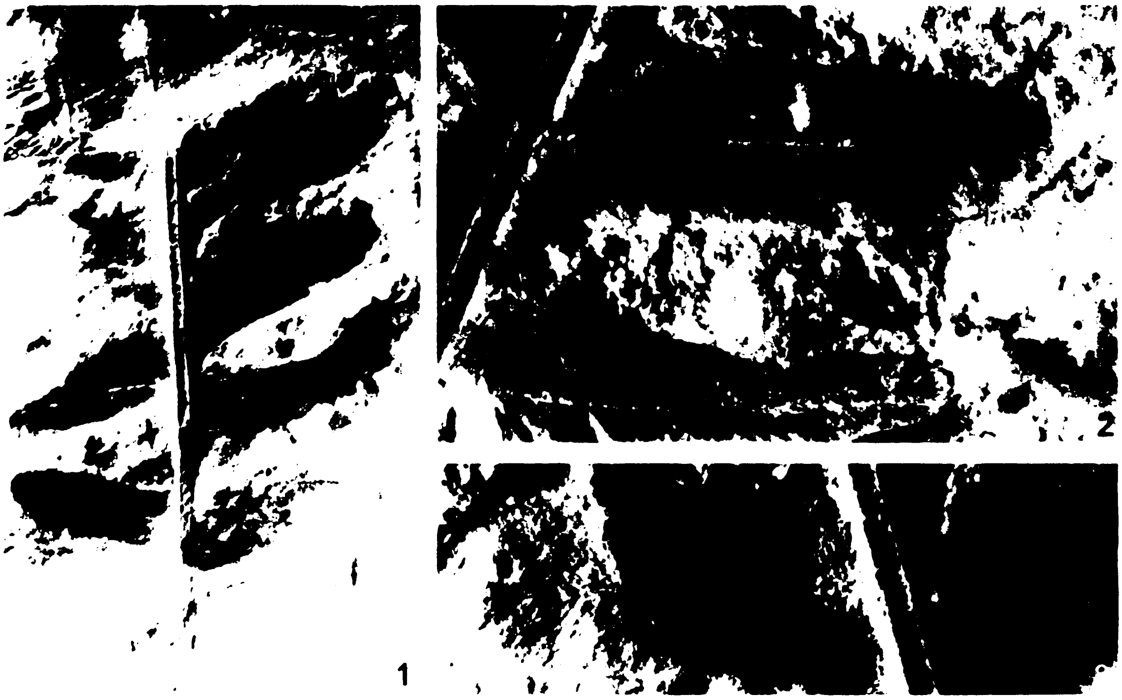

Plate IV.

1–3. '*Polypodium*' *alternatum* Pabst, Canyon Creek, Chuckanut Formation, NW USA.
1. Holotype, UCMP 10538A, re-figured from Pabst (1968, pl. 2, fig. 1a). ×2.
2. Detailed venation of two right pinnae from (1). ×5.
3. Detailed venation of one left pinna from (1). ×5.

pinna straight or slightly curved admedially, at an angle of 60–90° to rachis, secondaries dense, parallel, once forked close to costa, rarely simple, at angle of 40–50°, mostly reaching and merging with the margin; no sori observed on lamina.

Discussion: Pabst (1968) described this single fragmentary frond from the Chuckanut Formation of NW Washington as fertile. Fine particles of sediment (?concretions) spread on some parts of the frond may imitate sori, but the fragment is in our opinion sterile. The venation is different from that typical of the *Polypodium vulgare* complex. In particular, the lack of capitate endings of veinlets rule out the affinity to *Polypodium* in the restricted sense suggested by Ching (1978). Pabst

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Plate III.

1–6. *Polypodium fertile* MacGinitie, Redding Creek, Weaverville Formation, SEM micrographs.
1. Spore of ellipsoidal shape. ×1300.
2. Spore in equatorial view — kidney-shaped (reniform). ×1000.
3. Ellipsoidal spore in polar view. ×1000.
4. Detail of bulging, slightly wrinkled spore laesura. ×3000.
5. Spore wall (inner and outer exospore). ×5000.
6. Sculpture elements in distal area. ×8000.

(1968:48) suggested that *P. virginianum* was like the fossil in the positioning, size, and form of the pinnae, whereas *P. paradisiae* (= *Pecluma paradisiae*) had a similar venation. Dense parallel secondaries as seen on the pinnae can be found in several groups of ferns; in our opinion it corresponds best to the venation of *Blechnum*, but even of *Mattonia* and *Osmunda*. Some Neotropical species have similar simple pinnate fronds with alternate entire-margined pinnae and the same kind of venation patterns. As the character and topography of sori is uncertain in '*Polypodium*' *alternatum*, the affinity of this fern must remain open until more complete and fertile material is obtained.

4. Conclusions

While dispersed spores of the *Polypodium* type are widespread in the Cenozoic of North America, only a single Miocene species based on megafossils – *P. fertile* MacGinitie can be safely attributed to *Polypodium* sensu Ching. Evergreen fronds of rhizomatous mesophytic ferns have low chances to be fossilised. Only specific sedimentation settings, particularly in the volcanic ashes like in the case of this record, preserve megafossils of this kind (Collinson, 2002; Kolakovskii, 1957; Kvaček, 2001). In situ spore morphology is of great value in assessing affinities of such records. In view of discrepancies between the original description and the real morphology (here corrected) combined with the sterile condition of the frond of '*Polypodium*' *alternatum* Pabst, this fern must be excluded from the record of *Polypodium*.

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Scripta Fac. Sci. Nat. Univ. Masaryk. Brun., Vol. 30 (2000), Geology. Brno 2001 119

Nyssa - pollen in situ (Most Basin, Lower Miocene)

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Key words: palynology, palaeobotany, Tertiary, Miocene, pollen, *Nyssa*.

Abstract

Investigations of the pollen in situ (pollen in connection with male inflorescences/flowers) are important for understanding relations between maternal plants and dispersal pollen assemblages. Such a research has been carried out on recent and fossil pollen of the genus *Nyssa*; the fossil male inflorescence originates from the so called „Horizon No 30" in the roof of the main lignite seam in the Bílina Mine (Most Basin) of the Early Miocene age (Bůžek et al. 1992, Sakala 2000).

Localization

The Bílina Mine is located in the Most Basin (easternmost one of the Tertiary Krušné hory Piedmont Basins). The studied material is indirectly dated by mammalian fauna known from the nearby areas as the MN3 Zone (Eggenburgian, Early Miocene; Fejfar 1989, Fejfar and Kvaček 1993). Macroflora of the „Horizon No 30" was studied recently by Sakala (2000) and assigned to the Bílina - Brandis floristic assemblage of the Atlantic Boreal Bioprovince (sensu Mai 1995).

Fossil pollen material

Nyssa - fossil pollen in situ
(Bílina, Czech Republic)

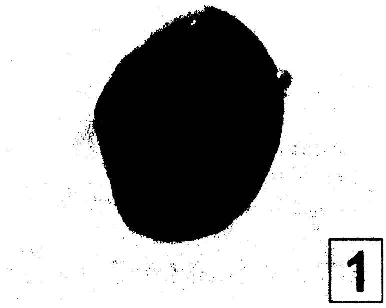
Tricolporate, tectate pollen grains. Size of grains (equatorial view): from 41x27 to 36x27 µm (mean: 38,8 - 27,6 µm). Remarks: Colpi at the angles, meridional, subprolate - prolate shape in the equatorial view, the exine below 0,5 µm thick, diameter of ellipsoidal pores: 3x2,5 µm - 1,5x1 µm (mean: 2,9x2 µm).

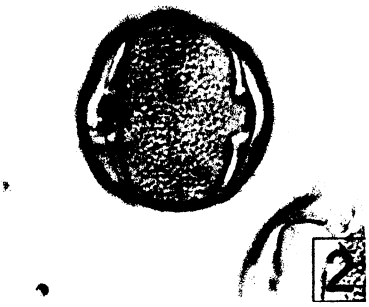
Remarks: Poor preservation of grains excludes a study in the polar view.

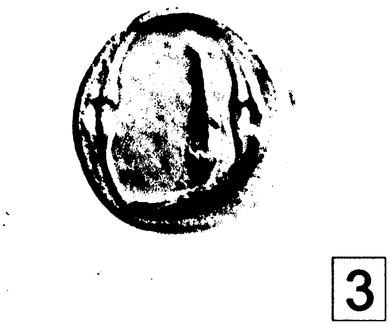
Recent pollen material

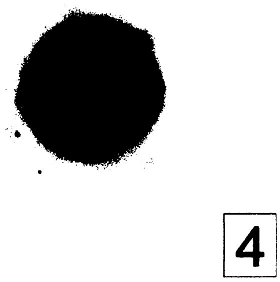
Nyssa javanica (BL.) WANGERIN
(Eastern and south-eastern Asia)

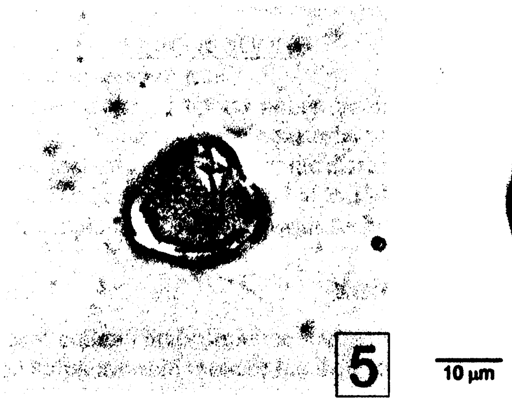
Tricolporate, tectate grains, triangular in polar view. Size of grains (equatorial view): from 31x23 µm to 24x23 µm (mean - 24,2 µm in width 25,7 µm in height), size in polar view: 38 - - 25 µm (mean - 28 µm). Exine about 1 µm (polar area) and 1,2 µm (equatorial area) thick,











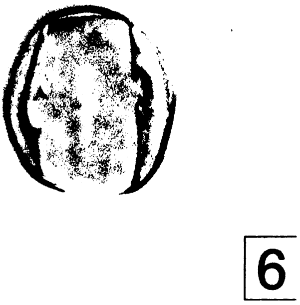


Figure 1 *Nyssa* - fossil pollen in situ
Figure 2 *Nyssa talamancana* HAMMEL & ZAMORA
Figure 3 *Nyssa ogeche* MARSHALL
Figure 4 *Nyssa javanica* (BL.) WANGERIN
Figure 5 *Nyssa wenshanensis* FANG & SOONG
Figure 6 *Nyssa sinensis* OLIVER

colpi at the angles, meridional, pores elipsoidal in shape (mean 3,3 µm - 2,6 µm), subprolate - - prolate spheroidal shape of the grain (equatorial view), triangular, convex (polar view).

Nyssa ogeche MARSHALL
(Eastern North America)

Tectate tricolporate pollen grains, almost round in polar view. Diameter in equatorial view: 42x36 µm - 36x31 µm (mean - 36,5 µm in width, 38,5 µm in height), mean of the size in polar view: 28 µm. Subprolate - prolate spheroidal (equatorial view), exina thick 1,1 µm (equatorial area), 1,3 µm (polar area), colpi at the angles, pores more - less round rectangular in the shape, size of pores 5x5 µm - 2,5x4 µm, with the prominent margin.

Nyssa talamancana HAMMEL & ZAMORA
(Central America)

Tricolporate pollen grain, triangulate, softly convex (equatorial view). Diameter in equatorial view: 32x39 µm - 27x34 µm (mean - 35,4 µm in width, 29,9 µm in height), size in polar view: 29 - 37 µm (mean - 28 µm).

Remarks: Colpi at the angles, meridional, pores very marked, also circular (diameter 4,7 - - 5,2 µm), exine thick 2,1 µm (equatorial area), 1,7 µm (polar area), suboblate shape of the grain (equatorial view).

Nyssa sinensis OLIVER
(Eastern and south-eastern Asia)

Tricolporate, isopolar, tectate pollen grains. Diameter in equatorial view: 34x31 µm 30x28 µm (mean - 29,2 µm in width, 31,8 µm in height), size in polar view: 32 µm - 36 µm (mean 33,5 µm). Grains prolate spheroidal in the shape (equatorial view), exina about 1,5 µm (in equatorial area), 1,2 µm in polar area) thick, pores ellipsoidal, diameter of pores: 6x4 µm 4x2,5 µm (mean: 4,5x3,5 µm).

Nyssa wenshanensis FANG & SOONG
(Eastern and south-eastern Asia)

Tricolporate, tectate, isopolar pollen grains, triangular shape in the polar view. Colpi at the angles, long, diameters in the equatorial view: 18 - 23 µm in height, 11 - 23 µm in width, prolate spheroidal - suboblate shape, the diameter of the pores: 1,5 - 2,5 µm.

Remarks: The herbarium material of this plant is almost sterile; consequently the measurements are incomplete and were not evaluated statistically.

Methods

The recent pollen comes from the herbarium specimens processed by means of acetic anhydride and sulphuric acid mixture (cooked for cca. 15 sec.), isolated pollen grains are stored in glycerine.

The fossil pollen grains were obtained from the male inflorescence by application of hydrofluoric acid, the Schulze solution and water; isolated pollen grains are stored in glycerine.

Both recent and fossil pollen grains were observed in the light microscope (Olympus BX 51) in Nomarski contrast (magnification 1000x).

Conclusions

The so far obtained data from the comparison of the fossil and extend species allow too much the fossil pollen grains with those of *Nyssa sinensis* OLIVER (Eastern Asia) and *Nyssa ogeche* MARSHALL (Eastern North America). Both extends species differ in other respect (leaf anatomy, fruits, male inflorescence) from the fossil representatives. There for our example is similar to some others Tertiary Europe's plants in which characters of extend representatives are combine. The research on the fossil and recent genus *Nyssa* is in progress. As a next step, the ultrastructure of surface sculptation of selected, well-preserved pollen grains will be studied using the SEM. Such a study is decisive for precise systematic evaluation of the studied material.

Recent (preliminary) observations show that there is very poor (limited) correspondence between taxa based on macroscopical remains and pollen taxa and are in agreement with the Sohma's opinion (Sohma 1963).

This investigation is a part of the complex study focused on the genus *Nyssa* from the Mine Bílina. The goal of this study is to try to combine information on all organs occurring in the same assemblage, in optimal case, coming from the same plant.

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DAŠKOVÁ, J. (v tisku): *In situ* pollen of *Alnus kefersteinii* (GOEPPERT) UNGER (Bechlejovice, Tertiary, Czech Republic). - Journal of the National Museum (Prague), Natural History Series.

***In situ* pollen of *Alnus kefersteinii* (GOEPPERT) UNGER (Bechlejovice, Tertiary, Czech Republic)**

Jiřina Dašková

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Abstract: Pollen grains of *Alnipollenites verus* - type isolated from male catkins are discussed here. It is the first proves of them from the Oligocene of North Bohemia.

Key words: pollen, palaeobotany, palynology, Tertiary, Bechlejovice, *Alnus*

Introduction

Studies of pollen *in situ* are important in view of taxonomical characteristics of the whole plants serving to the reconstruction of flowers and pollen of various plant groups (e.g. Kvaček et Konzalová 1996, Liu et al. 2001, Kohlman-Adamska et al. 2004). This paper demonstrates the first proves of pollen *in situ* of the genus *Alnus* from the Oligocene of North Bohemia. Pollen grains of *Alnipollenites verus* - type have been isolated from two well preserved catkins from the locality Bechlejovice. It represents important verification of the taxonomical classification of frequently found male alder inflorescences in this locality.

The palaeontology research of Bechlejovice locality has a long tradition. The first fossil plant macro remains were reported by Engelhardt (1895). Since that time numerous other palaeontological papers have been published from there. Comprehensive summary of palaeobotany research was given by Kvaček and Walther (2004).

Material and Methods

The locality Bechlejovice is situated in the Central part of České středohoří Mountains. Fossiliferous layers are located in south-east direction of the town of Děčín (fig. 1).
The age of the locality was determined by Konzalová (1981) as Early and early Late Oligocene. Her results are based on presence of index sporomorph *Boehlensipollis hohlii* W. KR. in Bechlejovice pollen spectra.
Pollen grains discussed in this paper were isolated from two specimens of *Alnus kefersteinii* (GOEPPERT) UNGER (fig. 2A, 3A) morphologically identical with other specimens described by Kvaček and Walther (2004, pl. 2, fig. 4). The plant remains are preserved in laminated diatomite as compressions/impressions with small amount of carbonized substance. Attempts to prepare pollen *in situ* were not always successful. Only two catkins yielded pollen described in here. Due to poor preservation, only hydrofluoric acid was used for maceration of samples, and than the samples were acetolysed (Erdtman 1954). In spite of a long maceration, the pollen grains had to be isolated mechanically from each other and from the matrix.
Collections from Bechlejovice are stored in various institutions: Czech Geological Survey (Prague), National Museum, Prague, Faculty Sciences of the Charles University, Natural History Musem in Viena, Humboldt University, Museum für Naturkunde (Berlin) and Staatliches Museum für Mineralogie und Geologie zu Dresden. The two specimens bearing catkins studied are stored in the collection of the National Museum, Prague.

Systematics

Family: Betulaceae S. F. GRAY

Genus: *Alnus* L.

Macroscopical remains of the mail catkins are assigned to *Alnus kefersteinii* (GOEPPERT) UNGER by Kvaček and Walther (2004). These cone-like infructescences are flattened, long stalked. They are 11-15 mm long and 5-8 mm wide. The inflorescences consist of units interpreted as male dichasia. Pollen isolated from stamens of these specimens was determined as *Alnipollenites verus* – type.

Alnus kefersteinii (GOEPPERT) UNGER
(Fig. 2A, 3A)

SYN:

1838 *Alnites kefersteinii* GOEPPERT 1838: 564, pl. 41, figs 1-5. (Salzhausen)

1847 *Alnus kefersteinii* (GOEPPERT) UNGER 1847: 113, pro parte, pl. 33, fig. 2 (non pl. 33, figs 1, 3-4). (Bílina)

1998 *Alnus kefersteinii* (GOEPPERT) UNGER 1847: Kvaček and Walther, 8, pl. 3, figs 5, 6, text-fig. 13.6. (Kundratice)

2004 *Alnus kefersteinii* (GOEPPERT) UNGER 1847: Kvaček and Walther, 20, pl. 2, figs 3, 4, text-fig. 11.8. (Bechlejovice)

Material: G08551 (Fig. 2A), G08552 (Fig. 3A)

Description: Male catkins fragmentary, more than 10 mm long, about 8 mm wide, with pollen *in situ* of the *Alnipollenites verus* – type (for description see below). Stamens and florets are not discernible due to poor preservation.
Remarks: The same type of inflorescences have been previously described from Bechlejovice by Kvaček and Walther (2004, p. 20, pl. 2, fig. 4) and Kundratice by the same authors (Kvaček and Walther 1998, p. 8, pl. 3, fig. 4). In both floras the catkins are associated with infructescences of *A. kefersteinii* and leaves of *Alnus gaudinii*. These organs obviously belong to the same alder, which is widely spread in the Oligocene to Pliocene of Europe (Mai and Walther 1988).

Alnipollenites verus (POTONIÉ 1931) POTONIÉ 1960
(Fig. 2B-D, 3B-D)

SYN:

1934 *Alnipollenites verus* R. POT.: 58-59, pl. 2, figs 13, 17, 18, 25, 26, pl. 6, fig. 28.

Description: Pollen grains have pentagonal shape (Fig. 3D); they are pentaporate with pores having vestibulum. They're 15-20 µm in size having granulate microstructure on the surface (Fig. 3C). Their garland-arranged folds of the exine extend from pore to pore (Fig. 2B, 3D) – this so-called *arci* is typical for genus *Alnipollenites*.

Remarks: Pollen grains of *Alnipollenites verus* (Pot.) Pot. are divided according to their size into 3 morphotypes (Nagy 1985). Present material shows pollen grains having 15-20 µm in diameter. They belong to *A. verus* f. *minor* in terms of Nagy (1985). This form is described as having 17-19 µm in diameter. There are only pentaporate pollen grains in this inflorescences but sometimes (in dispersed spectrum) are typical 4, 6 and 7 pored variants (e.g. Nagy 1985, Konzalová 1996).

Conclusions

The male catkins *Alnus kefersteinii* (Goeppert) Unger contain pentaporate pollen grains of *Alnipollenites verus* (Potonié) Potonié. The morphology of these grains is very typical due to pores having vestibulum and *arci* which are diagnostic features of the genus *Alnipollenites*. Isolated pollen grains verify the taxonomical classification of catkins assigned to *Alnus kefersteinii* (Goeppert) Unger occurring in Bechlejovice locality. This conclusion is in agreement with previous determinations by Göppert (1838) based on gross morphology.

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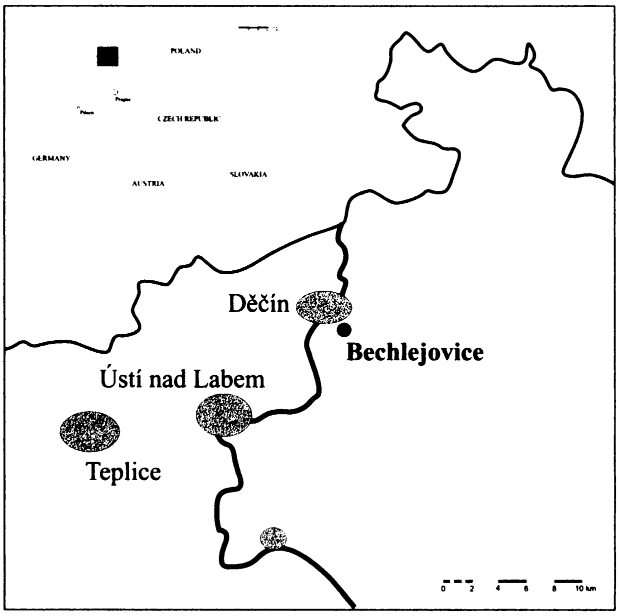
Figure 1. Map of the Central part of České středohoří Mountains – Bechlejovice locality.

Figure 2. A: *Alnus kefersteinii* (GOEPPERT) UNGER, male catkin (G08551); B-D: *Alnipollenites verus* (POTONIÉ) POTONIÉ, 5 porate pollen grains isolated from G08551

Figure 3. A: *Alnus kefersteinii* (GOEPPERT) UNGER, male catkin (G08552); B-D: *Alnipollenites verus* (POTONIÉ) POTONIÉ, 5 porate pollen grains isolated from G08552


POLAND
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Bechlejovice
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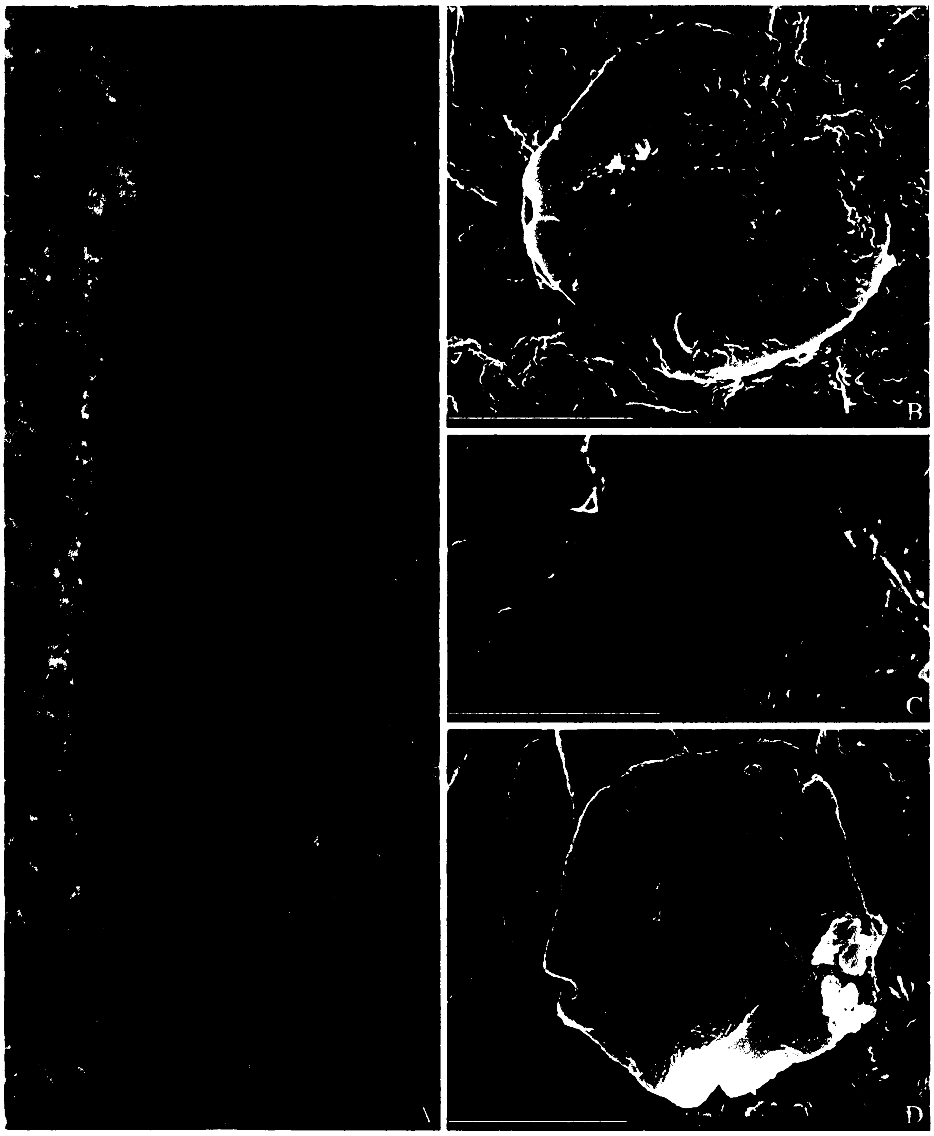
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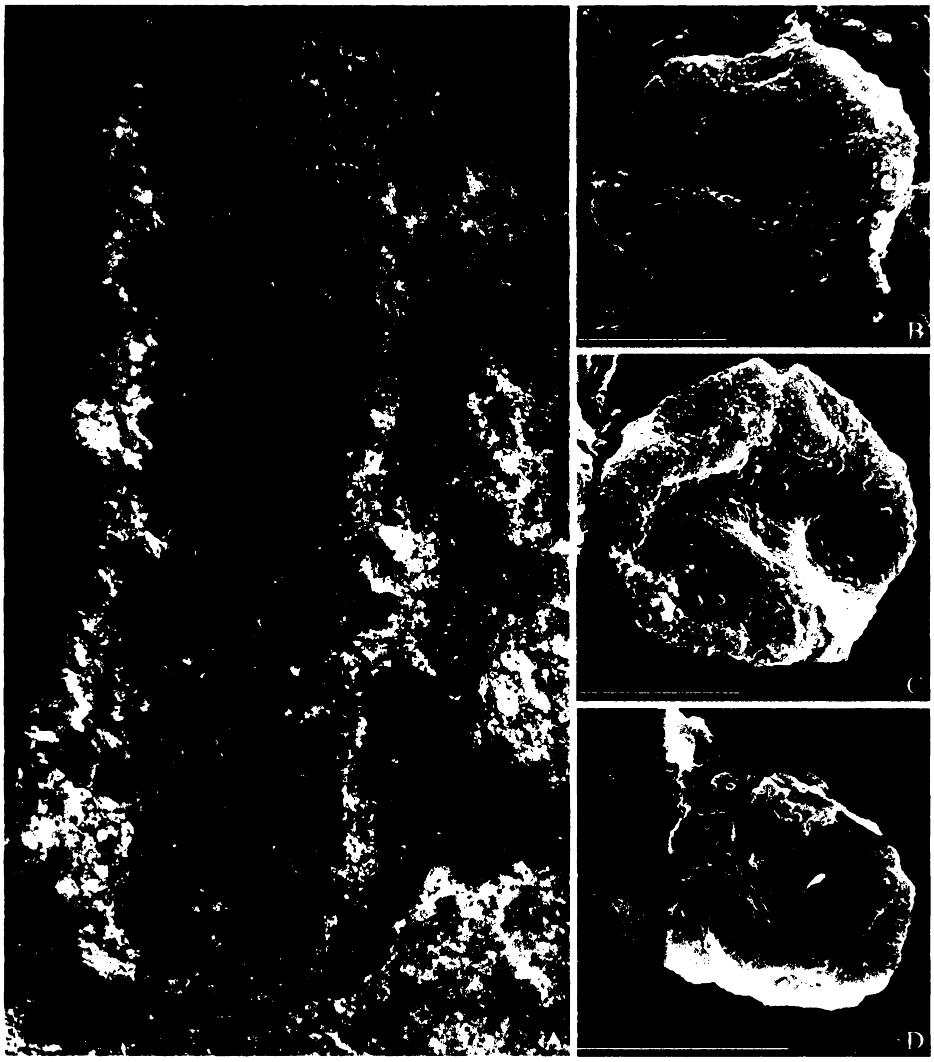
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KVAČEK, J., DAŠKOVÁ, J., PÁTOVÁ, R. (2006): A new schizaeaceous fern, *Schizaeopsis ekrtii* sp. nov., and its *in situ* spores from the Upper Cretaceous (Cenomanian) of the Czech Republic. - Review of Palaeobotany and Palynology, 140 (1–2): 51–60.

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A new schizaeaceous fern, *Schizaeopsis ekrtii* sp. nov., and its in situ spores from the Upper Cretaceous (Cenomanian) of the Czech Republic

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Abstract

A new fern, *Schizaeopsis ekrtii* sp. nov., is described from the Peruc-Korycany Formation (Cretaceous, Cenomanian) of the Czech Republic based on the morphology of its leaves and reproductive structures. It is compared to the similar, previously published fossil taxa. It is characterised by finely segmented, 4–5 times divided fronds. Each terminal segment bears one fertile tip. The tip is entire-margined, containing a single row of sporangia. *S. ekrtii* is very similar to the extant genus *Schizaea* in gross-morphology, but differs in its spore morphology. Extant *Schizaea* has monolete spores, whereas the *Schizaeopsis* has trilete spores. The spores of *S. ekrtii* are assigned to the *Cicatricosisporites–Appendicisporites–Plicatella* complex.

1. Introduction

The family Schizaeaceae represents one of the basal lineages of modern ferns with a long and well-documented history. Extant Schizaeaceae comprise three genera, *Lygodium*, *Anemia* (including *Mohria*) and *Schizaea*. The family is mainly distributed throughout the tropics and subtropics, being particularly abundant in South America. Morphological and genetic distinctions of the living genera, and a long fossil record, make the group ideal for phylogenetic analyses (e.g. van Konijnenburg van Cittert, 1992; Wikström et al., 2002).

Macrofossils and dispersed spores of fossil members of this family have been documented throughout the Mesozoic and Cenozoic. The first unequivocal members of the family are known from the Early Jurassic (*Stachypteris* Pomel; Zhou, 1995 and *Klukiopsis* Deng and Wang, 2000). Diversity increased during the Middle Jurassic with the appearance of *Klukia* Raciborski, 1890, *Stachypteris* Pomel, 1849 and *Sellingia* Lorch, 1967 (e.g. Harris, 1961; van Konijnenburg van Cittert, 1991; Cleal, 1993). In the Late Jurassic, several new taxa originated including *Ruffordia* Seward, 1894, *Mohriopsis* Appert, 1973 in Madagascar, and *Naktongia* Oishi, 1939 in Korea. Numerous taxa have been recorded from Cretaceous. In addition to the extant *Anemia* and *Lygodium*, they comprise the following genera: *Klukia* Raciborski, 1890, *Pelletixia* Watson and Hill, 1982, *Ruffordia* Seward (Dettmann and Clifford, 1992), *Schizaeopsis* Berry, 1911 (Skog, 1993), *Schizaeopteris* Stopes and Fujii, 1910 from Japan (Yoshida et al., 1996), *Schizaeangium* Bohra and Sharma, 1978 from India, *Paralygodium* Yoshida et al., 1997, and

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Mohriopsis Banerji, 1991. In contrast to the extant taxa, fossil representatives of the family are generally centred in the Northern Hemisphere.

New investigations in the Cretaceous (Cenomanian) of the Czech Republic, part of the ongoing studies of the Peruc Flora (e.g. Kvaček, 1995; 1997a,b; Kvaček and Knobloch, 1997; Eklund and Kvaček, 1998; Kvaček, 2000; Falcon-Lang et al., 2001; Kvaček and Pacltová, 2001; Kvaček and Eklund, 2003; Falcon-Lang, 2004; Kvaček et al., 2005) have revealed well-preserved fern taphocoenoses at various localities (Falcon-Lang et al., 2001). These comprise several types of fertile fronds with in situ spores. The first of these is described in this paper as a new species of the genus *Schizaeopsis*.

2. Material and methods

The studied material comes from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin in the Czech Republic (sensu Čech et al., 1980). This formation is assigned to the upper part of the Middle Cenomanian (Pacltová, 1977, 1978). The type locality at Kamenná Panna Quarry near Horoušany (50°07′17″, 14°44′09″E) is located 40 km east of Prague (Fig. 1). It is an active quarry containing a 32 m thick section through the upper part of the Peruc–Korycany Formation. The section (Fig. 2) was studied by Uličný and Nichols (1997), who interpreted the sediments as the deposits of gravely braided rivers (Unit 1), meandering streams and floodplains including lacustrine sediments of ephemeral lakes (Unit 2), anastomosed fluvial systems (Unit 3), tidally-influenced fluvial channels (Unit 4), supra-tidal marshes including a *Frenelopsis* assemblage (Unit 5), tidal flats and channels (Unit 6), shallow marine sub-tidal bars (Unit 7) and various marine shoreface settings (Units 8 and 9). The material described in this report comes from Unit 2, particularly from grey/green mudstone deposits, interpreted as the sediments of an ephemeral lake (Uličný and Nichols, 1997).

The material was examined using an Olympus SZX 12 binocular microscope, an Olympus BX 50 light microscope, and a Phillips 515 SEM. In situ spores were macerated using the standard methodology (e.g. Collinson, 1999; Batten, 1999). The selected fossil material was treated with hydrofluoric acid (HF, 4%) to remove silicates. This was followed by maceration in Schultze′s solution. The coalified material was washed in 5% KOH. Some of the extracted fossil remains were mounted in glycerine jelly (2 or 3 preparations from each sample) for examination by light microscopy. Part of the material was separated using a dissecting needle with a human hair glued near its tip (Zetter, 1989; Zetter et al., 2002). The samples were mounted on SEM stubs and observed using standard techniques (Collinson, 1999). All the studied material is housed in the collection of the National Museum, Prague.

Schizaeaceae Kaulf.
Schizaeopsis Berry, 1911
Syn.: Baieropsis Fountaine, 1889
Type: Schizaeopsis expansa Berry (1911), p. 194, text—fig. 1, pl. 12 = *Baieropsis macrophylla* Fountaine, 1889, p. 212, pl. 90, fig. 6 = *Schizaeopsis macrophylla* (Fontaine) Skog, p. 21, fig. 1 = *Schizaeopsis americana* Berry (1911), p. 214, fig. 2, pl. 22, figs. 1–9
Discussion: The newly described material shows diagnostic characters of the genus *Schizaeopsis* studied by Skog (1993). Fronds consist of repeatedly dichotomising narrow segments with terminally arranged sporangia aggregated into sporangiophores. The spores

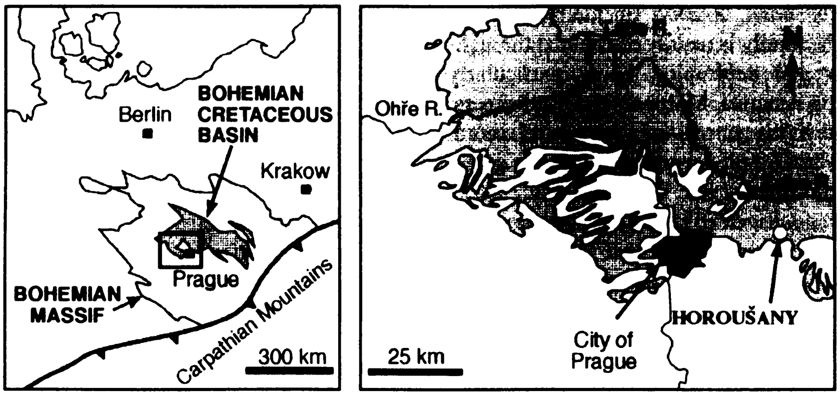

Fig. 1. Map showing the locality of Horoušany in the Czech Republic.

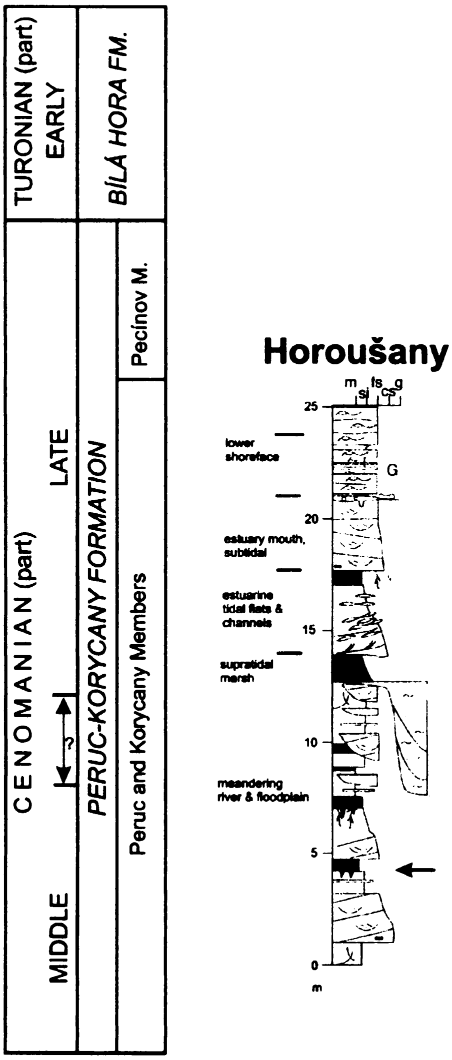

Fig. 2. Geological section and the basic palaeoenvironmental interpretation of the locality Horoušany (after Nguyen Tu et al., 2002). The type horizon indicated by arrow.

found in situ are cicatricose. Further characters noted below are typical of the family Schizaeaceae (Skog, 1993; Van Konijnenburg-van Cittert, 1991).

Schizaeopsis ekrtii sp. nov.
Plates I and II.
Type locality: Kamenná Panna Quarry, Horoušany, (50°07′17″, 14°44′09″E).
Type horizon: Late Cretaceous, Cenomanian, Peruc-Korycany Formation, Unit 2 (Uličný and Nichols, 1997).
Holotype: Designated here NMP F 3020, National Museum, Prague (Plate I,1).
Etymology: Named after our colleague Boris Ekrt, who found the best-preserved specimens of the described fossil fern.
Material: NMP F 3021–F 3032a,b, NMP F 3037.
Diagnosis: Frond more than 7 times dichotomously divided from the base. Both sterile and fertile fronds having narrowly lanceolate segments. Each segment forking in its terminal part into narrow strips. The sterile segments terminating with acute or rounded tips. Venation dichotomously branched, each terminal segment entered by one vein. The fertile segments terminated with sporangiophores bearing one row of semi-circular sporangia tightly packed together. Laminae of sporangiophores lined with trichomes, their tips terminating with cluster of long trichomes. Sporangia containing spores assigned to *Cicatricosisporites–Appendicisporites–Plicatella* Complex. Spores tetrahedral, and trilete with triangular amb. Leasurae raised, extending 2/3 of the spore radius. Muri smooth, arranged in three sets on both proximal and distal sides of the spore. The muri having anastomoses in each radial region extending from the equator towards the distal pole. Radial regions raised forming keels extending equatorially into the auriculae.
Description: The holotype shows a portion of a 5 times dichotomously divided fertile frond, 135 mm long, and flattened into one plane (Plate I,1). The frond consists of narrow, 0.8–1.5 mm wide, dichotomously branched segments. Other available material shows a variety of frond fragments from delicate segments to quite densely segmented fronds reaching at least 100 mm in length (Plate I,2). Two additional fertile specimens show sporangiophores (F 3025, Plate I,2; F 3037, Plate I,4). The fertile segments arising from the last dichotomies are very short (2–5 mm) bearing singularly attached sporangiophores (Plate I,6). Each sporangiophore is 3–5 mm long and 0.5–1 mm wide. It is usually preserved folded, forming a pod-like structure (Plate I,4,6). In some cases the sporangiophore shows impressed sporangia in a row (Plate I,6). There are usually 8–12 sporangia per sporangiophore. The sporangia are ovoid, and 300 µm in diameter (Plate II,1). No cellular structure of the sporangia is preserved. In the specimen F 3037, a thin cuticle like material bearing trichomes lines the sporangiophores. The same trichomes were observed in terminal parts of the sporangiophores (Plate I,5).

The sterile segments are generally broader (1–2 mm) than fertile ones, showing acute or rounded tips (Plate I,3,7). Veins are difficult to ascertain, but given the width of leaves, there is probably one vein per segment.

The trilete spores preserved in situ (Plate II,2) are mature, or nearly mature, and well-preserved (Plate II, 7–10). They are cicatricose, tetrahedral, about 80 µm in diameter, usually preserved slightly flattened, and show triangular amb. The laesurae are raised, but partly covered by parallel-arranged muri, extending 2/3 of the spore radius (Plate II,5,7). Muri are smooth, 3 µm broad, separated by 2 µm lumina (Plate II,6), and arranged in three sets on both proximal and distal sides of the spore. The muri having anastomoses in each radial region extending from the equator towards the distal pole (Plate II, 4). Radial regions are raised forming keels (Plate II, 4) extending equatorially into the auriculae (Plate II,3). *Discussion:* The type material of the previously monotypic genus *Schizaeopsis* Berry is based on *S. expansa* (Fontaine) Berry from the Lower Cretaceous of the Potomac Group, eastern USA. This taxon was revised by Skog (1993), who also elucidated nomenclatural problems concerning the genus, and showed that the valid name for this plant is *Schizaeopsis macrophylla* (Fontaine) Skog.

S. ekrtii sp. nov., the second species of the genus to be discovered, differs from *S. macrophylla* in the number of fertile tips per segment, in the construction of the fertile tip and in the different type of its spores. *S. macrophylla* has numerous fertile tips per segment (compare Skog, 1993, Fig. 1, 3) whereas *S. ekrtii* has only one. The fertile tips of *S. macrophylla* are pinnately lobed, showing the sporangia in two rows, whereas *S. ekrtii* has fertile tips always entire-margined showing only one row of the sporangia. Orientation of the sporangia in *S. ekrtii* is not known because they are always preserved completely covered by leaf lamina. The spores within the sporangia of *S. macrophylla* do not have auriculae, (Hughes and Moody-Stuart, 1966), in contrast with spores found in sporangia of *S. ekrtii*, which have them well-pronounced.

Schizaea-like fossil foliage, similar to *S. ekrtii* was described by Velenovský and Viniklář (1926) from the Bohemian Cenomanian as *Pseudoginkgo bohemica*. Unfortunately, there are no fertile specimens of *P. bohemica* available for the study, which could test its affinity to the Schizaeaceae.

In terms of frond macromorphology, *Schizaeopsis* is similar to some species of the extant genus *Schizaea* of the Schizaeaceae, particularly the sterile fronds of *Schizaea dichotoma* from New Caledonia (Plate III,1–3). This species bears trilete spores in rare cases (Selling, 1944). Although similar in frond topology *Schizaeaopsis ekrtii* differs from *S. dichotoma* in having: sporangia in single rows, trilete spores and cicatricose sculpture of exina. In terms of striate

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Plate I. *Schizaeopsis ekrtii* sp. nov., Kamenná Panna Quarry, Horoušany, general morphology. (see page 55)

1. Holotype, F 3020, ×0.75.
2. Six times dichotomised sterile frond, F 3031.
3. Detail of the sterile segment, F 3037, ×10.
4. Detail of the fertile segments, F 3025a, ×5.
5. Holotype, detail of Fig. 1, terminal part of the fertile tip showing trichomes, F 3020, ×30.
6. Holotype, detail of Fig. 1 showing the two fertile tips, one with trichomes (t), second with the distinct sporangia (s) in one row, F 3020, ×20.
7. Detail of the sterile segments, F 3030, ×5.

Plate II. *Schizaeopsis ekrtii* sp. nov., Kamenná Panna Quarry, Horoušany, spores. (see page 56)

1. Fertile tip showing the transversely broken sporangium with spores F 3025b, ×63.
2. Sporangium, detail of Fig. 1, F 3025b, ×220.
3. Detail of the distal surface of the spore showing auricule, F 3020c, ×1600.
4. Detail of the distal surface of the spore showing anastomoses in radial region extending from the equator towards the distal pole, F 3020d, ×1200.
5. Detail of the laesura, F 3020e, ×1700.
6. Detail of the muri, F 3020c, ×3400;
7. Spore in LM F 3020b, ×500.
8. Distal surface of the spore, F 3020c, ×250.
9. Distal surface of the spore, F 3020d, ×250.
10. Proximal surface of the spore, F 3020e, ×500.

Plate III. *Schizaea dichotoma* (L.) J.E. Smith. Recent, New Caledonia. (see page 57)

1. Herbarium specimens showing the sterile and the fertile fronds, ×1.
2. Portion of the fertile frond, detail of Fig. 1, ×2.5.
3. Cluster of sporangiophores, each showing two rows of sporangia, detail of Fig. 1, ×20.

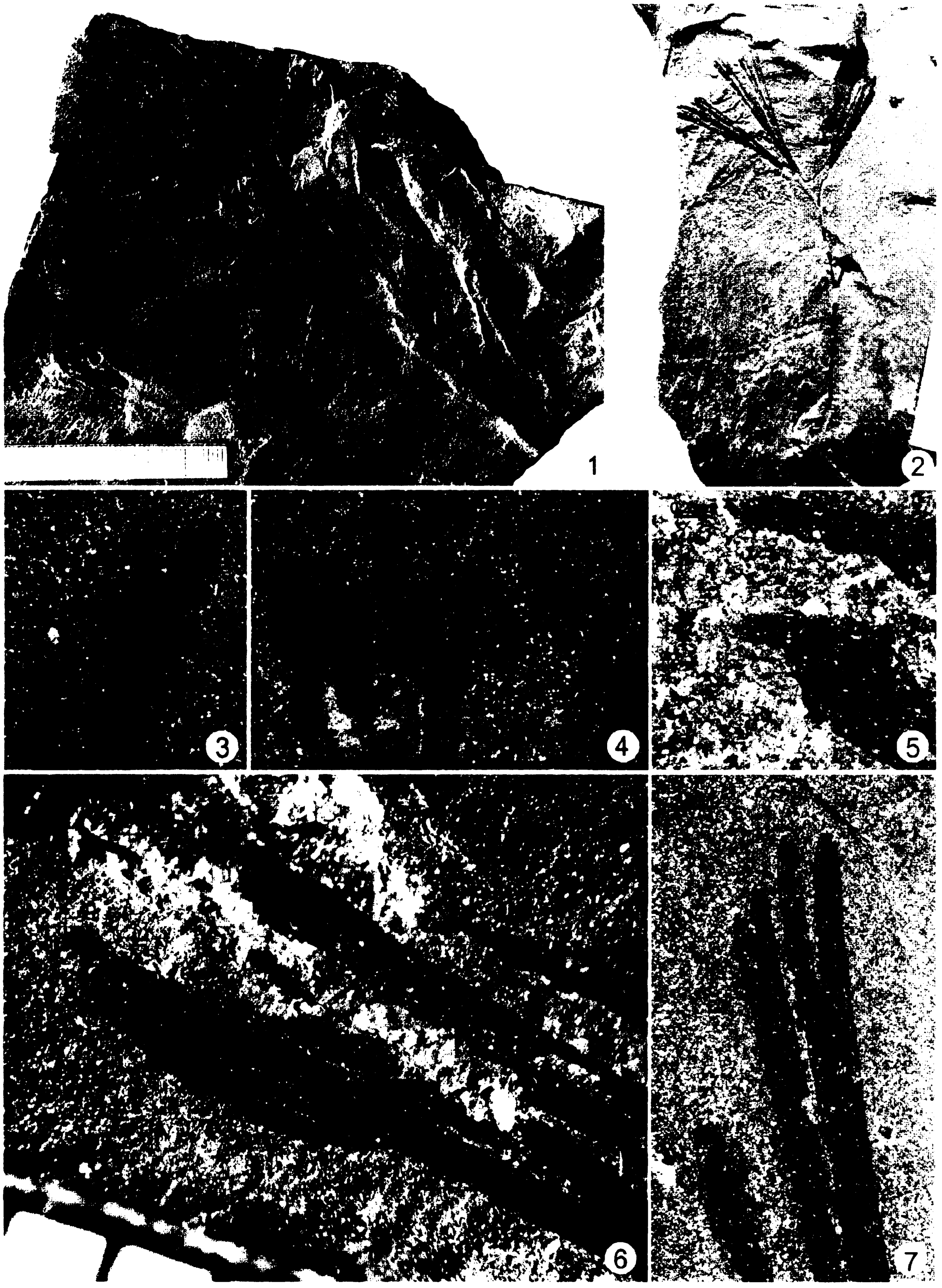

Plate I (*caption on page 54*).

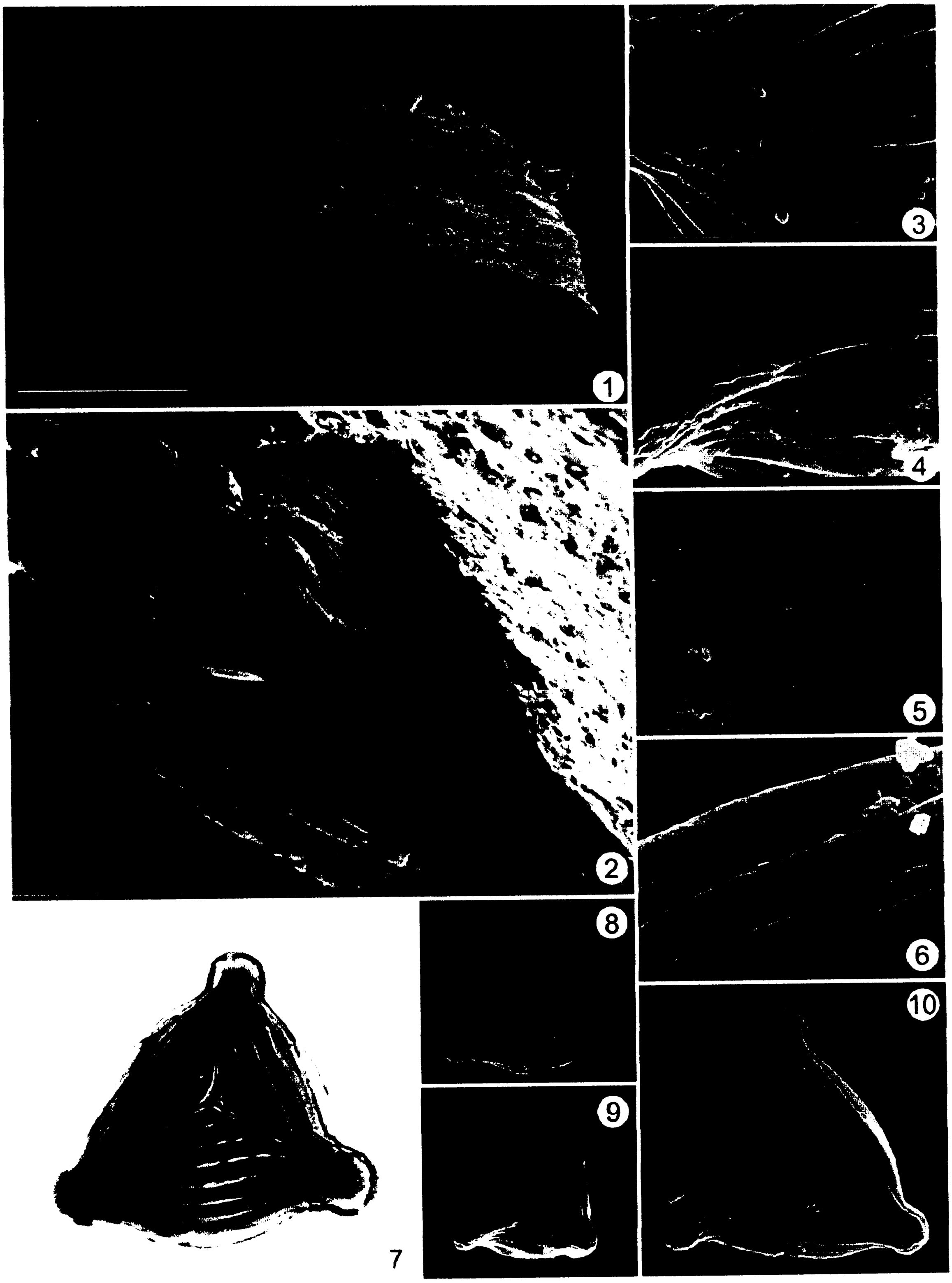

Plate II (*caption on page 54*).

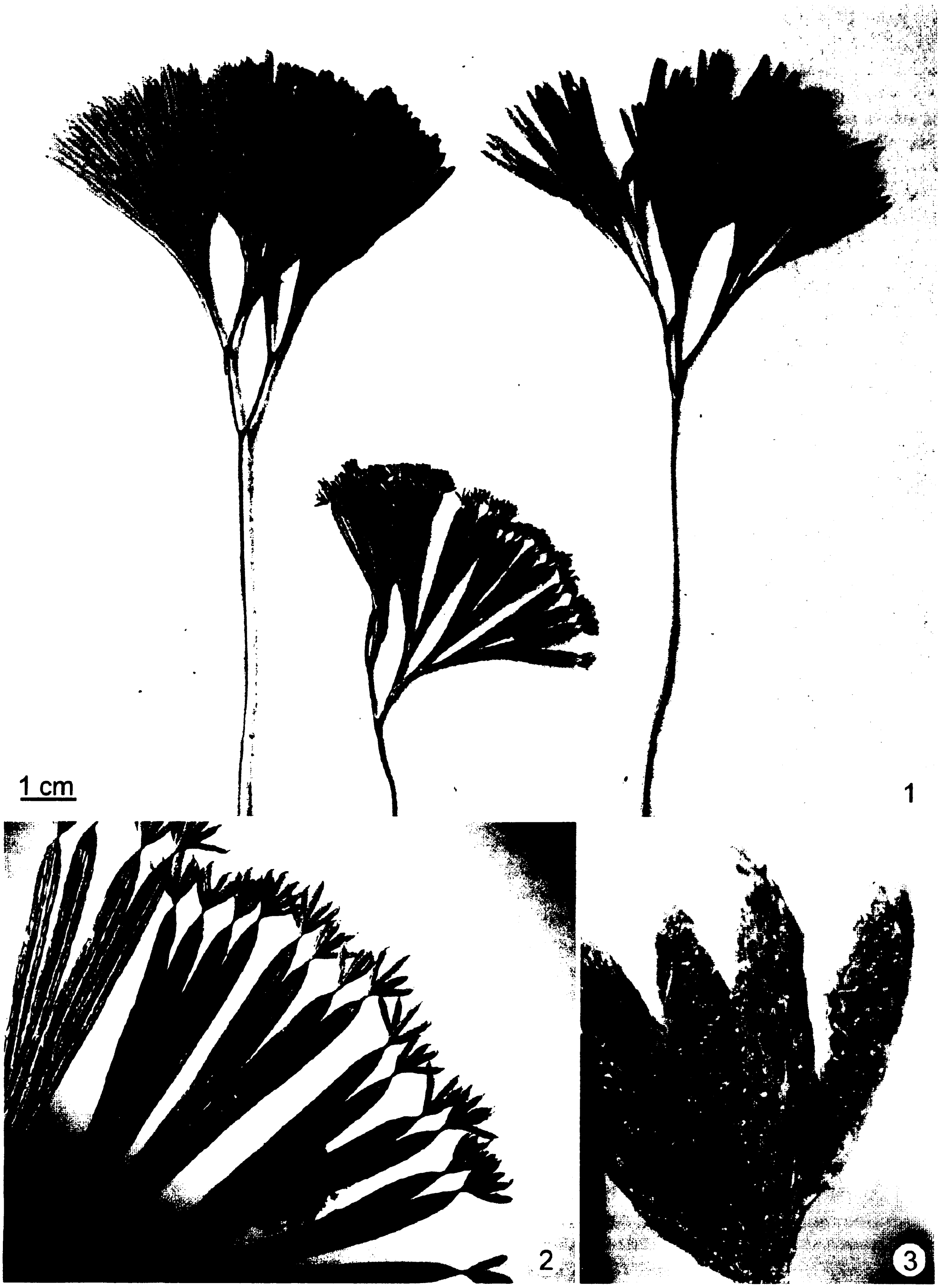

Plate III (*caption on page 54*).

ornamentation of the exina, *Schizaeopsis* is similar to the members of the subgenus *Actinostachys* Wallich (van Konijnenburg van Cittert, 1991). However it differs from spores of *S. ekrtii* in having monolete leasura. During their comparative studies van Konijnenburg van Cittert (1991) and Skog (1993) came to the conclusion that *Schizaeopsis* probably represents an early stage of the *Schizaea* evolution. Both authors based their argument on the occasional occurrence of trilete spores in the sporangia of extant *S. dichotoma*, as documented by Selling (1944). The basal position of *Schizaeaopsis* in the *Schizaea* clade was also suggested by Wikström et al. (2002, fig. 2).

The spores found in the sporangia of *S. ekrtii* show general characters of the *Cicatricosisporites–Appendicisporites–Plicatella* complex, which represents well-defined group. However delimitation of its genera is problematic. Following Dettmann and Clifford (1992) we prefer to assign our material to the genus *Plicatella* due to the presence of well developed auriculae. Dettmann and Clifford (1992) define *Plicatella* as a trilete tetrahedral spore with subtriangular to triangular amb. Leasurae occupy at least 2/3 of the spore radius. Exine is thickened in each disto-equatorial radial region where keel-shaped auriculae are developed. The spores of *Plicatella* differ from *Appendicisporites* in the absence of the discrete-element of each radial murus where the member of adjacent mural sets anastomose (Dettmann and Clifford, 1992). The spores of *Cicatricosisporites* Potonié and Gelletich, 1933 differ from *Plicatella* in absence of equatorial auriculae (Dettmann and Clifford, 1992).

Spores similar to *Schizaeopsis ekrtii* are recorded in certain species of the extant subgenus *Coptophyllum* of the genus *Anemia*. Spores bearing projections recalling appendices of *Appendicisporites* are known in *Anemia raddiana* (Detmann and Clifford, 1991). It differs from *S. ekrtii* having thicker muri and less pronounced auriculae. Spores of the *Appendicisporites–Plicatella* complex were recorded in the Cenomanian of Bohemia by Thiergart (1953) as *Appendicisporites* sp. Unfortunately, his illustrations are of very low quality and the repository of his material is unknown. Therefore no precise comparison is possible.

Plicatella tricornitata (Weyland et Greifeld) Deák et Combaz from the Santonian of Quedlinburg, Germany (Weyland and Greifeld, 1953), as far as we can observe from light microscope photograph, differs from the spores of *S. ekrtii* in having an equatorial amb with straight walls and less pronounced auriculae. *Plicatella distocarinata* (Dettmann et Playford) Davies from the Albian–Turonian of Australia (Dettmann and Playford, 1968) differs from the spores of *S. ekrtii* in having a very distinct radial region of anastomoses extending from the equator towards the distal pole and pronounced laesura extending to the equator.

Spores of the *Appendicisporites–Plicatella* complex were recorded in palynoassemblages from the Cenomanian of Bohemia (the Bohemian Cretaceous Basin, Peruc–Korycany Formation): from Čáslav, Central Bohemia (Svobodová, 1992) as *Plicatella* sp., from Pecínov (Svobodová et al., 1998) as *Plicatella tricornitata* (Weyland et Greifeld) Deák et Combaz (Svobo-Svobodová, 1992), from boreholes near Duchcov as *Appendicisporites* sp. (Svobodová, 1988) and from a borehole SK-9c near Svor in Northern Bohemia by Pacltová and Svobodová (1993) as *Appendiciporites tricuspidatus* Weyland et Greifeld.

Plicatella tricornitata (Weyland et Greifeld) Deák et Combaz sensu Svobodová (1992) from Čáslav is so similar to the spores of *S. ekrtii* described herein that we consider them identical. Other species described from the Peruc–Korycany Formation show differences. *Plicatella* sp. described by Svobodová et al. (1998) from Pecínov differs in lacking auricules, as far as we can observe from light microscope photographs. *P. tricornitata* (Weyland et Greifeld) Deák et Combaz sensu Svobodová et al. (1998) described from Pecínov differs from the spores of *S. ekrtii* in the presence of true appendices and well-pronounced laesura. Other recorded spore material is only mentioned in the text without illustration.

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Revision of the type material in the genus *Nathorstia* Heer (Filicales)

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ABSTRACT. **_Nathorstia angustifolia_ Heer from the Lower Cretaceous of Greenland has been revised and the true status of the genus _Nathorstia_ has been verified. _Nathorstia_ Heer is redefined here as a morphogenus of fern foliage recalling the family Matoniaceae, but lacking diagnostic characters of this family: sori consisting of radially arranged sporangia having _Matoniaceaeporites_ spores _in situ_. All the type material has been restudied and documented, including unsuccessful attempts in sampling for spores in situ. The lectotype of _Nathorstia angustifolia_ Heer is designed and its status is discussed.**

KEY-WORDS. **_Nathorstia_, morphogenus, Greenland, Lower Cretaceous.**

INTRODUCTION

Nathorstia Heer, a genus of Cretaceous ferns, was a source of numerous discussions for a long time (Seward 1927, Hirmer & Hörhammer 1936, Krasilov 1964, Andrews et al. 1970, Van Konijnenburg-van Cittert 1993, Tidwell & Ash 1994). The main reason of these discussions was a question whether this genus should belong to the family Matoniaceae or Marattiaceae. Several species of *Nathorstia* have been described from various stratigraphic horizons of the Cretaceous of both Hemispheres. Early Cretaceous records of *Nathorstia* are known from Greenland (Heer 1880), Russia (Krasilov 1967) and Argentina (Halle 1913, Passalia 2007). Late Cretaceous (Cenomanian) records came from Greenland (Nathorst 1908) and the Czech Republic (Bayer 1899, Nathorst 1908, Pátová & J. Kvaček 2006). The diagnosis of the genus has been gradually shifted far from its original content (Krasilov 1964) and now it seems to be quite different from that proposed originally by Heer (1880). Because of this difficult and unclear situation, we have decided to revise the genus *Nathorstia* based on Heer's type material in order to fix the status of the genus. In the present paper we suggest an emendation of its diagnosis using information gained from the revision of the type material of *N. angustifolia* housed in the Naturhistoriska Riksmuseet, Stockholm.

MATERIAL AND METHODS

All the material we have studied originated from the western coast of Greenland, locality Pattorfik [= Pátorfik, 70.72°N, 52.55°W], where it was collected by the Nordenskiöld's expedition in 1870. The Pattorfik locality shows large profiles of the Kome Formation, which belongs to the Lower Cretaceous (Pedersen 1976), more precisely to the Aptian-middle Albian (K. R. Pedersen, personal communication in 2007). The material is preserved as leaf impressions in dark grey brown mudstone. Its precise lithology is not known, because the section was not re-visited. All the studied material is housed in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

Material was examined by Zeiss Axioskop 2 plus stereomicroscope with Plan-neofluar objective and photographed by microscope camera AxioCam MRC and by digital camera Canon 300D with Sigma 1:2,8 macro lens. Images were adjusted in Adobe Photoshop. 7.0. Spores *in situ* were attempted to analyze using standard method published e.g. by Batten (1999).

SYSTEMATICS

Order Filicales

Family incertae sedis

Genus *Nathorstia* Heer 1880: 7

(non *Nathorstia* Seward 1894: 145)

Type: *Nathorstia angustifolia* Heer 1880: 7, pl. 1, figs 1-7. Accepted by Andrews (1970) and Van Konijnenburg-van Cittert (1993). For more arguments see below.

Nathorstia angustifolia Heer 1880

Text-figs 1a-d, 2a-f.

Syn: 1880 *Nathorstia angustifolia* Heer 1880: 7, pl. 1, figs 1-6.
?1880 *Nathorstia firma* Heer 1880: 7, pl. 1, fig. 7.
?1868*Danaeites firmus* Heer 1868: 81, pl. 44, figs 20-22.

Lectotype (designated here): S 112130a, figured on fig. 1a-c, (re-figured from Heer 1880, pl. 1, fig. 2).

Type locality: Pattorfik [= Pátorfik, 70.72°N, 52.55°W], Greenland.

Type horizon: Kome Formation, Lower Cretaceous.

Other material: S108097, S112129, S1121306b, S112131, S112132a,b, S112133.

Emended diagnosis: Simple pinnate fronds, pinnules entire-margined, lanceolate with bluntly acute apex and narrowing base. Main rachis robust. Rounded depressions representing possibly remains of sori arranged in one row on each side of the midrib. Primary vein reaching apex of the pinnule, secondary venation unclear.

Description: The lectotype (fig. 1a) represents a fragment of entire-margined pinnule with well impressed rounded bodies representing possibly impressions of sori. The pinnule is 108 mm long and 5 mm broad. Shallow rounded depressions (sori) are arranged in

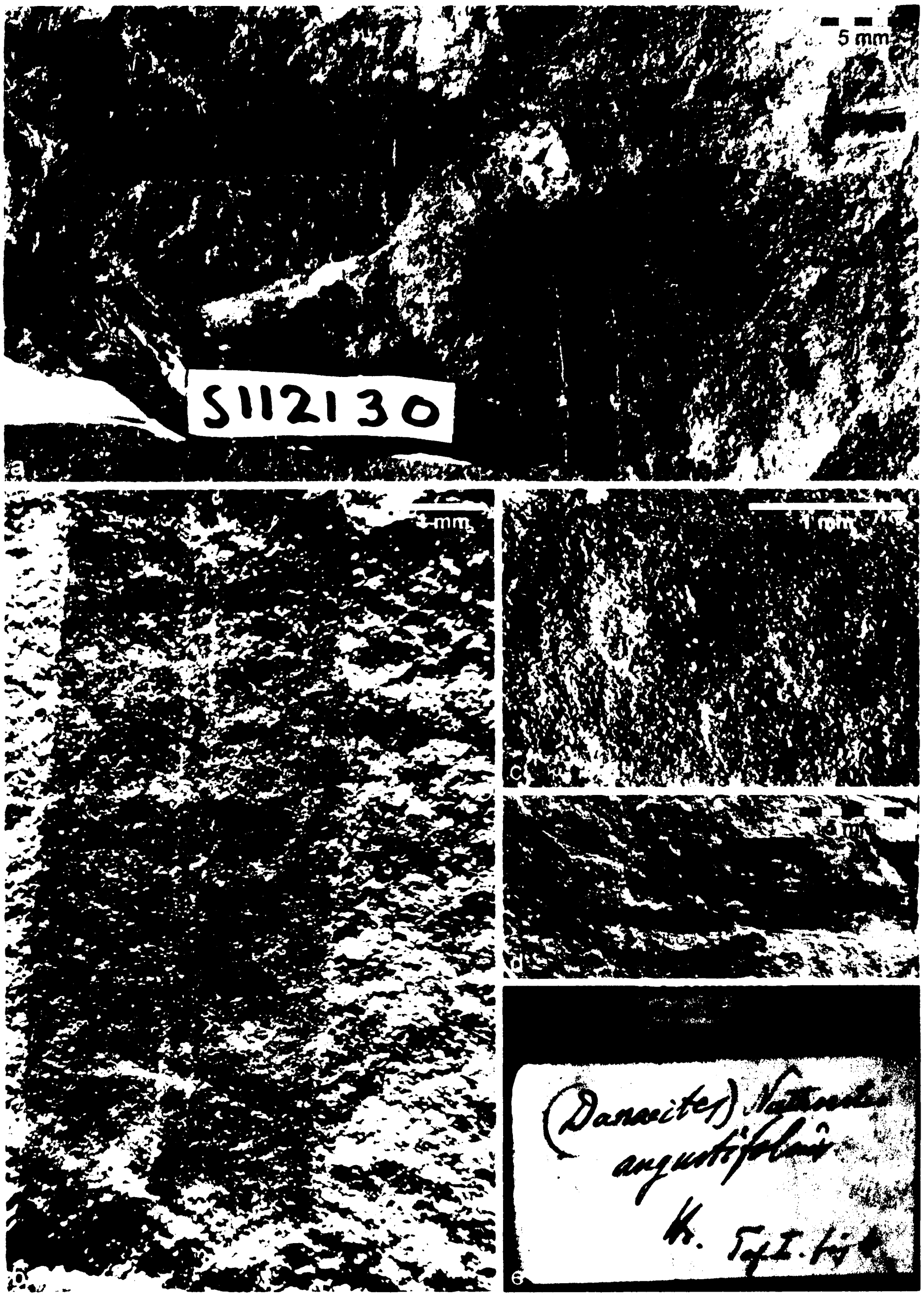

Fig. 1. *Nathorstia angustifolia* Heer, Pattorfik. a – lectotype (arrowed S112130a) and fragment of pinnule (S112130b), Heer 1880, pl. 1, fig. 2, S112130a; b – detail of lectotype showing secondary vein, arrowed, Heer 1880, pl. 1, fig. 2, S112130a; c – detail of circular depression, Heer 1880, pl. 1, fig. 2, S112130a; d – basal part of pinnule, Heer 1880, pl. 1, fig. 4, S112132a; e – original handwritten label by Heer.

two rows running parallel on each side of the primary vein (0.5 mm broad). Each depression (fig. 1b) is 0.8-1.1 mm in diameter. Some depressions are not completely rounded, showing slightly sinuate margin (fig. 1c). Venation of the pinnule is pinnate, but very poorly preserved. Secondary veins are leaving the midrib in right angles (fig. 2b). Further material described by Heer (1880) is represented by several fragments of pinnules having lamina 4-7.1 mm in breath and depressions 1-0.8 mm in diameter (fig. 1d, fig. 2 a-c, f). Two specimens from the type collection show fragments of compound leaves with pinnules narrowing to their base (fig 2 d,e). They are 15-34 mm in breath and 14-24 mm in length. Variability of the species is documented by additional fragments (No. S108097). All these specimens are accompanied with labels bearing Heer's autographs (fig. 1e).

DISCUSSION

The genus *Nathorstia* Heer (1880) is homonymous with *Nathorstia* Seward (*Nathorstia valdensis* Seward 1894, pl. 7, fig. 5, pl. 9, fig. 2) which represents a very different type of fern. The name *Nathorstia* Heer (1880) has priority over *Nathorstia* Seward (1894), which is illegitime.

In his paper on Greenland flora Heer (1880) mentioned two species: *Nathorstia angustifolia* Heer (1880) and *Nathorstia firma* (Heer) Heer (1880). The genus *Nathorstia* Heer is based on the type of *Nathorstia angustifolia* Heer, which is mentioned by Heer (1880) on the first place and mirrors his generic diagnosis. It is also generally accepted by other authors (Seward 1927, Andrews 1970, Van Konijnenburg - van Cittert 1993), although Farr et al. (1979) stated: "type non designatus" and Krasilov (1964) suggested *Reussia pectinata* as a type. The last suggestion would be only valid in case that Heer (1880) included *Reussia pectinata* Göppert in his protologue of *Nathorstia*. (*Reussia pectinata* Göppert is illegitimate name being based on illegitimate *Reussia* Presl 1838, non *Reussia* Endlicher 1836). However, Heer (1880) did not mention *R. pectinata* in his protologue and *R. pectinata* cannot be chosen for the type of the genus *Nathorstia*. Also the emendation of the genus *Nathorstia* by Krasilov (1964) is based on the specimens determined as *Nathorstia pectinata* (Göppert) Krasilov. These specimens are only slightly similar to *Nathorstia angustiloba* and the mutual comparison is not discussed by Krasilov (1964). He compares *N. pectinata* only to *Nathorstia latifolia* Nathorst from the Cenomanian of the Atane Formation in Greenland (Nathorst 1908).

Since times of Seward (1927) it is accepted that *N. angustifolia* includes *N. firma* from Kome in Greenland (Heer 1868, 1880). These two species differ only in the width of their pinnules and in the form of sori, which are oval in *N. firma*. After inspection of the specimens illustrated by Heer (1880) and housed in the Naturhistoriska Riksmuseet, Stockholm (Nr. S110074-01, S111082, S111144-02) we agree with Seward (1927) and Van Konijnenburg-van Cittert (1993) that a different shape of sori in *N. firma* was probably caused by deformation and that both species are very similar.

The type collection of *N. angustifolia* includes 5 specimens, which are poorly preserved impressions of sterile and fertile pinnules. Fertile pinnules show shallow rounded

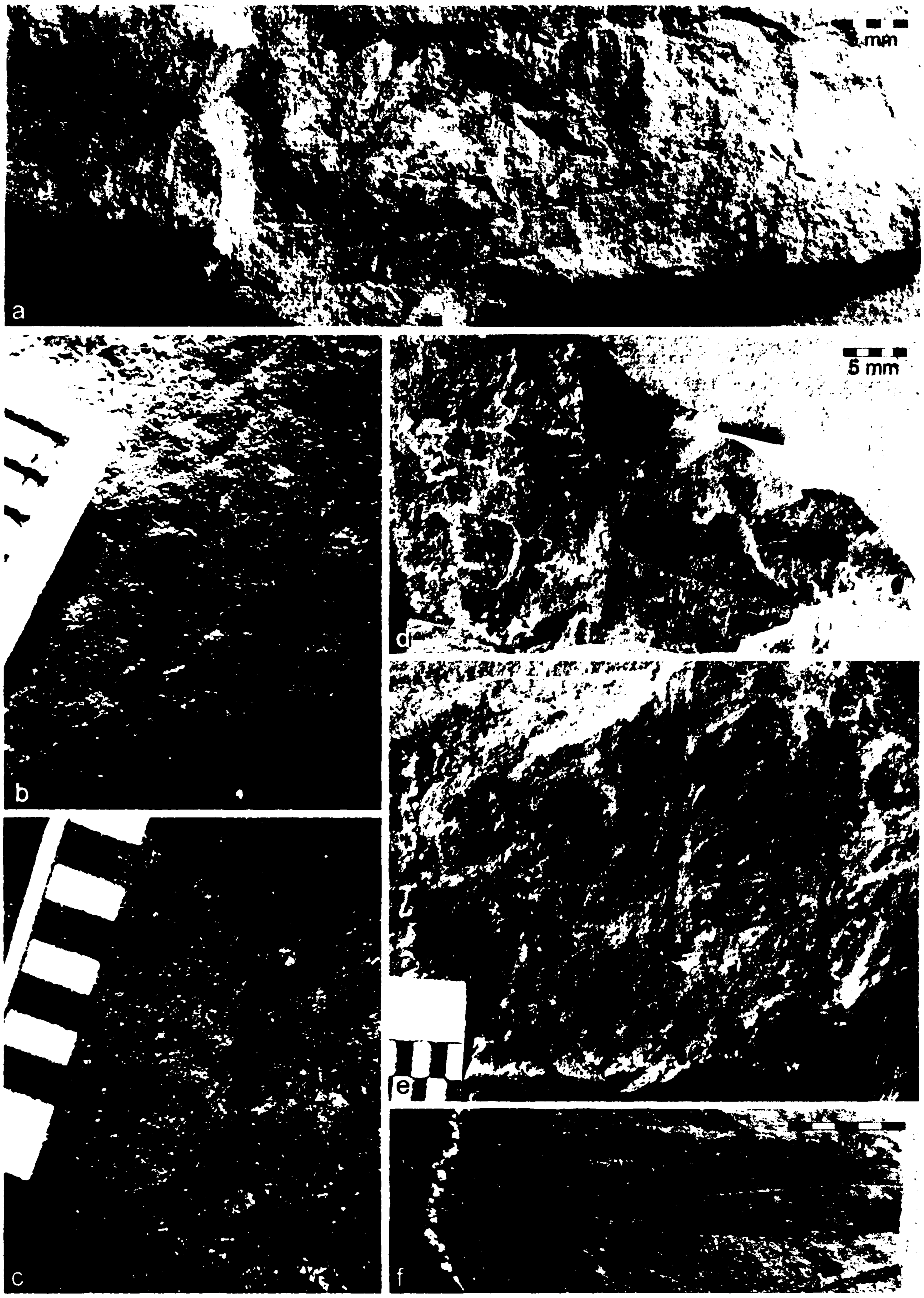

Fig. 2. *Nathorstia angustifolia* Heer, Pattorfik. a – two fragments of pinnule, Heer 1880, pl. 1, fig. 1, S112129; b, c – details of pinnule, Heer 1880, pl. 1, fig. 1, S112129; d – fragment of pinnate frond, Heer 1880, pl. 1, fig. 3, S112131; e – fragment of pinnate frond, Heer 1880, pl. 1, fig. 5, S112133; f – basal part of pinnule, S112132b.

depressions, probable remains of sori. It is not clear whether the sori are only impressed or whether they were detached before fossilization. Heer (1880) designating *Nathorstia* was not sure where the fern should be assigned systematically. He was discussing its similarity to "*Laccopteris dunkeri*" (Matoniaceae) and *Kaulfusia* (Marattiaceae). Later understanding of the genus *Nathorstia* was influenced by Nathorst (1808), who based his observations on *Nathorstia latifolia* interpreting its sori as fused in synangia. Nathorst (1908) compared *Nathorstia* with *Kaulfusia* and assumed that it belongs to the Marattiaceae. In the same way the genus was used by Halle (1913). Seward (1927) demonstrated that sporangia of *Nathorstia* are not fused and showed its great similarity to other fossil members of the Matoniaceae. However, Hirmer & Hörhammer (1936), revising fossil and recent genera of the Matoniaceae, excluded *Nathorstia* from the family and assigned it again to Marattiaceae. Krasilov (1964, 1967) in his studies on the Cretaceous flora from the Far East emended the genus *Nathorstia*. Unfortunately, for his emendation of the genus he used irrelevant material (see above). The material of *Nathorstia pectinata* (Göppert) Krasilov displays clearly isolated sporangia and spores of *Matoniaceaesporites* (Krasilov 1964, pl. 9) and other characters of the Matoniaceae. In the sense of Krasilov (1964) *Nathorstia* has been understood since its last revision (Van Konijnenburg-van Cittert 1993).

The present study of the type material of *Nathorstia angustifolia* reveals quite similar conclusions as suggested already by Seward (1927). However, it is absolutely impossible to show whether the depressions arranged in rows on pinnules represent sori or synangia (see figs 1 and 2). It is impossible to find clear diagnostic characters of the family Matoniaceae preserved in any specimen of the type collection. Poor impressions which could be interpreted as sporangia of *N. angustifolia* show that they were ovoid and not very many. The material definitely yielded no wedge-shaped sporangia, nor matoniaceous spores, which are preserved in many other species assigned to *Nathorstia* by later authors. Therefore, the genus *Nathorstia* is recommended here as a morphogenus accommodating impressions of fern fronds and isolated pinnae showing entire-margined lancoelate pinnules with clearly pronounced circular depressions (sori, synangia) running continuously on both sides of the midvein. Its systematic position is open. It probably belongs to the Matoniaceae, but could also represent poorly preserved fronds of ferns from other families, particularly from the Marattiaceae.

Those ferns recently assigned to *Nathorstia*, which show clear diagnostic characters of the family Matoniaceae (see Van Konijnenbirg-van Cittert 1993), should be transferred to another genus which will be published elsewhere (J. Kvaček & Dašková in prep.).

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A NEW LATE CRETACEOUS GINKGOALEAN REPRODUCTIVE STRUCTURE *NEHVIZDYELLA* GEN. NOV. FROM THE CZECH REPUBLIC AND ITS WHOLE-PLANT RECONSTRUCTION[1]

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During the Mesozoic Era, gingkoaleans comprised a diverse and widespread group. Here we describe ginkgoalean fossils in their facies context from the Late Cretaceous (Cenomanian) Peruc-Korycany Formation of the Czech Republic and present a reconstruction of tree architecture and ecology. Newly described in this study is the ovuliferous reproductive structure, *Nehvizdyella bipartita* gen. et sp. nov. (Ginkgoales). This ovuliferous organ consists of a bifurcating axis, terminated by large cupule-like structures, probably homologous to the collar of the recent *Ginkgo*. Each cupule encloses an orthotropous ovule. In specimens with the early developmental stages preserved, the entire ovule and young seed, with the exception of the micropylar area, is embedded in the cupule. Mature seeds consist of sclerotesta and sarcotesta. Monosulcate pollen grains of *Cycadopites*-type are found adhering to the seeds. Although similar to *Ginkgo* in terms of its large size and reduced number of seeds, *N. bipartita* differs from the extant genus in having ovules completely enclosed in a cupule-like structure. The co-occurrence of *N. bipartita* with ginkgoalean leaves of *Eretmophyllum obtusum* (Velenovský) Kvaček, J., ginkgoalean short shoots of *Pecinovicladus kvacekii* Falcon-Lang, and ginkgoalean trunk wood of *Ginkgoxylon gruettii* Pons and Vozenin-Serra in monodominant taphocoenoses at four geographically distant localities suggests that these remains all belong to one plant. This is supported by the close morphological and anatomical similarity between the different organs. Facies analysis of plant assemblages indicates that our Cretaceous tree occupied a water-stressed coastal salt marsh environment. It therefore represents the first unequivocal halophyte among the Ginkgoales.

Key words: Cenomanian; *Cycadopites*; *Eretmophyllum*; Ginkgoales; *Ginkgoxylon*; Late Cretaceous; *Nehvizdyella*; *Pecinovicladus*.

The order Ginkgoales contains a single extant species, *Ginkgo biloba*, but fossil studies demonstrate that this group of plants has, at certain times during its 200-million-year history, possessed much higher levels of diversity (Zhou, 1997). Peak diversity was attained in the Mesozoic Era, when ginkgoaleans comprised more than 13 genera (Tralau, 1968) and grew over much of the Pangean supercontinent (Royer et al., 2003). Although sterile ginkgoalean foliage is very common in Mesozoic strata, associated reproductive structures have only been documented very rarely. Furthermore, although fossil assemblages comprising both vegetative and reproductive organs are documented at some sites, only a few Mesozoic gingkoaleans have been reconstructed to date.

In this paper, we describe a new genus of ginkgoalean ovuliferous reproductive structure, *Nehvizdyella bipartita* gen. et sp. nov., from the Late Cretaceous (Cenomanian) of the Czech Republic. These fertile remains occur in facies-association with several other ginkgoalean morphotaxa, which all show strong morphological and anatomical similarities. Associated morphotaxa include tongue-shaped leaves referable to *Eretmophyllum obtusum* (Velenovský) Kvaček, J., pollen of *Cycadopites*-type, woody short shoots of *Pecinovicladus kvacekii* Falcon-Lang, and mature trunk wood of *Gingkoxylon gruettii* Pons and Vozenin-Serra (Uličný et al., 1997; Kvaček, 1999; Falcon-Lang, 2004). Based on these additional materials, we propose a whole-plant reconstruction for the ginkgoalean tree and utilize facies data to assess its paleoecology.

MATERIALS AND METHODS

The ginkgoalean plant material described here was collected at localities within the Peruc-Korycany Formation, the basal lithostratigraphic unit of the Bohemian Cretaceous Basin in the Czech Republic (sensu Čech et al., 1980). Palynological data indicate a late middle Cenomanian age for these beds (Pacltová, 1977, 1978). The four main sites are Hloubětín Brickpit (50°06'45" N, 14°32'02" E), a disused brick pit in the eastern part of Prague (material collected by Hluštík, 1973–1974), and three large working quarries, Pecínov Quarry near Rynholec (50°08'00" N, 13°54'34" E), Kamenná Panna Quarry near Horoušany (50°07'17, 14°44'09" E), and Vyšehořovice Brickpit (50°07'17", 14°45'12" E) east of the village of the same name (Fig. 1).

Geological mapping and sequence stratigraphic analysis has shown that the Peruc-Korycany Formation infills a series of palaeovalleys (Uličný and Špičáková, 1996). Palaeovalley-fill successions (Uličný et al., 1997; Uličný and Nichols, 1997) comprise the deposits of a variety of continental (braided rivers, meandering streams and floodplains, and anastomosed fluvial systems) and coastal environments (tidally influenced braided rivers, supratidal marshes, tidal flats, ebb-tidal deltas, estuaries, and lower shoreface). The ginkgoalean plant fossils were extracted from mudstone units interpreted as supratidal marsh facies at all four sites (Nguyen Tu et al., 2002). Ginkgoaleans form the dominant fossil component of these beds, which also contain the remains of the conifer *Frenelopsis alata* (K. Feistmantel) Knobloch, a few angiosperms, and a putative gnetalean (Uličný et al., 1997; Falcon-Lang et al., 2001).

Mudstone specimens dominated by ginkgoalean foliage (*Eretmophyllum*)

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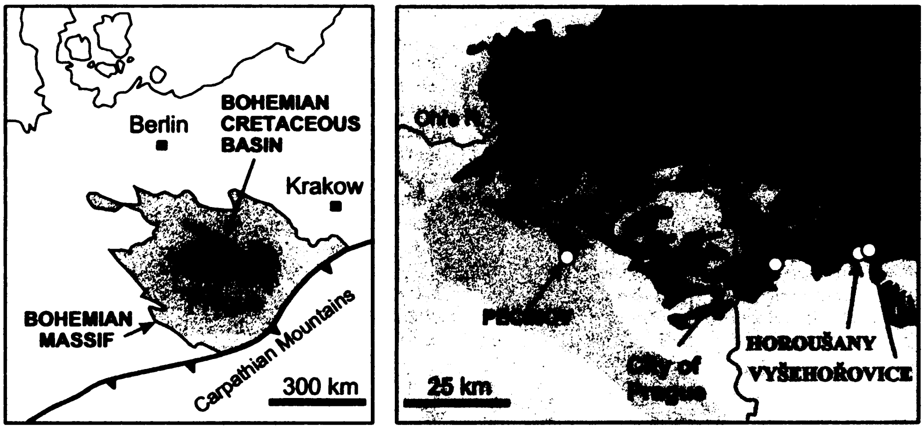


Fig. 1. Geological setting. Location of the Bohemian Cretaceous Basin in Central Europe (left) and location of the four fossil sites mentioned in this paper, surrounding Prague, Czech Republic (right). Dark grey area indicates Cretaceous Basin; light grey area indicates Bohemian Massif (after Uličný et al., 1997).

were treated in a solution of natrium carbonate. Other specimens were macerated for 8 h in diluted Schulze's solution and then stored in glycerine. After approximately 1 month, macerated specimens became partially translucent, although optimum translucence was not obtained until after 5 months of maceration and treatment in glycerine. Cuticles from the seed integument were then prepared using standard Schulze techniques (Kvaček, 1999, 2000). In addition to the ovules themselves, pollen grains that adhered to the seeds after maceration were separated using a dissecting needle with a human hair glued to its tip (Zetter, 1989; Zetter et al., 2002). Associated lignified and charred wood was also collected, and treated using standard HF techniques (Falcon-Lang et al., 2001). Resultant material was examined using an Olympus (Japan) SZX 12 binocular microscope, an Olympus (Japan) BX 50 light microscope, a Phillips (Germany) 515 SEM, and a Hitachi (Japan) S-3200 SEM. All specimens and preparations were deposited in the palaeobotanical collections of the National Museum, Prague (F 00003–15, F 00112–133, F 00189–191, F 02281, F 02293, F 02481–2483, F 02497–2500, F 02856, F 02886, F 02910–13, F 02926, F 02958, F 02972, F 03010–18, F 03038).

SYSTEMATICS

Genus—*Nehvizdyella* gen. nov. (Figs. 2–11)

Etymology—Diminutive drived from Nehvizdy, the village near where the fossils were found.

Type—*Nehvizdyella bipartita* gen. et sp. nov.

Generic diagnosis—Compound ovuliferous reproductive organ consisting of a main axis and two short secondary axes, each terminated by a large cupule-like structure. Each cupule encloses one orthotropous ovule. Seeds consist of sclerotesta and sarcotesta.

Species—*Nehvizdyella bipartita* gen. et sp. nov. (Figs. 2–11)

Synonym—*Nehvizdya obtusa* (Velenovský) Hluštík pro parte—seeds, megasporangiophores, Hluštík 1986: 100, pl. 1, figs. 1, 2, 6, text-fig. 8.

Specific diagnosis—Compound ovuliferous reproductive structure consisting of a main axis, stout and thick, which bears two short, apical secondary axes, each terminated by a cupule-like structure enclosing an ovule. In early developmental stages, the entire ovule, except the micropylar area, is embedded in the cupule. Ovule is orthotropous with micropyle facing distally. Seeds ovoid, having sclerotesta and sarcotesta. Remains of sarcotesta consisting of putative parenchymatous tissue. Outer cuticle of sarcotesta thick, bearing polygonal cells and stomata. Inner cuticle of sarcotesta very thin, bearing elongated cells. Sclerotesta hard and fragile. All the ovuliferous organs including main axis contain numerous resin bodies.

Holotype—Designated here F 03010, National Museum, Prague, (Figs. 3–5).

Paratype—Designated here F 03011, National Museum, Prague, (Fig. 2).

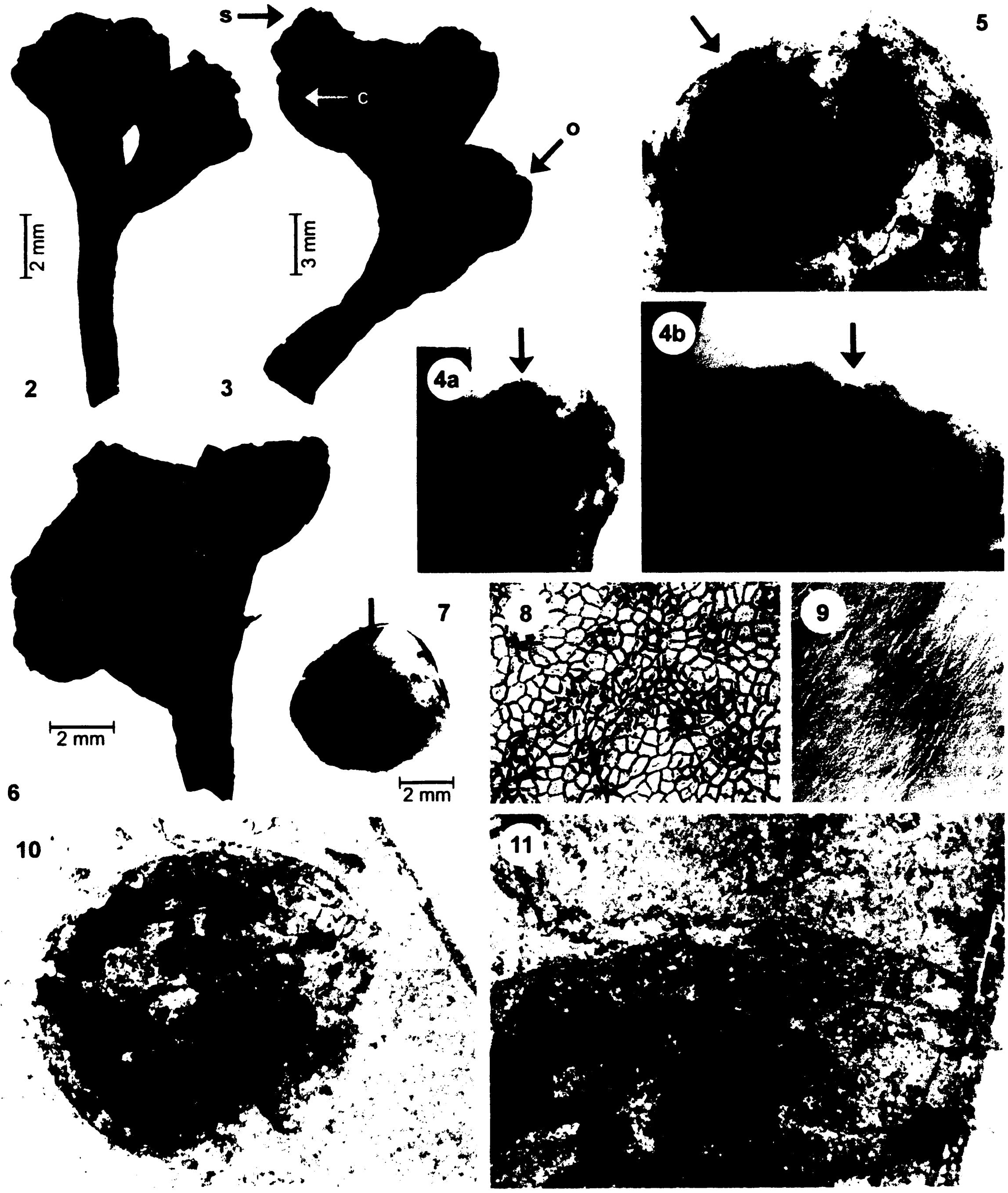
Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

Type locality—Horoušany, Kamenná Panna Quarry near Nehvizdy (holotype F 03010, paratype F 0301, F 03012–14, F 03018), Czech Republic (50°07′17″, 14°44′09″ E).

Other material—Prague, Hloubětín Brickpit (F 00189–91); Pecínov, unit 3 (F 03015–17), Vyšehořovice Brickpit (F 02497–99).

Etymology—Derived from bipartite nature of the organ.

Description—The holotype of *Nehvizdyella bipartita* (F 03010) is a 15 mm long ovuliferous reproductive structure bearing two cupules (Fig. 3). The main axis is 6 mm long and 2 mm in diameter and has fine longitudinal striations. Secondary axes, 3–5 mm long and 2 mm in diameter, are dichotomously attached to the terminal part of the main axis. Each secondary axis is wrinkled, and its apical part gradually passes into the cupule-like structure. The holotype shows two cupules. The larger cupule is 8.5 mm in diameter and bears the remains of a seed. The smaller cupule (Figs. 4–6) is 4.5 mm in diameter encloses an orthotropous ovule (2.5 mm in di-



Figs. 2–11. *Nehvizdyella bipartita* gen. et sp. nov. Horoušany, Kamenná Panna Quarry, general morphology. **2.** Paratype, ovuliferous organ, each secondary axis terminating with a cupule-like structure enclosing an ovule, F 03011, ×4. **3.** Holotype, ovuliferous organ showing partly preserved seed and one ovule. c = cupule, o = ovule, s = seed. F 03010.×4. **4a.** Ovule with micropyle (arrowed) enclosed in a cupule-like structure, detail of Fig. 3, holotype, macerated. F 03010. ×6.5. **4b.** Detail of micropyle (arrowed), detail of Fig. 3, holotype. F 03010. ×25. **5.** Detail of macerated ovule, full/deshed line indicating presumed boundary of ovule, detail of Fig. 3 (presumed micropyle arrowed), holotype. F 03010. ×15. **6.** Empty cupules attached to the main axis. F 03014. ×6.

ameter). There is an ovoid mass of tissue (1 mm in diameter), which differs from the surrounding cells (Fig. 5). It is interpreted as a nucellus or proembryo. The micropyle and pollen chamber are situated in the terminal part of the ovule (Fig. 4a, b). Other studied material includes five additional reproductive axes with or without seeds or ovules. They vary in length from 11 mm up to nearly 20 mm (paratype F 03011, Fig. 2). Their main axes are 5–9 mm long and 1–2 mm in diameter. Secondary axes are 2–3 mm in length. Cupule-like structures bearing mature seeds are 4–8 mm in diameter and have a well-cutinized rim (Fig. 6). All the ovuliferous organs except sclerotesta contain numerous resin bodies (Fig. 5).

Where the seeds are attached to an axis, they are always aborted at some stage of maturation. Fully mature seeds only occur in a detached state, typically filled with sediment (Fig. 10), which probably penetrated through the broken sclerotesta after burial. Furthermore, mature seeds are not usually preserved intact and therefore rarely occur in bulk-macerated material. The generally poor preservation of mature seeds is probably linked to the development of the sclerotesta, which would have accentuated fragmentation during attrition resulting from sedimentary transport, maceration, and postsedimentary compression. Another similar case of differences between the preservation of immature and mature seeds has been noted by Rothwell and Holt (1997) in Maastrichtian assemblages from Alberta, Canada.

The detached seed compressions (Fig. 10) are circular or slightly elliptic, 9–10 mm in diameter. They show two layers of coalified matter (Fig. 11). The inner layer, consisting of shiny black coalified matter, is usually 0.1 mm thick. It is interpreted as sclerotesta. The outer layer, consisting of faint (porose) matter, 0.2–4 mm thick, is interpreted as sarcotesta. It is covered by a thick cuticle (Fig. 11). The outer cuticle of the sarcotesta is easily macerated and comprises stomata surrounded by 6–7 subsidiary cells (15–25 μm by 20–35 μm) interspersed between isodiametric cells (10–25 × 20–35 μm, Fig. 8). The inner cuticle of the sarcotesta is poorly preserved and has elongated cells (Fig. 9). The sclerotesta is fragile and has a thin cuticle, which is difficult to prepare.

Some seeds are preserved intact (e.g., F 03018, Fig. 7), but do not possess sclerotesta, and when macerated, have a short, central stalk (2–3 mm). These fossils are interpreted as immature seeds.

GINKGOALEAN AFFINITY

The ovuliferous structure, *Nehvizdyella bipartita*, bears diagnostic characters of both living and fossil representatives of the Ginkgoales (e.g., Page, 1990; Stewart and Rothwell, 1993). The ovuliferous organ is characterized by bifurcating axes, that each bear one ovule; seeds with haplocheilic stomata, axes and seeds bearing resin bodies; and associated leaves having two vascular bundles in petioles and dichotomizing venation. Further evidence for ginkgoalean affinity is given by the facies-association of this ovuliferous organ and foliage with a variety of unequivocally ginkgoalean organs including pollen, foliage, woody short shoots, and trunks (details discussed later). The most remarkable feature of *Nehvizdyella* is the upward-oriented cupule-like structure. It is striated and probably built of nonwoody tissues. It encloses the ovule, and in later developmental stages supports a seed. Based on its position and function, we suggest that it is homologous with the collar of extant *Ginkgo*.

Similarity of *Nehvizdyella* to extant *Ginkgo* is evident in terms of the number of seeds per axis and their large size (length 20–22 mm in *Ginkgo*, 9–10 mm in *Nehvizdyella*). However, *Nehvizdyella* differs from *Ginkgo* in having ovules, which are mostly enclosed in a cupule-like structure, and in being facies-associated with the *Eretmophyllum* type of leaves (details discussed later). Although morphologically similar, *Nehvizdyella bipartita* is probably only distantly related to extant *Ginkgo biloba*. Reduction of the number of seeds per ovuliferous structure, the increasing size of the seeds, and the unification and expansion of the leaf lamina are probably general trends in several lineages of the Ginkgoales.

Nehvizdyella is most similar to ovuliferous reproductive structures associated with the genus *Grenana* Samylina from the Middle Jurassic of Angren, which have similarly sized seeds embedded in a large cupule (Appendix S1, see Supplemental Data accompanying online version of article). *Grenana* was originally described as a pteridosperm (Samylina, 1990), but later Zhou (1997) reinterpreted it as a member of the Ginkgoales. Although *Nehvizdyella* could be closely related to *Grenana*, detailed comparison between these two taxa is problematic because the holotype of *Grenana angrenica* Samylina (number 813/1N13) is a sterile leaf compression (Samylina, 1990). Although the aforementioned reproductive structures, including seeds and cupules, are facies-associated with the leaves, they never occur in an attached state. It is important to note that fig. 1 of Samylina (1990) is merely a hypothetic reconstruction and does not represent an actual specimen. Consequently, we consider the reinterpretation of *Grenana* by Zhou (1997, p. 185) to be misleading. We maintain that the genus *Grenana* is best reserved for the foliage alone and that the facies-associated reproductive structures should be classified as a new taxon.

The genus *Nehvizdyella* is also similar to the ginkgoalean ovuliferous reproductive structures *Umaltolepis* Krassilov from the Lower Cretaceous of Siberia (Krassilov, 1972) and *Toretzia* Stanislavski from the Triassic of Ukraine (Stanislavsky, 1973); they all have one or two ovules per axis (Appendix S1). However, *Umaltolepis* differs from *Nehvizdyella* in having a bract supporting the ovule, in having bracts at the base of the seed-bearing axis, and by the absence of a cupule-like structure. *Toretzia* differs from *Nehvizdyella* in having inverted anatropous seeds and in lacking cupule-like structures. Additionally, both *Toretzia* and *Umaltolepis* differ from *Nehvizdyella* in having linear ribbon-like leaves named *Pseudotorellia.*

Of the other fossil ginkgoalean reproductive structures described in the literature, all differ substantially from *Nehvizdyella* (Appendix S1). *Schmeisneria* Kirchner and Van Konijnenburg-Van Cittert from the Jurassic of Germany has small

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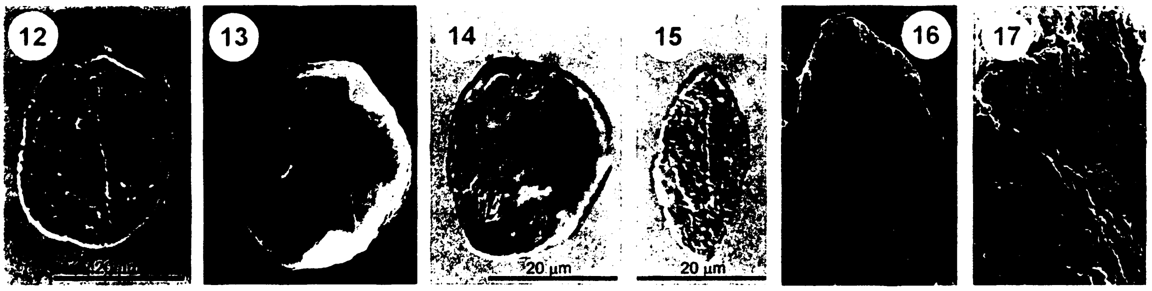
7. Dispersed seed with stalk (arrowed), macerated. F 03018. ×4. **8.** Outer cuticle of sarcotesta showing stomata. F 03018c. ×100. **9.** Inner cuticle of sarcotesta. F 03018b ×100. Figs. 10–11. *Nehvizdyella bipartita* gen. et sp. nov. Hloubětín Brickpit, seed morphology. **10.** Dispersed seed compression, F 00189. ×5. **11.** Detail of seed anatomy showing sarcotesta (sa), epidermis of sarcotesta (e), and sclerotesta (sc), detail of Fig. 10. F 00189. ×15.



Figs. 12–17. *Cycadopites* sp. Horoušany, Kamenná Panna Quarry, pollen morpology. **12.** Pollen grain showing concave sulcus, light microscopy (LM). F 03018c. ×1000. **13.** The same pollen grain as in Fig. 12, SEM. F 03018c. ×1000. **14.** Pollen grain showing irregularly open sulcus, LM. F 03018d ×1000. **15.** Boat-shaped pollen grain showing narrow sulcus, LM. F 03018e, ×1000. **16.** Partly fragmented pollen grain showing intrareticulate sculpture of sulcus, SEM. F 03018f ×1000. **17.** Detail of exine in sulcus, detail of Fig. 16, SEM. F 03018f. ×4000.

orthotropous ovules, and is locally attached to short shoots of *Glossophyllum* or *Eretmophyllum* type (Kirchner and Van Konijnenburg-Van Cittert, 1994). *Yimaia* Zhou and Zhang from the Middle Jurassic of China shows eight to nine sessile anatropous ovules, attached to or facies-associated with *Baiera* and *Ginkgoites* foliage (Zhou and Zhang, 1988, 1992). *Karkenia* Archangelsky from the Lower Cretaceous of Argentina has numerous small anatropous ovules per axis and is facies-associated with a variety of foliage types including *Sphenobaiera*, *Ginkgodium*, and *Eretmophyllum* (Archangelsky, 1965; Del Fueyo and Archangelsky, 2001). It probably represents a distinct, perhaps ancestral, lineage within the Ginkgoales, together with the Palaeozoic genus *Trichopitys* (Zhou, 1997).

FACIES-ASSOCIATED PLANT REMAINS

A variety of other unequivocally ginkgoalean morphotaxa co-occur in the same depositional facies as *Nehvizdyella bipartita* at four widely spaced localities. This assemblage comprises a single morphotaxon of pollen, sterile foliage, short shoot, and trunk wood, with fossil remains being preserved both as compressions and charcoal. The facies association, together with close anatomical similarities, strongly suggest that all these organs belonged to the same plant.

Pollen*—Cycadopites* sp. (Figs. 12–17)

Material studied—F 03018 c, d, e, f, National Museum, Prague.

Horizon and locality—Late Cretaceous (Cenomanian) Peruc-Korycany Formation, at Horoušany, Kamenná Panna Quarry near Nehvizdy.

Description—Eleven pollen grains and their fragments were found adhering to the exterior of the seed of *Nehvizdyella bipartita*. They were the only pollen grains adhering on seed no. F 03018. Pollen grains were photographed during maceration of the seed cuticle, so they are in various modes of preservation and fragmentation.

Pollen grains are boat shaped with a single sulcus, not more than 30 µm in diameter (Figs. 12–16). The sulcus occupies the entire length of the grain and is slightly concave (Figs. 12, 13). The pollen surface is scabrate, and microverrucate (Fig. 12). Auricular projections observed by Sahashi and Ueno (1986) are visible and have a reticular-like sculpture on the germinal aperture. This sculpture is also present in an internal part of the sulcus (Fig. 17).

Discussion—The pollen grains attached to seeds of *Nehvizdyella bipartita* agree with the genus *Cycadopites* Wodehouse (ex Wilson and Webster, 1946) in having the same size and shape and one colpus and a similar exine pattern. The genus was based on material from the Palaeocene of Red Lodge, Carbon County in Montana, USA (Wodehouse, 1933; Wilson and Webster, 1946) and later emended by Krutzsch (1970) and Nichols et al. (1973). The type species, *Cycadopites follicularis* Wilson and Webster 1946, differs from the present *Cycadopites* sp. in larger size and rather smoother surface. The most similar pollen taxa to *Cycadopites* sp. are *Cycadopites fragilis* Singh and *Cycadopites nitidus* (Balme) de Jersey (1964), which are commonly encountered in the same supratidal marsh facies that contain *N. bipartita* in the Bohemian Cretaceous Basin (e.g., Pacltová and Svobodová, 1993; Svobodová, 1990, 1992; Svobodová et al., 1998; Uličný et al., 1997). They both agree in general morphology with the material described herein attached to *N. bipartita*, having nearly smooth or faintly granulate exine.

Cycadopites fragilis was originally described from the Lower Cretaceous of Alberta (Singh, 1964) and is characterized by a sulcus extending the whole length of the grain and a smooth surface. *Cycadopites nitidus* was originally described from the Lower Cretaceous of Australia (Balme, 1957). It is characterized by a narrow sulcus extending the full length of the distal surface, which is slightly expanded at the extremities, and a faintly granulate exine. These two types of pollen primarily differ only in terms of size, and we therefore suggest that the two Czech species likely represent taphonomic or ontogenetic variants. This view has been previously discussed by Norris (1967), who identified a similar intergradational relationship between two other *Cycadopites* pollen species. In summary, we suggest that *C. fragilis* and *C. nitidus* in the Cretaceous Bohemian Basin of the Czech Republic were probably produced by the same species that bore *N. bipartita* organs.

According to the morphological classification scheme introduced by Thomson and Pflug (1953) the pollen grains described here are also similar to the genus *Monocolpopollenites* Pflug and Thomson in Thomson and Pflug 1953. However, *Monocolpopollenites* differs from our material in its shorter sulcus and in having marginal folds. It is also smaller and confined mostly to pollen derived from monocots.

Foliage—Eretmophyllum obtusum (Velenovský) Kvaček, J., 1998 (Figs. 18–24)

Holotype—F 00003, Velenovský 1885, pl. 1, fig. 8, National Museum, Prague, refigured herein (Fig. 18).

Type locality—Nehvizdy (old sandstone quarry in east surroundings of the village).

Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

Other material—Nehvizdy (holotype F 00003, F 00004–7, F 00012, 13); Prague, Vysočany (F 00010); Lipenec (F 00008, 9); Kralupy and Vltavou (F 00014, 15); Prague, Hloubětín (Velenovský type collection-F 00011); Prague, Hloubětín Brickpit (F 00112–133, F 00189–191, F 02856); Horoušany, Kamenná Panna Quarry (F 02886, F 02958, F 02972); Pecínov Quarry, unit 3 (F 02281, F 02293, F 2481–3, F 02497–2500, F 02856).

Description—Leaves of *Eretmophyllum obtusum* are large (up to 11 cm long and up to 2.5 cm at their widest point), tongue-shaped, coriaceous, and entire-margined with a typically obtuse apex and cuneate base (Figs. 18, 19). The massive well-pronounced petiole (3 mm in diameter) contains two veins (Fig. 19). The veins dichotomously branch near the base of leaf, run subparallel to leaf lamina, and converge near the apex at a high angle. Up to 8–12 veins per cm occur in the medial part of the leaf. The adaxial cuticle is very heavily cutinized, composed of polygonal, isodiametric to slightly elongate cells, that are arranged in longitudinal rows with anticlinal walls that are straight or slightly bent (Fig. 23). The abaxial cuticle is also heavily cutinized, with costal and intercostal bands (Fig. 20). Intercostal cells are polygonal, elongate, and occur in longitudinal rows. Costal bands are constructed of strongly cutinized polygonal, isodiametric cells, and stomata, which are randomly scattered or arranged in short rows (Fig. 24). Stomata are haplocheilic, deeply sunken, and surrounded by 4–6 subsidiary cells (Fig. 22). Subsidiary cells are strongly cutinized and typically bear papillae that form a raised coronal rim (Fig. 21). Numerous circular or spindle-shaped resin bodies occur in the mesophyll tissue (Fig. 20).

Discussion—These tongue-shaped leaves were first described from the Cenomanian of Bohemia as *Podozamites obtusus* (Velenovský, 1885), but their ginkgoalean affinity was later established by Velenovský and Viniklář (1926, 1927). Believing that the leaves were not arranged in bundles and given their superficial similarity to *Glossophyllum*, Hluštík (1977) erected the genus *Nehvizdya* for this foliage type. In his revision of gymnosperm foliage from the Bohemian Cenomanian, Kvaček (1998, 1999) transferred these fossil leaves to the genus *Eretmophyllum*, introducing a new combination *Eretmophyllum obtusum* (Velenovský) Kvaček J. (2000). Gomez et al. (2000) attempted to distinguish *Eretmophyllum* from *Nehvizdya* on the basis of the presence or absence of papillae on subsidiary cells as the differential character. However, this character is variable among genera in the Ginkgoales, and the suggested splitting of *Nehvizdya* and *Eretmophyllum* is consequently not accepted herein. The ginkgoalean affinity of *Eretmophyllum* is based on its dichotomous venation, which arises from the two main petiole veins, and its cuticle having haplocheilic stomata (Thomas, 1913).

Short shoots—Pecinovicladus kvacekii Falcon-Lang, 2004 (Figs. 25–34)

Holotype—F 02912; National Museum, Prague, refigured herein (Fig. 25).

Type locality—Pecínov Quarry, unit 3.

Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

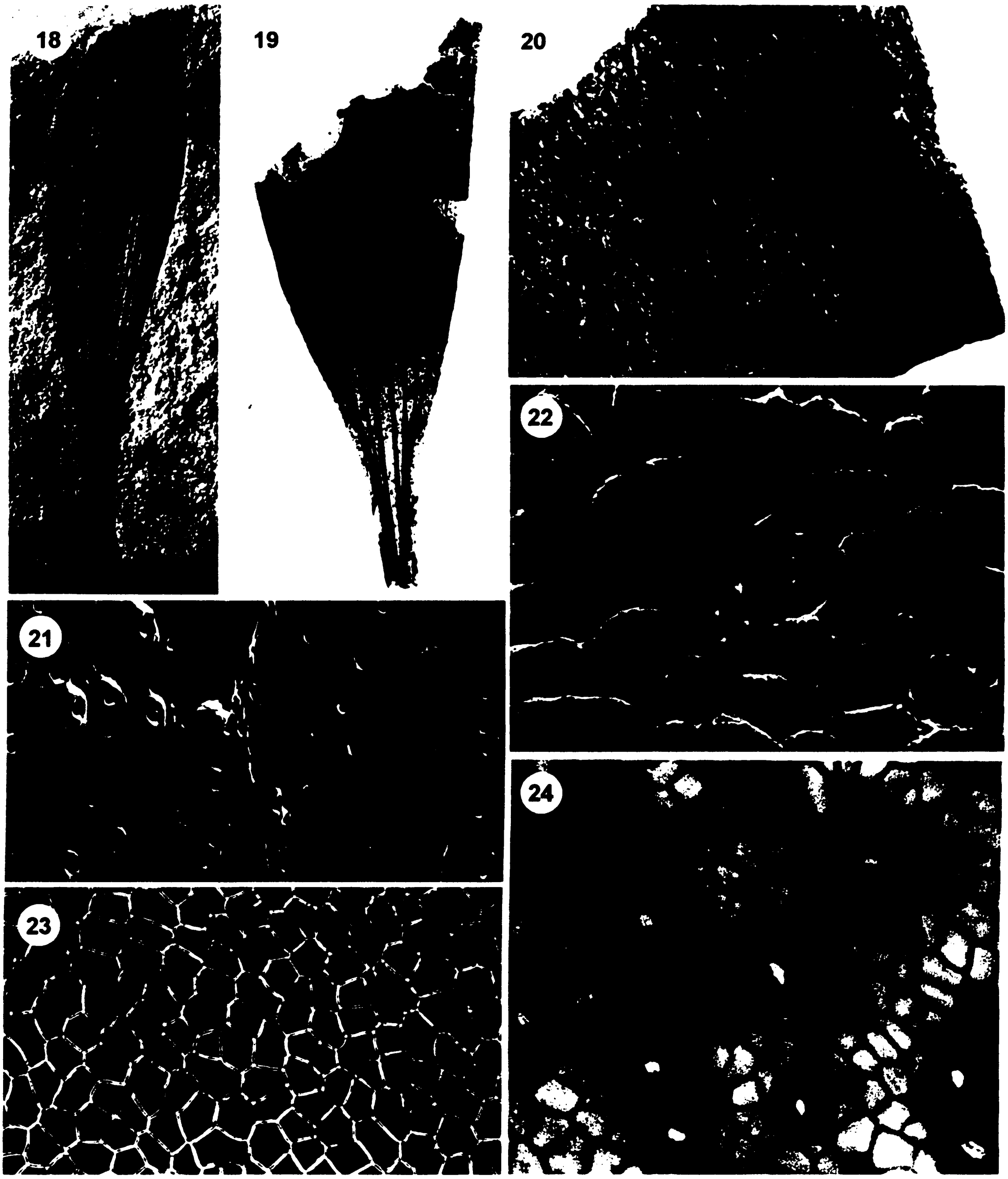
Other material—Pecínov Quarry, unit 3, F 02910, F 02911, F 02913-F 02926.

Description—*Pecinovicladus kvacekii* consists of 7–13 mm diameter shoots comprising pith, xylem, periderm, leaf traces, and branch traces (Fig. 25). The 1.6–2.2 mm diameter pith is parenchymatous. The xylem layer is 0.5–1.8 mm in radius (Fig. 26). Mucilage ducts (70–110 μm in diameter, >1.1 mm high) surrounded by axial parenchyma occur in the inner part of the secondary xylem (Fig. 27). Xylem comprises scalariformly-thickened primary and metaxylem succeeded by pycnoxylic secondary xylem composed of irregularly arranged tracheids (7–26 μm in diameter). Tracheids have 1–2-seriate, alternate or mixed, circular, bordering pitting on the radial walls (Fig. 28). Cross-fields comprise 1–6 taxodioid or cupressoid pits per field (Fig. 29). Axial parenchyma, arranged in vertical files may locally contain inflated cells, 25–45 μm in diameter, containing crystalline molds (Fig. 30). Rays are very short (1–7 cells high) and uniseriate, being spaced 5–11 tracheids apart (Fig. 31). The cambial zone, 55 μm radius, contains inflated parenchyma and rhombic crystal molds. The 2.5 mm radius periderm comprises parenchyma, resin-filled fibers and sieve cells.

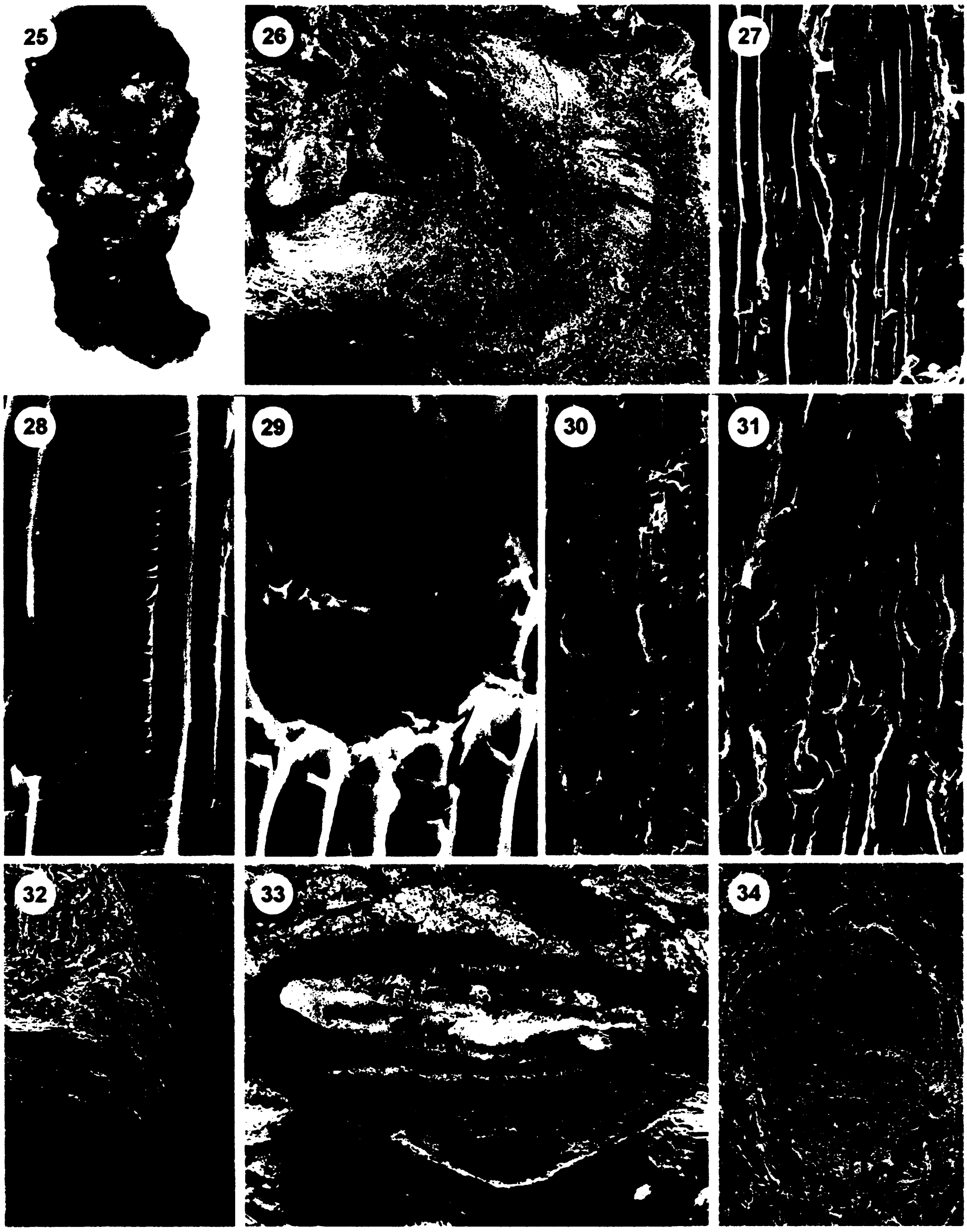
Leaf traces, comprising an oval adaxial xylem strand and a crescent-shaped abaxial phloem strand, are 1.0–1.5 mm in diameter at the point of departure from the secondary xylem, and arranged with a 5/13 helical phyllotaxy (Figs. 25, 32). Leaf bases preserved on the exterior of the axis, 2.7–3.5 mm wide and 1.45 mm thick, comprise xylem, phloem, mesophyll and epidermis (Fig. 33). The vascular bundle ramifies into >6 veins at the leaf base. Some shoot specimens have fewer leaf traces, but have secondary branch traces (1.8–2.1 mm diameter) comprising a 0.8 mm diameter pith and a 0.8 mm radius secondary xylem layer. A few secondary branches are positioned in the leaf axil (bracts) and may represent the detached peduncle of reproductive structures (Fig. 34).

The gingkoalean affinity of this morphotaxon is indicated by a combination of features including, most importantly, the presence of inflated axial parenchyma in the secondary xylem, which demonstrably once contained crystalline druses (Gunckel and Wetmore, 1946; Greguss, 1955; Scott et al., 1962). Additional ginkgoalean features are irregularly arranged files of wide and narrow tracheids in the secondary xylem (Srivastava, 1963), and very short rays (Mastogiuseppe et al., 1970).

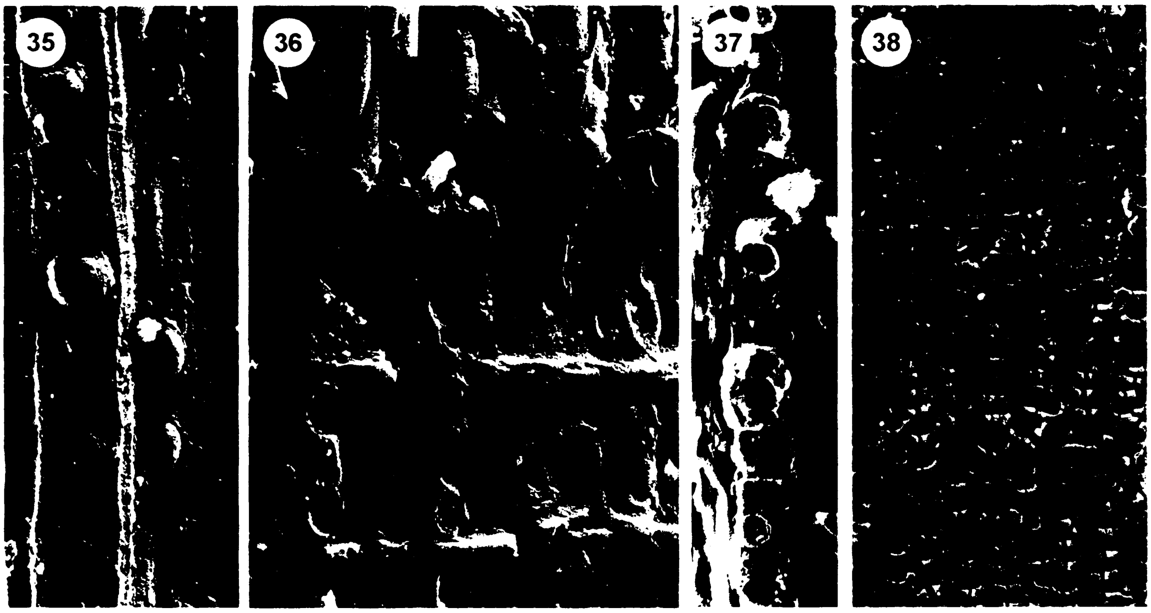
Mature wood—Ginkgoxylon gruettii Pons and Vozenin-Serra 1992 (Figs. 35–38)



Figs. 18–24. *Eretmophyllum obtusum* (Velenovský) Kvaček, J., leaf morphology and anatomy. **18.** Holotype, leaf impression, Nehvizdy. F 00003. ×1. **19.** Basal part of naturally translucent leaf showing venation pattern, Prague, Hloubětín Brickpit. F 00116. ×2.5. **20.** Macerated leaf showing resin bodies, Pecínov Quarry, unit 3. F 02483. ×10. **21.** Outer part of abaxial leaf cuticle, SEM, Pecínov Quarry, unit 3. F 02481b. ×100. **22.** Inner part of abaxial cuticle, SEM, Pecínov Quarry, unit 3. F 2481b. ×500. **23.** Adaxial cuticle, type collection of Velenovský, LMM, Prague, Hloubětín. F 0008. ×200. **24.** Abaxial cuticle, type collection of Velenovský, LMM, Prague, Hloubětín. F 0008. ×200.



Figs. 25–34. *Pecinovicladus kvacekii* Falcon-Lang, anatomy. **25.** Holotype, longitudinal view of branch, Pecínov. F 02912. ×2.5. **26.** Primary branch in transverse section (TS) with secondary branch, Pecínov. F 02912. ×10. **27.** Mucilage duct surrounded by epithelial cells, Pecínov, radial longitudinal section (RLS). F 02909. ×180. **28.** Tracheid with alternate and opposite bordered pits, Pecínov, RLS. F 02910. ×650. **29.** Cross-field pitting, Pecínov, RLS. F 02909. ×1000. **30.** Inflated axial parenchyma, Pecínov, tangential longitudinal section (TLS). F 02909. ×150. **31.** Uniseriate rays, Pecínov, TLS. F 02910. ×300. **32.** Departing leaf trace, Pecínov, RLS. F 02910. ×30. **33.** Leaf trace showing xylem and phloem bundles, Pecínov, TLS. F 02910. ×18. **34.** Reproductive axis (peduncle) embedded in branch, position in leaf axil, Pecínov, TLS. F 02911. ×40.



Figs. 35–38. *Ginkgoxylon gruettii* Pons and Vozenin-Serra, wood anatomy, Hloubětín Brickpit. **35.** Uniseriate, spaced tracheid pits, radial longitudinal section (RLS). F 03038. ×1000. **36.** 2–8 cupressoid cross-field pitting, RLS. F 03038. ×1250. **37.** Chains of inflated axial parenchyma, RLS. F 03038. ×200. **38.** Tracheids in transverse section (TS) showing faint growth interruption. F 03038. ×250.

Holotype—10532, Palaeobotany Laboratory, Pierre and Marie Curie University, Paris.

Type locality—Carrière du Bouillard, Nord d'Angers, France.

Type horizon—Late Cretaceous (Cenomanian), Jumelles and Brissac Formation.

Material studied—F 03038, National Museum, Prague.

Horizon and Locality—Late Cretaceous (Cenomanian) Peruc-Korycany Formation, at Prague, Hloubětín Brickpit.

Description—Mature ginkgoalean wood is known from a single trunk specimen, 13 cm in diameter and >1.09 m in length, preserved in the salt marsh peat facies at Hloubětín Brickpit. Anatomically, the wood is pycnoxylic, consisting only of tracheids and rays. In radial longitudinal section (RLS), tracheids are characterized by uniseriate bordered pits which are typically spaced at least one pit diameter apart (Fig. 35). Both borders (9–10 μm in diameter) and apertures (2–3 μm in diameter) are circular. Rays are composed of parenchyma cells that are 50–75 μm long, 20–30 μm high, and 20–30 μm wide, and have well-preserved cross-field pitting. Typically 2–8 circular cupressoid pits, each 5–6 μm in diameter, occur clustered in the cross-field region (Fig. 36). Chains of inflated axial parenchyma, 3–12 cells in length are common (Fig. 37). Axial parenchyma cells are large (25–45 μm in diameter), locally thick-walled (up to 8 μm thick), and may contain moldic preservation of crystalline druses. In tangential longitudinal section (TLS), rays are uniseriate and short (1–12 cells high). Tangential tracheid pits are absent. In transverse section (TS), rays are spaced 90–210 μm apart, and may be up to 3–4 mm long. Tracheids have tangential diameters of 14–22 μm and radial diameters of 12–21 μm. Middle lamellae are present between adjacent trachieds indicating that the wood is lignified, not charred. Growth rings are absent over several centimetres, but subtle growth interruptions do locally occur with an irregular spacing (Fig. 38).

This wood corresponds closely to *Ginkgoxylon gruettii* Pons and Vozenin-Serra from the Cretaceous (Cenomanian) of Anjou, France. This species differs from the Czech specimens in exhibiting rare biseriate trachied pitting, rare biseriate rays that are 1–26 cells high, and fewer cross-field pits (1–6). Such differences are of little taxonomic significance and likely reflect ontogenetic variability (Falcon-Lang, 2005a). For these reasons, our mature woods are assigned to *Ginkgoxylon* cf. *G. gruettii*. This morphotaxon has also recently been discovered in Cenomanian deposits at Charente in western France (Perrichot, 2000). One of the key features that allows this morphotaxon to be referred to the Ginkgoales is, as previously noted, the presence of druse-filled, inflated axial parenchyma chains (Gunckel and Wetmore, 1946; Greguss, 1955; Scott et al., 1962).

WHOLE-PLANT RECONSTRUCTION

Despite the abundance and diversity of Cretaceous ginkgoalean remains, assemblages of isolated morphotaxa have rarely been reconstructed in terms of a whole-plant. However, it is important that such attempts are made in order to gain a true sense of ginkgoalean diversity and phylogeny (Tralau, 1968; Zhou, 1997; Czier, 1998). Some ginkgoalean taxa show a high degree of polymorphism with up to three genera of sterile foliage associated with one reproductive structure, and locally one genus of sterile foliage may have several associated reproductive structures (Zhou, 1997). Consequently, analysis of isolated morphotaxa may result in either an overestimate or underestimate of biological diversity.

Whole-plant reconstruction—In this paper we demonstrate the common affinity of *Nehvizdyella bipartita* ovuliferous organs, *Cycadopites* pollen, *Eretmophyllum obtusum* leaves, *Pecinovicladus kvacekii* short shoots, and *Ginkgoxylon gruettii* trunk wood based on (1) the facies co-occurrence of parautochthonous remains at four sites, and (2) the precise anatomical correspondence between adjacent morphotaxa.

Specifically, *Cycadopites* pollen is found adhering to *Nehvizdyella*, whereas other pollen morphotaxa are absent. Furthermore, *Cycadopites* pollen is always highly abundant in the salt marsh facies dominated by *Eretmophyllum*. Leaf bases preserved on the external surface of *Pecinovicladus* are anatomically and morphologically identical to the leaf bases of *Eretmophyllum*, indicating a close association between the two morphotaxa (Falcon-Lang, 2004). Furthermore, secondary axes preserved in leaf axils (bracts) on *Pecinovicladus* are of identical size and shape to the main axis of *Nehvizdyella*, and closely correspond anatomically. The secondary wood of *Pecinovicladus* is almost identical to *Ginkgoxylon* wood, the only minor differences probably being related to wood ontogeny (Falcon-Lang, 2005a). Finally, *Nehvizdyella* bears the same type of stomata and contains the same type of resin bodies as leaves of *Eretmophyllum*, indicating a common affinity (compare Fig. 8 and Figs. 5, 20, 24).

Previous studies have also hinted at this same association, although only in part. For example, Velenovský and Viniklář (1926, 1927) described poorly preserved isolated axes (putative long shoots) and seeds, which they tentatively associated with *Eretmophyllum* foliage. Preliminary cuticular studies of seed sarcotesta were carried out by Hluštík (1986), who also noted an association with *Eretmophyllum* foliage. In both cases, the seeds were of the same type as those described herein as *Nehvizdyella bipartita*. Hluštík (1986) attempted a partial reconstruction of these remains, depicting them in terms of a long shoot with helically arranged leaves, a reconstruction based on Velenovský and Viniklář (1926)'s poorly preserved specimen (which is now lost). During the course of our investigation, we did not find similar long shoot material. It is possible that the *Nehvizdyella* whole-plant possessed both short shoots and long shoots, as in recent *Ginkgo*, but in the absence of well-preserved long shoot material we are unable to confirm Hluštík's reconstruction.

Based on the fossil assemblage described, we maintain that the *Nehvizdyella* whole-plant was a small tree or large shrub. The maximum recorded trunk diameter of only 13 cm suggests a height of no more than a few meters given biomechanical considerations (Niklas, 1994). Lateral branches with short shoots, and possibly long shoots, bore helically arranged tongue-shaped leaves up to 11 cm long with ovules locally positioned on stalks within the leaf axils. A representative branch of *Nehvizdyella* whole-plant is illustrated in Fig. 39.

Paleoecology—The ginkgoalean assemblage is exclusively associated with salt marsh peat facies at four different localities spanning the entire basin (Uličný and Nichols, 1997). These units were formed during periods of marine transgression and represent a saline, water-stressed environment (Uličný et al., 1997). Tree-rings in facies-associated woods additionally suggest a seasonally dry subtropical climate (Falcon-Lang et al., 2001). The ginkgoalean remains, especially *Eretmophyllum obtusum* leaves, occur in very high concentrations in these units, locally forming the dominant component of the peat (Kvaček, 1999). These data, together with presence of roots below the peat and the taphonomic co-occurrence of organs with varying hydrodynamic properties (Nichols et al., 2000), indicate that this is an autochthonous or parautochthonous assemblage. Therefore, the ginkgoaleans, together with co-occurring cheirolepid conifers, putative gnetaleans, and a few angiosperms, are best characterized as a mangrove or salt marsh community (Hluštík, 1986) with trees adapted for growth in saltwater environments (Tomlinson, 1994). No modern coniferopsids utilize the mangrove or saltmarsh strategy (Hogarth, 1999), although rare putative examples have been reported from the fossil record (Falcon-Lang, 2005b).

Fig. 39. Reconstructed short shoot bearing *Nehvizdyella* reproductive structures by Jiří Svoboda. ×0.5.

Carbon isotopic studies of plants from the salt marsh peat facies allow more detailed palaeoecological interpretation. The angiosperm, gnetalean, and cheirolepid conifer remains have highly positive $\delta^{13}C$ values (−23‰) compared to the mean value for the whole Peruc-Korycany Formation, consistent with growth under highly water-stressed conditions (Nguyen Tu et al., 1999, 2002). Additionally, these plants have very thick cuticles and show a variety of xerophytic characters including deeply sunken stomata (Uličný et al., 1997). In contrast, $\delta^{13}C$ values for *Eretmophyllum* are consistently more negative (−25.5‰) than the other salt marsh plants, although more positive than for plants in freshwater facies (−27‰). Furthermore, *Eretmophyllum*, being a broadleaf, is less characteristically xeromorphic, although such characters as sunken, papillate stomata certainly suggest xeromorphy (Kvaček, 1999). An additional xeromorphic character in *Nehvizdyella* is the enclosure of ovules in sterile tissues (presumably to limit water loss), a feature also seen in *Alvinia bohemica*, the ovuliferous cone of *Frenelopsis alata* (Kvaček, J., 2000). Isotopic data perhaps imply that the *Nehvizdyella* tree grew in less saline regions of the salt marsh, either in a supratidal setting landward of the other trees, or adjacent to lower salinity drainage channels that locally cut into the salt marsh peat facies (Uličný et al., 1997).

The absence of tree-rings in the woody cylinder of *Peci-*

novicladus may suggest that all of the short shoots were less than 1 year old and were therefore seasonally shed as in *Metasequoia*. However, tree-rings are also absent in the mature wood, *Ginkgoxylon gruettii* so the age at which short shoots were shed cannot be assessed with certainty. Nor can the occurrence of discrete *Eretmophyllum*-rich laminae be used as an indicator of seasonal leaf shedding because this may simply represent a taphonomic phenomenon. Furthermore, *Eretmophyllum* leaf bases and leaf scars attached to *Pecinovicladus* show evidence for mechanical breakage rather than abscission, perhaps indicating an evergreen habit. Whilst the phenology of the *Nehvizdyella* tree cannot be determined with certainty, it is worth noting that all modern trees adapted to salt marsh or mangrove settings have a physiological necessity for an evergreen canopy. It is therefore likely that our Cretaceous ginkgoalean tree was similarly evergreen, in contrast to its nearest living relative, *Ginkgo biloba*.

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Original article

Two new species of *Kladnostrobus* nov. gen. and their spores from the Pennsylvanian of the Kladno-Rakovník Basin (Bolsovian, Czech Republic)

Deux nouvelles espèces de *Kladnostrobus* nov. gen. et leurs spores du Pennsylvanien du bassin de Kladno-Rakovník (Bolsovien), République Tchèque

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Abstract

A new lycopsid family Kladnostrobaceae is proposed, based on the type of sporangia, their attachment by a pedicel and the type of reticulate spores enclosed. All these characteristics distinguish the Kladnostrobaceae from all other lycopsid families. A new lycopsid genus *Kladnostrobus* nov. gen., consisting of two new species *Kladnostrobus clealii* nov. sp. and *Kladnostrobus psendae* nov. sp., is described from the Kladno-Rakovník Basin (Lower Bolsovian) of the central and western Carboniferous continental basins of the Czech Republic. Helically arranged distal laminae and pedicels are relatively primitive, suggesting that *Kladnostrobus* may represent a new, primitive type of lycopsid cone produced by some unknown, probably arborescent lycopsid parent plant. Spores of *Kladnostrobus* are about 90–100 µm in diameter, and possess reticulate sculpture. The proximal contact area of spores is laevigate. In situ spores can resemble some dispersed species of the genera *Convolutispora* Hoffmeister, Staplin and Malloy, *Camptotriletes* (Naumova) Potonié and Kremp, *Reticulatisporites* (Ibrahim) Neves and mainly *Dictyotriletes* (Naumova) Smith and Buttterworth.

Résumé

Une nouvelle famille Kladnostrobaceae est proposée, basée sur le type des sporanges, leur mode d'attachement par un pédicelle et le type de spore inclus. Tous ces caractères distinguent les Kladnostrobaceae de toutes les autres familles de lycopsides. Un nouveau genre de lycopsides *Kladnostrobus* nov. gen., qui contient les deux nouvelles espèces *Kladnostrobus clealii* nov. sp. et *Kladnostrobus psendae* nov. sp., est décrit en provenance du Bassin de Kladno-Rakovník (Bolsovien inférieur) parmi les bassins carbonifères continentaux centraux et occidentaux de la République Tchèque. Les lames distales et les pédicelles distribués de manière hélicoïdale sont relativement primitifs, suggérant que *Kladnostrobus* peut représenter un nouveau type primitif de cônes lycopsides produits par une plante mère inconnue. Les spores de *Kladnostrobus* ont un diamètre de 90 à 100 µm et possèdent une sculpture réticulée. L'aire de contact proximal est lisse. Les spores in situ ressemblent aux espèces de spores dispersées des genres *Convolutispora* Hoffmeister, Staplin et Malloy, *Camptotriletes* (Naumova) Potonié et Kremp, *Reticulatisporites* (Ibrahim) Neves et même à *Dictyotriletes* (Naumova) Smith et Butterworth.

Keywords: Lycophyta; *In situ* spores; Pennsylvanian; Czech Republic

Mots clés : Lycophyta ; Spores *in situ* ; Pennsylvanien ; République Tchèque

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1. Introduction

Palynological research on Carboniferous in situ spores began with the study of lycopsid cones. Early diagnoses and descriptions of Carboniferous spore-bearing lycopsid specimens focused on megaspores (e.g. Witham, 1833; Morris, 1840; Goeppert, 1848; K. Feistmantel, 1881); most authors tended merely to mention the presence of spores, giving no detailed descriptions or measurements. Chaloner (1953) and Felix (1954) were the first authors who emphasised the real importance of spore content for more precise determination of lycopsid fructifications. Brack-Hanes and Thomas (1983) subsequently emphasised the need to study holotypes (if they are available) from both, the macrofloristic and palynological perspectives.

Spore descriptions allowing comparison with well-defined dispersed species have become critical for cone determination (Thomas, 1970). Spores should be accepted as a part of the diagnoses or descriptions of fructifications, and of the whole parent plant, if the natural and consistent association of organs can be demonstrated.

The preservation of the cones or fertile fronds can be poor (especially in several compressed specimens) and in situ spores are often very important feature of specific or generic (e.g. *Kladnostrobus* nov. gen.) diagnoses. Moreover, studies of in situ spores isolated from several specimens of one cone species can show the natural morphological variations of spores within a cone (e.g. due to different ontogenetic stages). Results of the palynological study of in situ spores and their parent fructifications can, therefore, help in the recognition of natural species, and allow meaningful comparison of in situ spores of one natural species with dispersed form-taxa. Macrofloristic and palynological approaches must be roughly equally important.

In some cases, spores isolated from one parent plant fructifications are all very similar and clearly belong to one dispersed spore species (e.g. spores of *Kladnostrobus*), so that one natural species correlates with one artificial species. In other cases spores of one parent plant species belong to several dispersed spores species of one or more genera (Laveine, 1969, 1970; Leisman, 1970; Bek and Straková, 1996; Bek, 1998; Bek and Opluštil, 1998; Bek and Pšenička, 2000); and so one natural species correlates with several artificial spore taxa. In other cases, identical spores were produced by several parent plant species of several genera of different plant groups.

2. Materials and methods

The holotype of *Kladnostrobus clealii* (E6001) was found at the Kladno locality (Fig. 1), the Kladno-Rakovník Basin (Lower Bolsovian, Pennsylvanian). The holotype of *Kladnostrobus psendae* is from the Max Mine, Libušín, near Kladno, the Kladno-Rakovník Basin (Lower Bolsovian, Pennsylvanian). Spores were recovered by dissolving small portions of sporangia with the aid of 35% hydrofluoric acid for 24 h and in nitric acid for 24–40 h and in KOH for 1 h. All spores were mounted in glycerine jelly for direct microscopic examination, and selected spores were examined under a CAMECA SX100 scanning electron microscope. Photographs were taken using a digital camera Olympus C330s and Olympus BX51 microscope. The terms used for the descriptions of in situ spores are the same as those in the latest edition of the *Glossary of pollen and spore terminology* (Punt et al., 1994). In situ spores are compared using the system of classification of dispersed spores developed by Potonié and Kremp (1954, 1955); Dettmann (1963); Smith and Butterworth (1967). The holotypes, slides with spores and digital photos of both holotypes are stored in the National Museum, Prague. Digital photos and negatives of spores are stored in the Institute of Geology, Academy of Sciences, Prague.

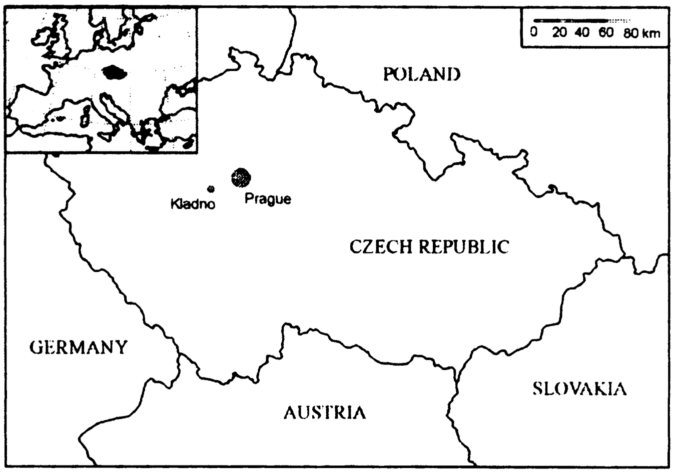

Fig. 1. Geographical position of the central and western Bohemian Carboniferous continental basins of the Czech Republic.

3. Systematics

Class LYCOPSIDA Scott, 1909.

Family KLADNOSTROBACEAE nov. fam.

Etymology: The family name *Kladnostrobus* refers to Kladno, the type locality and the centre of the Kladno-Rakovník Basin.

Type genus: *Kladnostrobus*, nov. gen.

Diagnosis: Stalked strobili. Helically arranged sporophylls. Relatively poorly developed distal laminae and sporophylls. Fusiform sporangia attached by the whole basis with pedicel. Circular trilete spores possess irregular reticulum. Proximal contact area of the spores is laevigate.

Remark: Cones of Lepidocarpaceae possess distal laminae prominently developed from pedicel. Sporangia of Lepidocarpaceae have regularly circular and oval shape, but sporangia of Kladnostrobaceae possess irregular (fusiform) shape. Sporangia of Sigillariaceae are attached to the pedicel only by a small part at the base, whereas sporangia of Kladnostrobaceae are attached by the whole basal part. The shape of sporangia of Sigillariaceae is mostly circular and not fusiform like sporangia of Kladnostrobaceae. Sporangia of Chaloneriaceae, Pleuromeiaceae and Isoetaceae are organised in fertile zones and not in strobili like sporangia of Kladnostrobaceae. Cones of Kladnostrobaceae differ by the fusiform shape of sporangia, their association with pedicel, by relatively poorly developed distal laminae and by the type of spores from all other lycopsid plants.

Genus ***Kladnostrobus*** nov. gen.

Etymology: The generic name *Kladnostrobus* refers to Kladno, the type locality Kladno and the centre of the Kladno-Rakovník Basin.

Type species: *K. clealii*, nov. sp.: Figs. 2 and 3.

Holotype: E6001, the National Museum, Prague, Czech Republic.

Type locality: Kladno, the Kladno-Rakovník Basin, central and western Carboniferous Bohemian continental basins.

Diagnosis: Stalked strobili. Helically arranged sporophylls. Long lanceolate distal laminae with pedicel 6 mm long. Fusiform sporangia. Trilete circular microspores. Reticulum with irregular muri and lumina of irregular shape. Laevigate sculpture of spores on proximal surface.

Kladnostrobus clealii nov. sp.

Fig. 2; Fig. 3 (1–3, 5).

Etymology: The specific names honours Dr. Chris J. Cleal, eminent British palaeobotanist from the Museum of Wales, Cardiff, UK, and friend.

Holotype: E6001, the National Museum, Prague.

Type locality: Kladno, the Kladno-Rakovník Basin, central and western Carboniferous Bohemian continental basins.

Material: Holotype is the only specimen.

Type horizon: The holotype comes from the Kladno Formation, Lower Bolsovian, Pennsylvanian.

Diagnosis: Stalked strobilus 70 mm long, 16 mm wide. Helically arranged sporophylls 11 mm long. The angle between sporophyll and the axis is 33°. Distal laminae 3 mm long, pedicel 6 mm long. Fusiform sporangia 8 mm long, 2 mm wide. Circular to subcircular trilete microspores 68(91.3)102 μm in diameter. Rays of trilete mark one third to half of the radius. Exine 4–6 μm thick, irregular reticulum. Muri 3–9 μm high and wide. Lumina of irregular shape, 7–17 μm in diameter. Contact area on proximal surface laevigate.

Remarks: All the microspores closely resemble each other and differ only in diameter.

Kladnostrobus psendae nov. sp.

Fig. 3 (4, 6); Figs. 4 and 5.

1998. *Sphenophyllostachys* sp. A - Bek, pp. 81–82, Pl. 78, Figs. 1–5, Pl. 147, Figs. 2–4.

Etymology: The specific names honours Dr. J. Pšenička, Czech palaeobotanist from the West-Bohemian Museum in Plzeň, Czech Republic.

Holotype: E3660, the National Museum, Prague, Czech Republic.

Type locality: Max Mine, Libušín, near Kladno, the Kladno-Rakovník Basin, central and western Carboniferous Bohemian continental basins.

Material: Holotype is the only specimen.

Type horizon: The holotype comes from the Kladno Formation, Lower Bolsovian, Pennsylvanian.

Diagnosis: Strobili more than 80 mm long, 10 mm wide. Helically arranged sporophylls 1 mm wide, 4 mm long. Circular to subcircular trilete spores 87(101.2)116 μm in diameter. Rays of trilete mark one third to one half of the radius. Exine 3–6 μm thick, irregular reticulum. Muri 2–8 μm high and wide. Lumina of irregular shape, 6–10 μm in diameter. Muri and lumina bear finely microgranulate sculpture. Contact area on proximal surface laevigate.

Remarks: All the microspores closely resemble each other and differ only in diameter.

4. Discussion

The preservation of the type specimens of both species, *K. clealii* and *K. psendae*, is poor. We cut one section near the apex of *K. clealii* to examine its internal morphology and the arrangement of sporophylls and sporangia, with the aim of determining the affinity of the cone (lycopsid or sphenopsid or progymnosperm). The simple sporangia of *K. clealii* are attached to the sporangiophore by the whole of its basis. Each fusiform sporangium contains a mass of spores (Fig. 2(3–5)).

The preservation of the type specimen of *K. psendae* is very poor. From the whole cone only the middle part 80 mm long is preserved. The entire length can be only estimated to be about 150 mm. The specimen is preserved as an impression with coalified tissue limited to ca. 10 mm fragment in the central part of the cone. We tried to macerate a small piece of this coal to observe the morphology of the sporophylls, type of sporangia, sporangiophores and spores. However, it

Fig. 2. 1–6. *K. clealii* nov. sp., Kladno locality, the Kladno-Rakovník Basin, E6001, National Museum, Prague. 1. General view of the holotype. 2. Upper portion of the holotype showing axis, sporophylls and sporangia. 3. Detail of upper portion of the holotype showing sporophylls, sporangia and spores. 4, 5. Details of spores in sporangium. 6. Spore of the *Dictyotriletes*-type × 500.

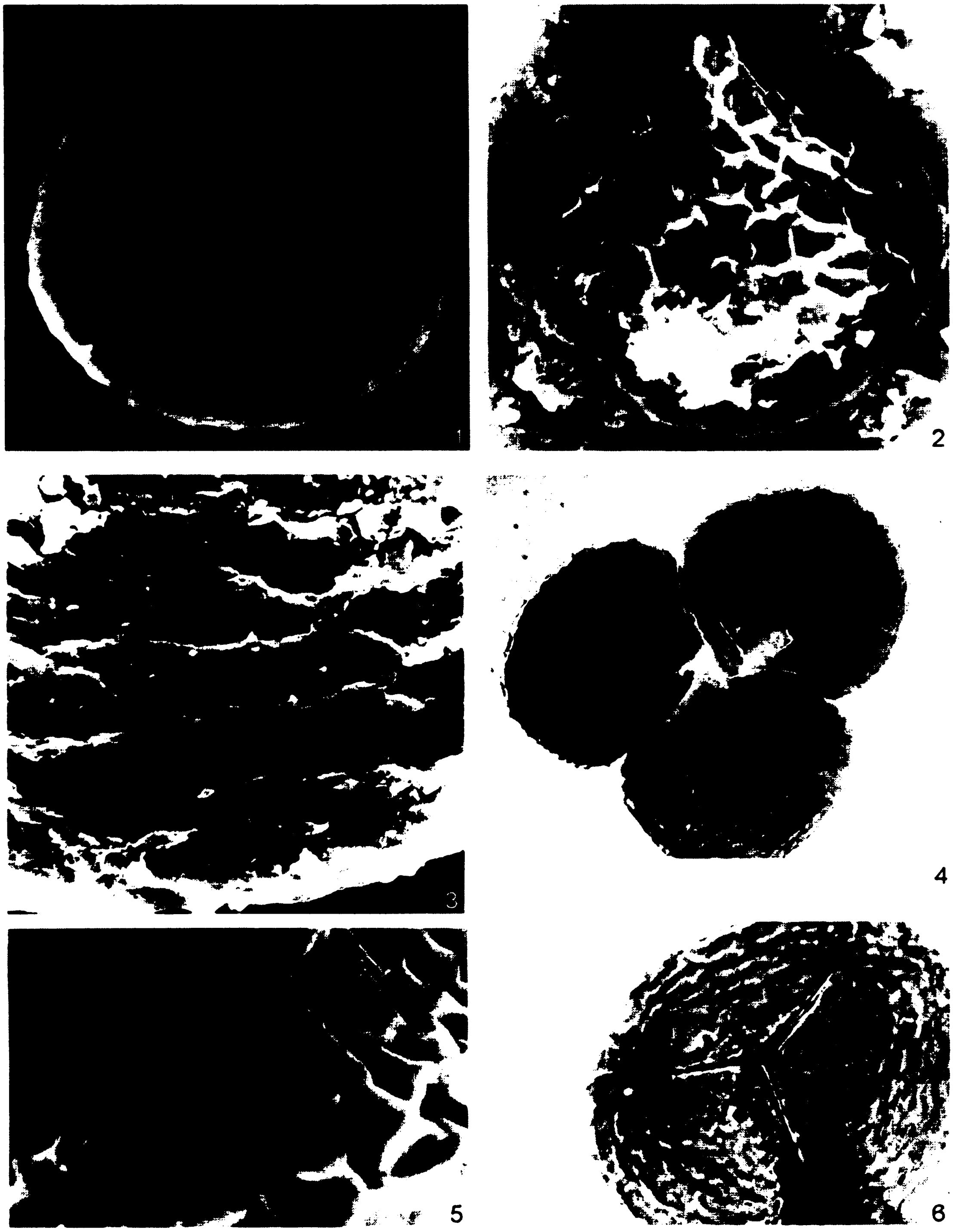

Fig. 3. 1–3. 5. *K. clealii* nov. sp., Kladno locality, the Kladno-Rakovník Basin, E6001, National Museum, Prague. 1. Spore of the *Dictyotriletes*-type, proximal view. Notice that the sculpture of the contact area is different from the sculpture of proximal surface. SEM. × 800. 2. Spore of the *Dictyotriletes*-type: distal view, showing reticulate sculpture. SEM. × 800. 3. Detail of Fig. 1 showing irregular muri and lumina of the proximal surface. × 3000. 5. Detail of Fig. 2 showing muri and lumina of the distal surface. × 1500. 4. 6. *K. psendae*. sp. nov., Max Mine, Libušín, near Kladno, the Kladno-Rakovník Basin, E3660, National Museum, Prague. 4. Tetrad of spores of the *Reticulatisporites–Dictyotriletes*-type. × 500. 6. Proximal surface and contact area of the spore of the *Reticulatisporites*-*Dictyotriletes*-type. × 1000.

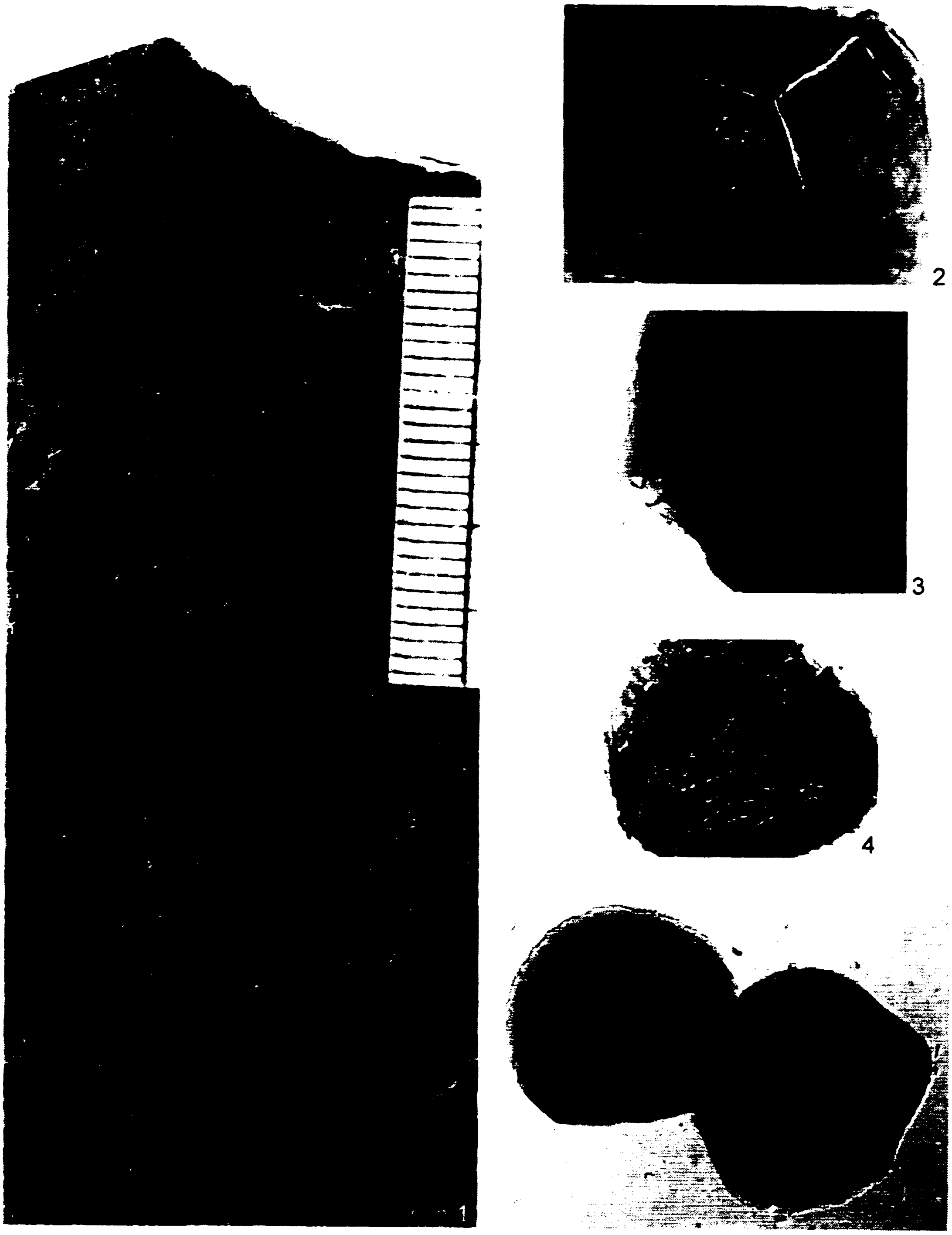

Fig. 4. 1–5. *K. psendae*. nov. sp., Max Mine. Libušín. near Kladno. the Kladno-Rakovník Basin. E3660. National Museum. Prague. 1. General view on holotype. 2–3. Details of the proximal contact area of the spore of the *Dictyotriletes*-type. Notice laevigate sculpture of proximal contact area. All × 1000. 4–5. Spores of the *Dictyotriletes*-type. Notice prominent reticulate sculpture. All × 500.

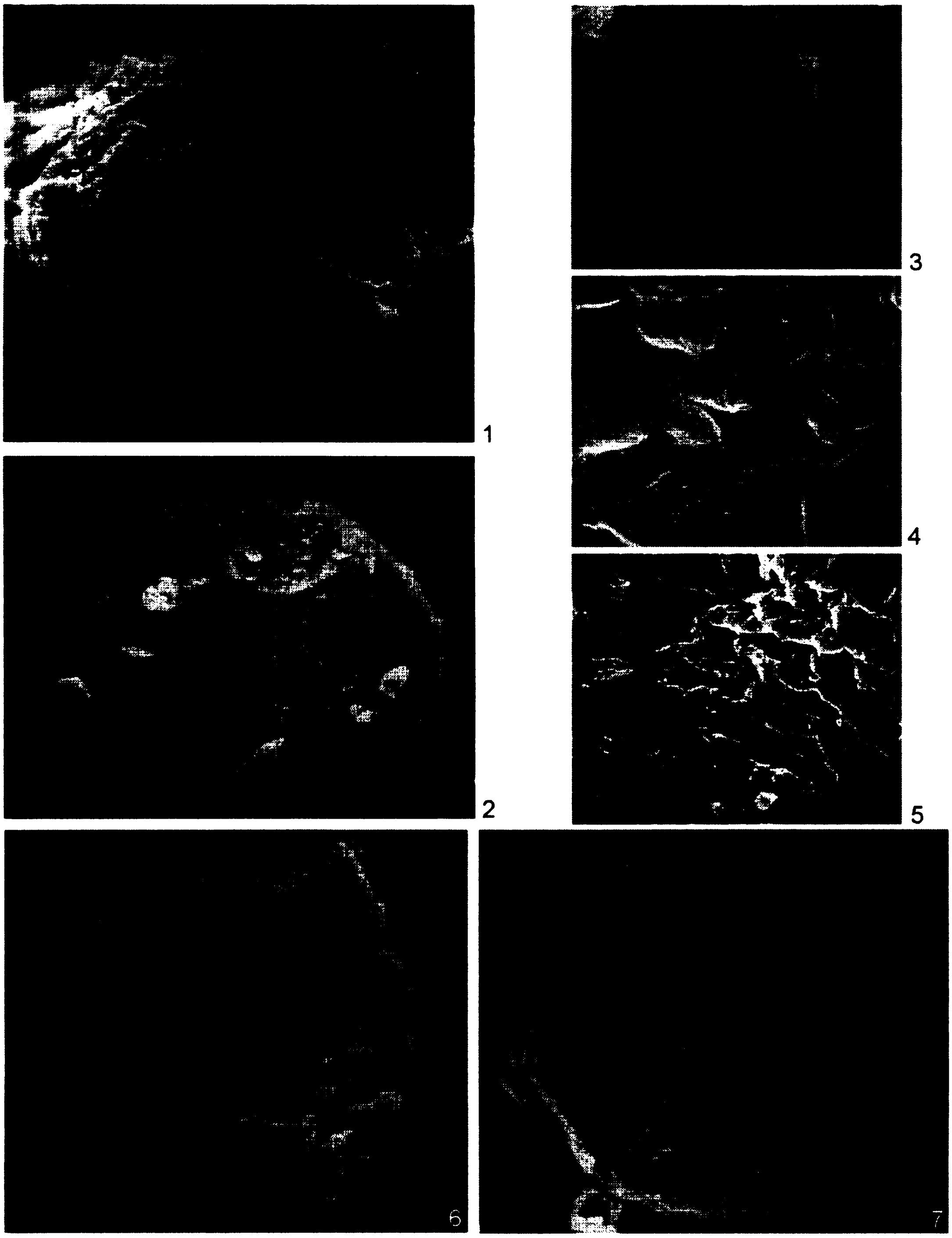

Fig. 5. 1–7. *K. psendae*, nov. sp. Max Mine, Libušín, near Kladno, the Kladno-Rakovník Basin, E3660, National Museum, Prague. 1. Tetrad of spores of the *Dictyotriletes*-type. Distal views. SEM × 500. 2, 6, 7. Spores of the *Dictyotriletes*-type. Distal views, SEM, All × 500. 3–5. Details of muri and lumina (primary sculpture) showing their microgranulate sculpture of muri and lumina (secondary type of sculpture). SEM. Fig. 3 × 4500; Fig. 6 × 4000; Fig. 7 × 1500.

was possible to recognise only the spores and the helical arrangement of the sporophylls indicating its clear lycopsid affinity.

Spores of both new species are morphologically similar. *K. psendae* possesses larger (more than 100 µm in diameter) spores with a laevigate contact area and reticulate sculpture, but the surface of the muri and lumina (primary sculpture) bears a finely scabrate to microgranulate secondary sculpture (Fig. 5(3–5)). Spores of *K. clealii* are smaller (about 90 µm in diameter) with a similar type of reticulum, but the surface of the muri and lumina is laevigate (Fig. 3(3, 5)) and does not possess secondary sculpture like spores of *K. clealii*.

Spores of *Kladnostrobus* cones can resemble some species of the dispersed spore genera *Convolutispora* Hoffmeister, Staplin and Malloy, *Camptotriletes* (Naumova) Potonié and Kremp, *Reticulatisporites* (Ibrahim) Neves and mainly *Dictyotriletes* (Naumova) Smith and Butterworth. Miospores of these genera have rugulate, cristate, reticulate, verrucate or granulate sculpture. The laevigate contact area is the main feature that distinguishes spores of *Kladnostrobus* from the miospores of these dispersed genera. Species of *Convolutispora* have vermiculate ridge-like processes, often causing a convoluted or coarsely reticulate–punctate appearance. The character of the ornament within the genus is variable; rugulae, vermiculae or verrucae dominate, although muri also occur. The contact area of spores of *Convolutispora* is not described. Almost all *Camptotriletes* species are smaller than spores isolated from both new Bohemian species and have different sculpture elements (ridges, cristae, striae or verrucae).

Kladnostrobus spores are broadly similar to dispersed miospore species *Reticulatisporites splendens* Kosanke and/or *Dictyotriletes maculatus* (Ibrahim) Potonié and Kremp and/or *Camptotriletes falkenbergensis* Venkatachala and Bharadwaj. *D. maculatus* possesses a similar sculpture and thickness of exine but a smaller diameter (only 53–70 µm) and it lacks a contact area. *C. falkenbergensis* is comparable in the diameter (90–120 µm) but it lacks a contact area too.

It may be strange, that *Kladnostrobus* spores are compared with miospore species assigned to two or three genera. The problem is, that not all Palaeozoic palynologists determined *Dictyotriletes* and *Reticulatisporites* miospores in the same way.

The genus *Dictyotriletes* was emended by Potonié and Kremp (1954: p. 144) for the first time and later, Smith and Butterworth (1967: p. 194) for the second time to include certain spores formerly assigned to *Reticulatisporites*. Miospores of the genus are considered to be azonate (lack an equatorial thickening) with reticulum developed on the distal and sometimes also on the proximal surfaces.

The genus *Reticulatisporites* was proposed by Ibrahim (Potonié, Ibrahim and Loose in 1932) for azonate spores lacking cingulum and emended by Neves (1964: p. 1066) for trilete spores with a differentially thickened cingulum. Potonié and Kremp (1954, 1955); Neves (1961, 1964); Neves and Playford (1961); Playford and Helby (1968); Smith and Butterworth (1967) have tried to elucidate uncertain determination of species of genera *Dictyotriletes* and *Reticulatisporites*.

Neves (1964) in his revision of *Knoxisporites* (Potonié and Kremp) Neves examined the holotype of *Reticulatisporites reticulatus* (Ibrahim) Ibrahim and interpreted it as an cingulate specimen. This idea is not supported by all palynologists, because e.g. Playford and Helby (1968) and authors suppose, that the structure of the holotype of *R. reticulatus* referred by Neves as a differentially thickended cingulum is no more than an equatorial or subequatorial murus seen in optical section. It means, that Neves (1964) distinguished *Reticulatisporites* and *Knoxisporites* as cingulate genera from *Dictyotriletes* that is azonate with reticulum mainly on the distal surface. Alternative interpretation is, that *Dictyotriletes* and some miospores referred to *Reticulatisporites* (*R. reticulatus*-type) represent azonate reticulate taxa, while *Knoxisporites* and other *Reticulatisporites* species are cingulate.

Kladnostrobus spores are not cingulate and can be assigned to the dispersed miospore genus *Dictyotriletes*.

Identical in situ spores (i.e. reticulate spores with contact area) have not been reported elsewhere. Broadly similar spores have been isolated from some filicalean plants. Table 1 summarises parent plants of spores of the *Convolutispora–Camptotriletes–Reticulatisporites–Grumosisporites*-type.

The spores of *Kladnostrobus* are morphologically unusual among other in situ lycopsid spores. Large trilete reticulate spores of the *Reticulatisporites–Dictyotriletes*-type are not known from any lycopsid cones. We believe that there is a close relationship between *K. clealii* and *K. psendae*, of both taxa have similar type of their spores. Both cones also possess a helical arrangement of sporophylls indicating clearly their lycopsid affinity. It is not possible to compare the macroscopic details of both holotypes due to the very poor preservation of *K. psendae*.

The morphology of the spores is quite different from those isolated from any other Carboniferous lycopsid strobili. Pseudoherbaceous lycopsids of the genera *Chaloneria* (Newberry) Pigg and Rothwell, *Omphalophloios*, *Porostrobus* Chaloner, *Spencerites* (Scott) Drábková, Bek and Opluštil and herbaceous *Selaginella*-like plants all yielded different spores of the genera *Endosporites* Wilson and Coe, *Densosporites* (Berry) Butterworth, Jansonius, Smith and Staplin, *Cristatisporites* (Potonié and Kremp) Butterworth, Jansonius, Smith and Staplin, *Spencerisporites* (Chaloner) Drábková, Bek and Opluštil and *Cirratriradites* Wilson and Coe. Cones of arborescent lycopsids such as *Lepidostrobus* (Brongniart) Brack-Hanes and Thomas, *Flemingites* (Carruthers) Brack-Hanes and Thomas, *Bothrodendrostrobus* Hirmer, *Sigillariostrobus* (Schimper) Feistmantel, *Mazocarpon* Benson and *Achlamydocarpon* Schumaker-Lambry produced spores of the genera *Lycospora* (Ibrahim) Schopf, Wilson and Bentall, *Crassispora* (Bharadwaj) Sullivan and *Cappasporites* Urban.

Table 1
Review of parent fructifications produced microspores of the *Camptotriletes*, *Convolutispora*, *Dictyotriletes* and *Grumosisporites*-type

Parent fructifications	Diameter of spores (μm)	Classification of spores	References
Waldenburgia corynepteroides Gothan	100–120	*Convolutispora–Verrucosisporites*	Gothan, 1950; Remy, 1953; Remy and Remy, 1955, 1957
Botryopteris americana Graham	23–59	*Convolutispora–Verrucosisporites*	Graham, 1934; Delevoryas and Morgan, 1953; Phillips and Rosso, 1970
Botryopteris cratis Millay and Taylor	55–110	*Convolutispora ampla* Hoffmeister, Staplin and Malloy	Millay and Taylor, 1980
Botryopteris globosa Darrah	25–58	*Convolutispora* sp.	Darrah, 1939; Murdy and Andrews, 1957; Brush and Barghoorn, 1964; Phillips and Rosso, 1970; Millay and Taylor, 1982
Botryopteris fecunda Mamay	Ca. 36	*Camptotriletes* sp.	Mamay, 1950
Botryopteris illinoensis Mamay	Ca. 23	*Camptotriletes* sp.	Mamay, 1950
Senftenbergia pennaeformis (Brongniart) Stur	48–112	*Convolutispora-Camptotriletes*	Radforth, 1939; Remy and Remy, 1955, 1957; Laveine, 1969
Biscalitheca kansana Cridland	72–88	*Convolutispora* sp.	Cridland, 1966
Nemejcopteris feminaeformis (Schlotheim) Barthel	70–100	*Convolutispora–Verrucosisporites*	Abbott, 1961; Galtier and Grambast, 1972; Barthel, 1976; Brousmiche 1983
Chacassopteris concinna Radchenko	90–110	*Convolutispora–Reticulatisporites*	Balme, 1995
Paulophyton cuyanum Leguizamon and Archangelsky	Ca. 90	*Convolutispora* sp.	Leguizamon and Archangelsky, 1981
Phillipopteris globiformis Hamer and Rothwell	27–48	*Grumosisporites–Convolutispora*	Hamer and Rothwell, 1983
Eoangiopteris andrewsii Mamay	29–45	*Convolutispora*	Mamay, 1950; Millay, 1978
Millaya tularosana Mapes and Schabilion	90–113	*Convolutispora–Verrucosisporites*	Mapes and Schabilion, 1979
Kladnostrobus clealii nov. sp.	68–102	*Dictyotriletes*	Herein
Kladnostrobus psendae nov. sp.	87–119	*Dictyotriletes*	Herein

5. Conclusion

The spores of *K. clealii* and *K. psendae* are morphologically different from those found in any other lycopsid and represent quite new group of lycopsid spores. Spores with reticulate ornament have not been previously recorded from Carboniferous lycopsids. We have found only presumed microsporangia but no megasporangia, so we cannot determine whether the cone was bisporangiate.

Distal laminae and pedicels are poorly developed, supporting our hypothesis that *Kladnostrobus* may represent a new, relatively primitive type of lycopsid cones. The helical arrangement of the sporophylls provide the only criterion for the classification of *Kladnostrobus* as a lycopsid cone, due to poor preservation of the specimens.

We can presume that parent plants of *Kladnostrobus* were not pseudoherbaceous lycopsids of the *Chaloneria, Omphalophloios* or *Spencerites*-type, because the sporangia of these plants are organised in fertile zones lying directly on vegetative stems and not in discrete strobili. It unlikely that *Kladnostrobus* belonged to herbaceous lycopsids, because strobili of these heterosporous *Selaginella*-like plants are much smaller, narrower and possess a quite different type of spore. Sporangia of selaginellalean cones are attached by a stalk at the axil of the sporophylls. It is probable that *Kladnostrobus* were cones of some type of arborescent lycopsid. If so, *Kladnostrobus* would have a special position among lycopsid plants, with its relatively primitive type of sporophylls, fusiform sporangia attached by a pedicel, and strange type of spores. It supports our opinion that *Kladnostrobus* represents a new lycopsid family.

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The sub-arborescent lycopsid genus *Polysporia* Newberry and its spores from the Pennsylvanian (Bolsovian-Stephanian B) continental basins of the Czech Republic

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Abstract

About fifty compression specimens belonging to four species of *Polysporia* from the Kladno-Rakovník Basin of the central and western Bohemian Carboniferous continental basins and Intra-Sudetic Basin of the Czech Republic were studied macromorphologically and for *in situ* spores. Their stratigraphic range is from the Bolsovian to the Stephanian B. *Polysporia rothwellii* sp. nov., *P. drabekii* sp. nov. and *P. radvanicensis* sp. nov. are proposed as new species. *Polysporia* is reconstructed as a sub-arborescent plant with a principal axis with sterile and fertile apical portions. *P. rothwellii* and *P. drabekii* are preserved only as clusters of micro- and megasporophylls on specimens not in connection to an axis, and their identification and classification is based mainly on *in situ* spores. Micro- and megasporangia of some specimens of *Polysporia* occur together on axes, however, usually they are not arranged in a distinct pattern and only ocasionally the distinct transition among micro- and megasporangia is to be seen. *In situ* megaspores are correlated with the dispersed species *Valvisisporites auritus* (*Polysporia radvanicensis* and *P. drabekii*), *Expansisporites westphalensis* (*Polysporia rothwellii*) and *Triletisporites bohemicus* (*Polysporia robusta*). *In situ* microspores are correlated with the dispersed species *Endosporites zonalis* (*Polysporia robusta*), *E. globiformis* (*Polysporia rothwellii*) and *E.* cf. *formosus* (*Polysporia drabekii*). Some of Kidston's type material of *Polysporia* from UK was re-examined and yields megaspores of the *Expansisporites valvatus*-type and microspores of the *Endosporites* *globiformis*-type. A review of *in situ* and dispersed occurrences *Valvisisporites*, *Pseudovalvisisporites*, *Triletisporites*, *Expansisporites* megaspores and *Endosporites* miospores is given.

Key words: Polysporia, *Chaloneria*, *Endosporites*, *Valvisisporites*, *Triletisporites*, *Expansisporites*, Carboniferous, *in situ* spores

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1. Introduction

Carboniferous sub-arborescent lycopsids represent a small but important group of fossil plants. All of them are characterized by central principal, sometimes branched axis. Another significant morphological feature is the fertile apex (not strobilus) with sporangia. Subarborescent lycopsids were not so tall as the arborescent lycopsids (e.g. *Lepidodendron* Sternberg and *Lepidophloios* Sternberg) which grew up to 20-30 m in height, but they were much higher and more robust than herbaceous forms like selaginellas. Their reconstructions (Pigg and Rothwell, 1983a; Drábková et al., 2001; Wagner et al., 2003; Libertín et al., in press) usually show plants of only a few meters high with almost upright to horizontal leaves and prominent fertile apices.

Subarborescent lycopsids and their spores are stratigraphically and mainly palaeoecologically significant (e.g, Bartram, 1987; DiMichele et al., 1979). We recognise four genera of subarborescent lycopsids; i.e., *Spencerites* Scott, *Omphalophloios* White, *Chaloneria* Pigg and Rothwell, and *Polysporia* Newberry. All four genera are usually grouped together, although there are some differences among them (DiMichele et al., 1979).

Little has been published on the Carboniferous compression genera *Polysporia*, *Spencerites* and *Omphalophloios*. Most authors refer them to isoetalean plants (Chitaley and Pigg, 1996; Pigg, 2001; Grauvogel-Stamm and Lugardon, 2001, 2004 and others); a phylogenetic line which began within the Upper Devonian (Bek et al., 2006, Bek and Chitaley, in prep.) and continues throughout the Carboniferous, Mesozoic, Cenozoic and to the recent.

We have studied more than fifty compression specimens of *Polysporia* based on macroscopic observations and especially microscopic studies of *in situ* spores. Most of the *Polysporia* specimens are preserved as isolated clusters of fragments of sporophylls not connected to a principal vegetative axis. Because the potential of macrofloristic studies of compressed *Polysporia* material is limited, we had to concentrate especially on the palynology of their *in situ* micro- and megaspores, thereby demonstrating that the combination of *in situ* micro- and megaspores is crucial for the specific determination and classification of all *Polysporia* species.

Only two species of *Polysporia* were known; *P. mirabilis* Newberry and *P. doubingeri* Grauvogel-Stamm and Langiaux. Innitially, we assumed that this genus was very homogeneous and that the species had a very similar gross morphology and very similar spores. After the study of specimens from the Czech Republic the most suprising is the number of *Polysporia* species (*P. robusta* Drábek, *P. rothwellii* sp. nov., *P. drabekii* sp. nov. and *P. radvanicensis* sp. nov.) that occur in the Pennsylvanian of the Czech Republic and their variability. All *in situ* microspores belong to different species of the dispersed miospore genus *Endosporites* Wilson and Coe, but it is very surprising is that *in situ* megaspores are to be assigned to three dispersed megaspore genera [(*Valvisisporites* Ibrahim, *Triletisporites* (H.Potonié) Potonié and Kremp and *Expansisporites* Loboziak)]. In fact, all of *in situ* megaspores share similar morphological features, i.e., a central body, a cingulum and auriculae and they all have the same gross morphology. The differences are in the sculpture of the distal surface (different in *Triletisporites*), the width of the cingulum and the size of the auriculae (both can vary within one sporangium, see e.g. Taylor, 1994), features which necessitate to accommodate them into three different morphogenera of dispersed megaspores.

We use the generic name *Polysporia* and not *Chaloneria* because we do not have enough information about the anatomy of specimens as they are preserved as compressions. Of some specimens of the *Polysporia* species from the Czech Republic vegetative and fertile parts are known, like *P. robusta* and partly *P. radvanicensis*, but most are known only as clusters of fragments of micro- and/or megasporophylls like *P. drabekii* and *P. rothwellii.*

The present specimens of *Polysporia* represent the largest collection of this type of plant and they provide important information about their diversity and stress the great importance of palynological studies of *in situ* spores for palaeobotanical research. The study of *Polysporia* specimens from the Czech Republic confirms that palynology is the main criterion for the determination of fertile compression specimens of *Polysporia,* because sterile parts of *Polysporia* are very rarely described, the preservation of their fructifications is usually poor and does not allow the description of their morphology.

2. Previous studies

The genus *Polysporia* was established by Newberry (1893) for compressions of fertile axes with sporangia, or isolated sporangia containing microspores of the *Endosporites*-type from the Pennsylvanian of Ohio, USA. Important is the work of Kidston (1897) who described similar specimens (pl. ii, fig. 1a,b) and a sporangium (pl. ii, fig 12a-b) as *Sigillariostrobus* Hirmer and *Sporangium sensu* Kidston from the Duckmantian of Ayrshire, UK. Another significant paper was published by Chaloner (1958) who re-examined holotypes of *Polysporia mirabilis, Lepidophyllum truncatum* Lesquereux and *Lepidostrobus* (*Macrocystis*) *truncatus* Lesquereux and emended the generic diagnosis of *Polysporia.* He synonymised all three species together with the specimens previously described him as *Lepidostrobus zea* Chaloner (Chaloner, 1953), isolated mega- and microspores from all these species, and considered them all to be identical.

New data on the morphology, the anatomy of the stele, the cortex, secondary tissues, the leaves, the reproduction, the palaeoecology and sporangia and spores of these plants were published by DiMichele et al. (1979) from coal-ball specimens from the Middle Pennsylvanian of the Illinois Basin, USA. They provided an excellent reconstruction of the sterile and fertile portions of the plant. The whole plant is interpreted with shoots having alternating fertile and vegetative zones. *Polysporia/Chaloneria* may have grown in marginal wetland environments where herbaceous low shrubby plants predominated, and is found mostly in marshland peats (DiMichele et al., 1979).

Pigg and Rothwell (1983a) reported several hundred permineralized fragments of a single type of plant occurring in Upper Pennsylvanian coal balls from the Appalachian Basin, USA on which they based their description and a whole plant reconstruction of the new genus *Chaloneria* and the heterosporous species *Chaloneria cormosa* Pigg and Rothwell. This species was interpreted as an unbranched plant, about 2 m tall with a rounded rooting base. Alternating regions of mega- and microsporophylls are visible in the fertile zones. A second new species *C. periodica* Pigg and Rothwell has alternating vegetative and fertile zones and is based on Middle Pennsylvanian specimens that were previously referred to *Polysporia mirabilis* by DiMichele et al. (1979). Spores of both species are assignable to *Valvisisporites* (megaspores) and *Endosporites* (microspores). Pigg and Rothwell (1983a) stated that the compression specimens of *Polysporia* cannot provide precise data regarding the morphology and anatomy and therefore they proposed *Chaloneria* as the probable petrified counterpart of the compression taxa of *Polysporia.* Accordingly, they suggested to use the name *Chaloneria* only for permineralized specimens showing several anatomical details with the same micro- and megaspores.

Taylor (1994) published TEM photographs of the ultrastructure of *Valvisisporites* megaspores and SEM photomicrographs evidential, that megaspores of different stage of maturity may occur in the same sporangium.

2. Material and methods

Most specimens (E) are housed in the National Museum, Prague, some others are stored in the West-Bohemian Museum, Pilsen (F), specimens (ZS) from the Intra-Sudetic Basin and (JD) from the Kladno-Rakovník Basin are from the Czech Geological Survey, Prague, all in the Czech Republic. All numbers of specimens, their localities and storage are mentioned in the text below. *Polysporia* specimens from the Kidston collection are from the British Geological Survey, Keyworth, UK. Some palynological slides of microspores, their digital photomicrographs and negatives of SEM photos, digital photographs of specimens are stored in the Institute of Geology, Academy of Sciences of the Czech Republic, Prague. Some slides with microspores are housed in the National Museum, Prague and digital photos of megaspores are in the Czech Geological Survey, Prague.

Spores were recovered by dissolving small portions of sporangia with 35 % hydrofluoric acid (HF) for 24 h, in nitric acid (HNO_3, 40%) for 24-40 h and in potassium hydroxide (KOH, 10%) for 1 h. All microspores were mounted in glycerine jelly for direct microscopic examination. Some spores were examined with a CAMECA SX100 scanning electron microscope. Photographs were made with an Olympus C330s digital camera attached to an Olympus BX51 microscope. The terms used for the descriptions of *in situ* spores are in accordance with the latest edition of the Glossary of pollen and spore terminology (Punt et al., 2007). *In situ* spores are classified according to the system for dispersed spores suggested by Potonié and Kremp (1954, 1955), Dettmann (1963), and Smith and Butterworth (1967).

3. Systematic part

Order Isoetales
Family Chaloneriaceae

Genus ***Polysporia*** (Newberry) DiMichele, Mahaffy and Phillips, 1979

Type species: ***Polysporia mirabilis*** (Newberry) DiMichele, Mahaffy and Phillips, 1979

Diagnosis: see Chaloner, 1958, p. 201.

Polysporia rothwellii sp. nov. Plates I-III

Holotype: E6016, National Museum, Prague, Czech Republic (Plate I, 1-6).

Type locality: Kladno, Libušín (former Schöller) Mine, Kladno-Rakovník Basin.

Type horizon: Radnice Member, Kladno Formation, Bolsovian, Pennsylvanian.

Etymology: In honour of Prof. G.W. Rothwell, American palaeobotanist, who studied plants of the *Polysporia/Chaloneria*-type.

Material: The holotype E6016 (Radnice coal seam, Radnice Member, Kladno Formation, Libušín Mine, Kladno-Rakovník Basin) is kept in the National Museum, Prague; specimen ZS 309 from the Slaný Mine, Lower Lubná coal seam, Radnice Member, Kladno Formation is stored in the Czech Geological Survey, Prague. Both are from the Kladno-Rakovník Basin from the same stratigraphical level (Radnice Member) and from two localities a few kilometres apart.

Diagnosis: Sporophylls with micro- and megasporangia oval in outline. Claviform sporangia. Megaspores triangular to subcircular in outline, cingulate, with prominent triradiate ridges and distinct semicircular to obtuse auriculae. A vestibulum or gula-like extension is developed in the proximal polar area. Cingulum less than 5 % of the total diameter. The exine is divided into a thicker ectexine and a thinner endexine. Pseudosaccate trilete microspores, subtriangular to circular amb; central body one-third of the radius. The thickened rays of the trilete mark almost reach outer margin of the pseudosaccus. The central body sometimes has distinctly darker peripheral zone. Central body circular in outline, laevigate and pseudosaccus micropunctate.

Description: One specimen shows mega- and microsporangia (Plate I, 1). The microsporangia (Plate I, 3) are 8-9 mm wide and 20-22 mm long; the megasporangia (Plate I, 2, 7) are 6-7 mm wide and 12-16 mm long, i.e. microsporangia are larger than megasporangia. Eight microsporangia and two megasporangia are preserved (Plate I, 1, 4-5) on a specimen. The surface of the microsporangia seems to be longitudinally striated. The axis and other vegetative parts of the parent plant are not preserved. The outline of the megaspores is roundly triangular to almost circular (polar and semipolar compressions are more abundant than lateral compressions). Megaspores are 600-1100 (average 812) μm in diameter (Plate I, 6; Plate II, 1-2, 5, 7). Triradiate ridges 30-50 μm high and their height is constant toward to the apex, sometimes the ridges can be slightly higher (Plate II, 4, 7). Well developed auriculae, 125-150 μm wide at their base (Pl. II, 9-10), are developed at the extremities of the triradiate ridges (Plate II, 1-2, 4, 6). The endexine is thin and homogeneous. The ectexine is 8-10μm thick, whereas the endexine is thinner, only 0.3 μm thick (Plate III, 1-2). The ectexine is horizontally stratified (Plate III, 1-3). Ubisch bodies sometimes occur (Plate II, 3, 11). The sculpture of gula-like extension is different from the surface of contact area (Pl. II, 8).

Microspores are 68-121 (average 88) μm in diameter (Plate III, 4-9). The amb of the pseudosaccus is rounded-triangular, circular to sometimes elongated. Laesurae have weak, straight or flexuous ridges. Three proximal interradial papillae may sometimes be visible. The pseudosaccus is thin, often folded with a microreticulate sculpture. The limbus is usually 2-5 μm wide (Plate III, 4-5).

Remarks: The megaspores isolated from *Polysporia rothwellii* are closely comparable to the dispersed species *Expansisporites westphalensis* (Bharadwaj) Loboziak. *E. westphalensis* megaspores have never been reported *in situ*. The relatively small vestibulum or gula-like extension in proximal polar area is the most significant morphological features of this species. Microspores (Pl. III, 4-9) are identified as the dispersed spore species *Endosporites globiformis* (Ibrahim) Schopf, Wilson and Bentall.

Polysporia rothwellii differs from all other *Polysporia* species in its megaspores. These *in situ* megaspores differ especially in having more developed auriculae and a thinner exine than the megaspores isolated from specimens of *P. mirabilis* described by Chaloner (1953) which we identified as the dispersed spore species *Expansisporites valvatus* Loboziak and Soyez (see Discussion).

Polysporia radvanicensis sp. nov. Plates IV-V.

Holotype: Specimen ZS-322, Czech Geological Survey, Prague, Czech Republic (Plate IV, 1-4).

Type locality: Radvanice, Intra-Sudetic Basin, Czech Republic.

Type horizon: Odolov Formation, Jívka Member, Stephanian B, Pennsylvanian.

Etymology: After Radvanice, the type locality of the species.

Diagnosis: Helically arranged sporophylls. Sporophylls with mega- and microsporangia oval in outline with prominent transition zones between microsporophylls and megasporophylls. Triradiate cingulate subtriangular to subcircular megaspores with semicircular auriculae. Tip of the proximal pole distinctive. Prominent triradiate ridges. Cingulum about 20% of the total diameter. Two-layered exine, ectexine ten times thicker than endexine.

Description: Sporangia are broader near the distal end. Megasporangia 10-11 mm long, 6-7 mm wide; microsporangia 15-18 mm long, 5-6 mm wide. The microsporangia are larger than the megasporangia (Plate IV, 1-2). The surface of the microsporangia is longitudinally striated. Megaspores, 480-1225 (average 1010) µm in diameter (Plate IV, 4). Semicircular auriculae 150-170 µm wide. Cingulum 75-150 µm wide. The triradiate ridges of megaspores are low, only 30-40 µm high near the proximal pole (Plate V, 2; Plate IV, 5-7). Semicircular auriculae are developed at the apical area (Plate IV, 6-7, Plate V, 2, 4). Fragments of the tapetum or its imprints occur on the surface of the exine (Plate V, 3). The exine consists of two layers (Plate V, 1). Ectexine 20-25 µm thick on the distal and 25-30 µm thick on proximal surface. Endexine less than 2 µm thick on both surfaces.

Only individual inner bodies of microspores occur in slides and SEM samples (Plate V, 5-9). No complete specimen of a microspore was macerated.

Remarks: Only a part of the axis is preserved. Megaspores are correlated to the dispersed species *Valvisisporites auritus sensu* Bharadwaj. Zerndt (1937, p. 594) described dispersed megaspores from the Radvanice locality, Stephanian of the Czech Republic (i.e. the same horizon as *Polysporia radvanicensis*) as *Triletes auritus* var. *grandis* Zerndt (Type 11^a) which is synonymous with *Valvisisporites auritus sensu* Bharadwaj.

Not only megasporangia with rough surface but also smooth sporangia occur on the specimen (Plate IV, 1, 3). All previous macerations of all the smooth *Polysporia* sporangia confirmed that they are microsporangia so we suppose that smooth sporangia of *P. radvanicensis* are not exceptional and also represent microsporangia. Repeated maceration of these sporangia was not successful probably due to immature stage of microspores. Single palynomorphs highly probably represent inner bodies of *Endosporites* microspores. We observed identical inner bodies in some other slides with *in situ Endosporites*, e.g., from Devonian *Polysporia* from USA (Bek and Chitaley, in prep.). In these slides inner bodies occur together with fully matured *Endosporites* microspores and it is evident that they belong to these microspores.

Polysporia drabekii, sp. nov. Plates VI, VII, 1-3.

1967 Lepidostrobus ovatus Němejc; Drábek pp. 28-31.

1977a Polysporia mirabilis Newberry; Drábek pp. 94-96.

Holotype: Specimen E1805 (megasporangiate), National Museum, Prague (Plate VI, 1).

Paratype: Specimen E1605 (microsporangiate), National Museum, Prague (Plate VI, 2).

Type locality: Nýřany, central and western Bohemian Carboniferous basins.

Type horizon: Sapropelic coal, Nýřany Coal Group, Nýřany Member, Westphalian D.

Etymology: In honour of Dr. K. Drábek who studied plants of the *Polysporia*-type from the Czech Republic.

Material: Twelve specimens of sporangia E1605, E1612-1615, E1618, E1803-8 from the sapropelitic coal of the Nýřany Member, Nýřany locality stored in the National Museum, Prague.

Diagnosis: Micro- and megasporangia oval in outline. Megaspores roundly triangular to subcircular in outline. Semicircular to obtuse auriculae in apical area. Cingulum about 20-25% of the total diameter. Distinct triradiate ridges. Tip of the proximal pole well developed. The exine is thick, laevigate, divided into a thicker ectexine and a thinner endexine. Microspores trilete, pseudosaccate, subcircular to subtriangular pseudosaccate in outline. Punctate pseudosaccus with microreticulate sculpture enveloping the central body with the trilete mark. Limbus sometimes visible.

Description: Specimen E1805 (Plate VI, 1) shows a transverse section of five fragments of megasporophylls associated with an axis 14 mm wide. Distal laminae are broken and only the sporangial part of the sporophyll is seen. The axis is very poorly preserved (mouldering) and the connection of sporangia with the axis is not visible. Megasporangia 25-34 (average 27.5) mm long, 8.9-14.0 (average 12.1) mm wide (Plate VI, 1, 7), oval in outline. Only one fragment of a microsporophyll (E1605, Plate VI, 2) is preserved, not showing any connection or association with sterile parts of the parent plant. Sporangial wall 0.4 mm thick.

Microsporangium oval in outline 29 mm long, 8.3-11.8 mm wide (Plate VI, 2).

Megaspores 1090-1530 (average 1352) µm in diameter in proximal-distal orientation, including auriculae (Plate VI, 3-4; Plate VII, 3). 60% of megaspores are equatorially flattened. The proximal portions of these megaspore are obtuse-triangular in outline or pyramidal. Distinct auriculae and overhanging cingulum occur in the equatorial region. The outline of the distal portion is sometimes semicircular (Pl. VI, 4). Distinct triradiate ridges extend mostly to the equator, and are sometimes higher near the proximal pole. The surfaces of the cingulum and auriculae are sometimes radially undulated. The thickness of ectexine is 45-48 µm on the proximal surface and endexine is 0.16 µm thick (Plate VII, 1-2). The ectexine appears to be stratified throughout its vertical extent. The surface layer (1.25 µm thick) consists of closely vertically positioned, short sporopollenin particles (Plate VII, 2). The next layer is 33-35 µm thick, anastomosing sporopollenin rods are farther apart near the outer surface of the ectexine (Plate VII, 1-2). Sporopollenin rods are arranged more horizontally and more closely spaced toward to the endexine. The compaction of this layer is higher close to the base. The ectexine of the distal part is thinner (20-22µm) and less well stratified than that on proximal side (Plate VII, 1-2).

Microspores 58-97 (average 81) µm in diameter. Central body 37-64 (average 49) µm in diameter (Plate VI, 5-6, 8).

Remarks: Megaspores isolated from the specimens of *Polysporia drabekii* are closely comparable to the dispersed species *Valvisisporites auritus sensu* Bharadwaj. One specimen (E1602, Plate VI, 2), interpreted by Němejc (1954) as the holotype of *Lepidostrobus ovatus* Němejc, is in fact the only known microsporangium of *Polysporia drabekii*. Microspores are poorly preserved (Plate VI, 5, 6, 8), and all of them are in clusters. Only the pseudosaccus, part of the trilete mark and the central body can be seen. Hence, they can be identified as *Endosporites* cf. *formosus*.

Comparisons: Megaspores isolated from *Polysporia radvanicensis* are morphologically similar to those of *P. drabekii*. The main diference is, that they are smaller on average, usually have narrow and less prominent triradiate rays, and that the exine is thinner.

Megaspores isolated from *P. mirabilis* are 520-1024 (average 800) µm in diameter (Chaloner, 1953), i.e. they are smaller on average, and triradiate ridges are less developed. Some megaspores from the groups of megasporangia from Yorkshire, UK (No. 1273, Kidston´s Collection, British Geological Survey, Keyworth, UK), were re-examined (Pl. XII, 1-2, 4, 8-10). These specimens are from the same locality as the types formerly identiefied as *Lepidostrobus zea*, a possible synonym of *Polysporia mirabilis*. The diameter of thirty-three specimens is 700-875 (average 785 µm). Triradiate ridges and auriculae are less well developed and a pronounced gula-like extension or vestibulum is present at the apex. Chaloner (1958) designated these megaspores to *Valvisisporites auritus*. *V. auritus sensu* Potonié and Kremp (1955), and included specimens with a vestibulum or gula-like extension developed in proximal polar area. These specimens were transferred to *Valvisisporites westphalensis* Bharadwaj (Bharadwaj, 1957) that was later accommodated in the genus *Expansisporites* (Loboziak, 1965), based on the occurrence of the gula-like extension at the proximal polar area. Loboziak and Soyez (1967, p. 142) proposed another species, *E. valvatus*, which is very similar to the megaspores isolated from the megasporangia of *Polysporia mirabilis*. *P. mirabilis* differs from *P. drabekii* in having megaspores of the *Expansisporites*-type and in the smaller diameter of the sporangia. Chaloner (1958, pl. 31, fig. 5) illustrated a megaspore which is about 840 µm in diameter, that was isolated from the lectotype of *Polysporia mirabilis*. This specimen is distinctly smaller than the megaspores of

P. drabekii. However, megaspores from the syntype of *Lepidophyllum truncatum* from Mazon Creek of Illinois, USA, figured by Chaloner (1958, pl. 31, figs. 1- 2) are morphologically very similar to the megaspores isolated from *Polysporia drabekii.*

DiMichele et al. (1979) reported megaspores (Tab. 2), 900-1560 µm in diameter, and compared them to the dispersed species *Valvisisporites auritus* var. *grandis*.

Polysporia robusta Drábek, 1976 Plates VII-XI

1977b Polysporia robusta Drábek, Drábek, pp. 205-7.

Holotype: E1467, National Museum, Prague (Plate VIII, 1).

Type locality: Max Mine, Kladno, the Kladno-Rakovník Basin.

Type horizon: Kladno Formation, Bolsovian, Pennsylvanian.

Material: Specimens E1467-8 (Max Mine, near Kladno), E1469-73 (Schöller Mine near Kladno), E1600-01, E2282-84 (Ronna, near Kladno) and E5627 (Svinná, near Radnice, Radnice Basin), all stored in the National Museum, Prague. Specimens F669 (Dubí, near Kladno), F03712, F03718, F03727, F03731 and F03733 (Kladno locality), all housed in the West Bohemian Museum in Pilsen. Specimen JD 0045 from the Prago Mine, Kladno-Rakovník Basin, stored in the Czech Geological Survey, Prague.

Diagnosis: Fructifications of cylindrical shape. Axis makes up about two-thirds of the diameter of the whole fructification. Sporangia more-or-less oval, 6 to 10 mm long, 4 to 6 mm wide, and 3.5 to 6 mm. The length and width of sterile free part is above 35 and 2 mm, respectively. Microsporangia and megasporangia are in separate zones. Megaspores include the species *Pseudovalvisisporites flavus* var. *sculptus* (Bharadwaj) Lachkar; microspores are ranged to the genus *Endosporites* (from Drábek 1977b, p. 86).

Description: The longest, but still incomplete specimen of *Polysporia robusta* (Plate VIII, 2-4, 7) is 0.46 cm long. The preservation is very poor due to oxidation; the specimen is probably immature. Only hardly visible imprints of megaspores (Plate VIII, 3) are visible and poorly preserved microspores are interpreted as immature. The end of the fertile zone is not the apex of the whole plant (Plate VIII, 2 up), but the axis is sterile again. The leaves are arranged helically on the principal axis. The angle between axis and leaves is 80°. Narrow lanceolate leaves 60-80 mm long with one vein. Fertile zones consist of irregularly positioned micro- and megasporophylls. The widest microsporophyll zone is 40-60 mm thick (Pl. VII, 4). The most complete specimen (Pl. VIII, 2-4) possesses only one megasporophyll zone of 30 mm wide. The distal laminae is 60 mm long and the angle between the axis and the laminae is 45°. Microsporangia on sporophylls are oval to subtriangular in shape. The length of microsporangia is 12-16 mm, their width is 5-6 mm. The surface of microsporangia is smooth. Megasporangia on megasporophylls are 6-7 mm long and 4-5 mm wide with a circular to oval outline. The surface of megasporangia is undulated.

Trilete cingulate megaspores, 800-1625 (average 1245) µm in diameter. Amb subtriangular sometimes with auriculae at the apices (Plate IX, 5). Top of the auriculae is rounded sometimes undulate (Plate X, 5). The triradiate ridges are prominent and the ridges of the trilete mark are narrow, straight or flexuous, usually 200 µm high (Plate IX, 2-3; Plate X, 5, 7). The cingulum is smooth, waved or folded, up to 250 µm wide (Plate IX, 2; Plate X, 1, 7). The surface structure of the proximal contact area is variable. from a more-or-less distinct negative reticulum to a vermiculate-like sculpture (Plate X, 7). The distal surface shows a variable number (8-18) of smaller or higher tubercules with circular and polygonal bases (Plate X, 6). Most megaspores possess relatively densely spaced, saddled, S-shaped or star-like elements on the distal surface (Plate IX, 5, 6). Many small brown or red-brown globules, being fragments of the tapetum, or their imprints occur on the surface of megaspores Plate IX, 5, 6).

The thickness of ectexine on the proximal surface is 45-50 µm. On the distal surface the ectexine is about 30 µm thick, but its thickness reaches up to c. 100 µm including tubercules. The endexine is 0.6-0.7 µm thick. The ectexine appears to be stratified throughout its vertical extent. The surface layer (6 µm thick) consists of closely spaces, short particles of sporopollenin. The outer part of ectexine usually occupies two-thirds to three-quarters of the vertical thickness. Anastomosing sporopollenin rods are further apart near the outer surface of the ectexine (Plate XI, 3). Sporopollenin rods are better, more horizontally arranged and closely spaced toward to the endexine.

Trilete pseudosaccate microspores 61-99 (average 79) µm in diameter (Plate VIII, 5-6; Plate IX, 4). Amb circular, subcircular to subtriangular. Laesurae with weak ridges, straight or flexuose, extending the radius of the inner body. The rays of the trilete mark continue to the margin of the pseudosaccus. The pseudosaccus is often folded, finely microreticulate; the limbus is 2-5 µm wide (Plate VIII, 5-6). The central body usually with a darker peripheral zone. Inner body 35-69 (average 49) µm in diameter: the pseudosaccus is more than a half, usually two-thirds, of the total diameter including.

Remarks: All *in situ* megaspores are comparable to the dispersed spore species *Triletisporites bohemicus* Kalibová and microspores are assigned to the dispersed miospore species *Endosporites zonalis* Kosanke.

Discussion: Drábek (1977b) identified *in situ* megaspores from *Polysporia robusta* as *Pseudovalvisisporites flavus* var. *sculptus*. Lachkar (1965, p. 12, tab. 2, fig. 6) included rounded triangular megaspores with a pseudocingulum and prominent auriculae in *P. flavus* var. *sculptus*. The proximal and distal surfaces of the auriculae are covered by small pustulae which form negative reticulum-like pattern. Megaspores isolated by Drábek (1977b) from

Polysporia robusta do not correspond with the diagnosis of *Pseudovalvisisporites flavus* var. *sculptus* given by Lachkar (1965). The main differences are that *P. flavus* var. *sculptus* has very small auriculae, exine of the distal and proximal surfaces is uniformly sculptured with regularly and closely spaced pustulae.

Ischenko and Semenova (1962, p. 69, pl. VI, figs. 4 a,b) described megaspores similar to those of *Polysporia robusta* as *Megastriatiti sulcatus* Ischenko and Semenova from the Bolsovian of the Donbas Basin, Ukraine. The diameter (1375 µm) and ornamentation of these megaspores are very similar to those of *Triletisporites bohemicus*, however, the cingulum is not well-defined.

Polysporia robusta is characterized by axes bearing sterile leaves with a single vein. Zones with microsporangia irregularly alternate with megasporangiate zones. The axis is 8-35 mm wide, the largest fragment is 373 mm long. Linear leaf scars are helically arranged. Sterile leaves occur sporadically in the fertile zones. Lanceolate leaves are narrower in fertile (up to 2 mm) than in sterile zones (4 mm). The longest leaves are 140 mm long (Plate IX, 1).

Elongated sporangia, oval in outline, have a narrow base and are inclined to the axis with an angle of 12°. Microsporangia are usually larger than megasporangia. Megasporangia are 6-8 mm long and 3-3.5 mm wide. Microsporangia are 9-10 mm long and 4-5 mm wide. Some sporangia have an apical longitudinal groove. The surface of sporangia is longitudinally striated.

4. Discussion of the spores

4.1. Microspores

4.1.1. In situ Endosporites

All the microspores isolated from various *Polysporia* and *Chaloneria* specimens are of the *Endosporites*-type. Most of authors classified them as *E. globiformis* (Chaloner, 1953, 1958;

Brack and Taylor, 1972; DiMichele et al., 1979), some others as *E. ornatus* Wilson and Coe (Pigg and Rothwell, 1983a) and *Endosporites* sp. (Drábek, 1977a). Three *in situ*, i.e. natural species of *Endosporites* isolated from *Polysporia/Chaloneria* plants are known to date. The first type of *in situ Endosporites* microspores is characterized by the occurrence of three prominent papillae on the proximal contact area (corresponding with the dispersed species *E. plicatus* Kosanke and probably *E. vesicatus* Kosanke). The second and most often reported type possesses a relatively small, circular central body and a large pseudosaccus, i.e., a small body-pseudosaccus ratio, as in the dispersed species *E. globiformis*, *E. formosus* and *E. pellucidus* Wilson and Coe. The third *in situ Endosporites* type has a relatively large, triangular central body and a high body-pseudosaccus ratio, occasionally with a limbus, as in the dispersed species *E. zonalis*, *E. ornatus*, *E. angulatus* Wilson and Coe, *E. breviradiatus* Guennel, *E. delicatus* Singh, *E.? parvus sensu* Staplin, *E. triangularis* Pi-Radondy and Doubinger, *E. rotundus* (Ibrahim) Schopf, Wilson and Bentall, *Wilsonia granulata* Dybová and Jachowicz, *W. punctata* Dybová and Jachowicz and *Zonotriletes punctulosus* Luber).

4.1.2. Dispersed *Endosporites* species

The genus was established by Wilson and Coe (1940) for trilete pseudosaccate microspores in which the endospore and exospore are separated distally. The endospore (central-inner body) is surrounded by the pseudosaccus which usually possesses a limbus. The type of the genus is *E. ornatus*. *Endosporites* spores appear to be susceptible to swelling after maceration with Schulze‘s reagent and treatment with potassium hydroxide. Therefore, the diameter is not a reliable criterion to distinguish species. Hence, some of the dispersed *Endosporites* species are probably synonyms. More than 25 dispersed species of the *Endosporites*-type have been described from the Carboniferous in the palynological literature (Table 1). Not all of them belong to *Endosporites*. For example, *E. parvus*, *E. uniformis* Gupta and Boozer and *E. vesicatus* may be referred to *Florinites* Schopf, Wilson and Bentall (due to different connection of exine layers and character of the pseudosaccus) and *E. magnificus* (Horst) Potonié and Kremp (due to different morphology) was transferred to the genus *Remysporites* Butterworth and Williams. Many dispersed *Endosporites* species are very similar to each other. The body-pseudosaccus ratio and the occurrence of three papillae on the contact area of central body seem to be the only reliable criteria to distinguish them. The diameter of the spores varies within all *Endosporites* specimens isolated from one parent plant species. The outline varies from circular to oval and triangular. The sculpture of the pseudosaccus and the length of trilete ray are constant. Sometimes three small papillae occur on the proximal surface of the central body (*E. plicatus*, *E. vesicatus*) or on the limbus (*E. globiformis*, *E. triangularis*).

Dispersed *Endosporites* species may be divided into four main morphological groups on the basis of the body-pseudosaccus ratio and the nature of the central body (Table 2).

The presence of three papillae on proximal central body of *E. globiformis* might be questionable. Ibrahim (1933, p. 28) did not mention these papillae in his original diagnosis. However, Potonié and Kremp (1955) illustrated papillae on the specimens they studied (pl. 20, figs. 460-461) and they also refigured Ibrahim's holotype (pl. 20, fig. 459) showing papillae. Smith and Butterworth (1967, p. 272, pl. 22, figs 1, 2) figured and mentioned papillae of specimens identified as *E. globiformis*. It is probable that *E. globiformis* possessing three prominent papillae on proximal contact area also belongs to the third group of *Endosporites*.

Endosporites circularis Guennel apparently has a special position due to its relatively small diameter (about 35 μm), the prominent labrum and the dark ring on the margin of the central body.

Brack and Taylor (1972) considered *E. vesicatus* and *E. plicatus* to be different ontogenetic stages of the same biological species, based on the comparable diameter and the three papillae on proximal contact area of central body. This seems to be correct. Chaloner (1953) suggested that *E. globiformis*, *E. zonalis*, *E. ornatus*, *E. formosus* and *E. vesicatus* are conspecific. Based on our knowledge about *in situ Endosporites* microspores, we cannot agree with this interpretation. DiMichele et al. (1979) regarded *E. globiformis* as a synonym of *E. ornatus sensu* Potonié and Kremp, but for the same reason we cannot support this.

On the other hand, some authors (Tryon and Lugardon, 1991; Grauvogel-Stamm, 1999) assume, that all inner bodies of all *Endosporites* miospores possess three proximal papillae, interpreted (in ultrastructural sections) as laminated zones.

4.2. Megaspores

4.2.1. *In situ Valvisisporites*, *Pseudovalvisisporites*, *Triletisporites* and *Expansisporites* megaspores

The majority of the megaspores isolated from *Polysporia* and *Chaloneria* specimens are regarded to be of the *Valvisisporites auritus*-type (Chaloner, 1953, 1958; Drábek, 1967, 1977a; DiMichele et al., 1978; Gastaldo, 1981; Pigg and Rothwell, 1983a,b; Doubinger and Langiaux, 2001). Subtriangular, cingulate megaspores with prominent triradiate ridges, auriculae and distinct distal sculpture of variously compressed tubercules, isolated from the species *Polysporia robusta* and described by Drábek (1977b) are assigned to a diferent megaspore genus, although they are still of the same morphological type like *Valvisisporites* megaspores.

DiMichele et al. (1979) compared megaspores isolated from sporangia of *Polysporia mirabilis* to the dispersed spore species *Valvisisporites auritus* var. *grandis*, *V. nigrozonalis* (Stach and Zerndt) Lachkar, *V. augustae* (Loose) Potonié and Kremp and *V. flavus* Zerndt. Gastaldo (1981) described megaspores of the *Valvisisporites auritus*-type (as "*Valvisporites*") from *Lepidocystis* Lesquereux fructifications and described some ultrastructural features.

Pigg and Rothwell (1983b) reported megaspores and megagametophytes of *Chaloneria cormosa* and demonstrated a wide range of variability, with many of the stages often preserved in a single sporangium. The smallest megaspores occur in tetrahedral tetrads while larger specimens are preserved individually.

4.2.2. Dispersed *Valvisisporites*, *Pseudovalvisisporites*, *Triletisporites* and *Expansisporites*

The genus *Valvisisporites* was erected by Ibrahim (1933) for triangular-shaped megaspores with auriculae at the radial extremities. Later, the generic diagnosis of *Valvisisporites* was emended by Potonié and Kremp (1954) to accommodate trilete, cingulate megaspores being roundly triangular to trilobate in outline due to the presence of exine extensions (auriculae) at the radial extremities. Reviews of all dispersed *Valvisisporites* species were given by Potonié and Kremp (1955, 1956), Bharadwaj (1957), Piérart (1965) and Żoldani (1966). Potonié and Kremp (1956) transferred *Triletes auritus* I *sensu* Zerndt to *Valvisisporites*. Bharadwaj (1957) did not agree with Potonié and Kremp's broad and general concept of *Valvisisporites auritus* (Potonié and Kremp, 1956, p. 94) and proposed the new species *V. westphalensis* in which he included some specimens previously identified by Potonié and Kremp as *V. auritus*. *Triletes auritus* I (Zerndt 1930, pl. 1, fig. 4) is the holotype of *Valvisisporites auritus*. Bharadwaj (1957) synonymised *V. auritus* var. *grandis* with *V. auritus*. Kalibová (1959) accepted Bharadwaj's concept of *V. auritus* and referred some megaspores (0.6-1.6 mm in diameter) from the Westphalian D-Stephanian of the Czech Republic to this species. Żoldani (1966) raised *V. auritus* var. *grandis* to the rank of a species [(*V. grandis* (Zerndt) Żoldani)] with the holotype *V. auritus* var. *grandis* (Zerndt 1937, pl. 10, fig. 4) from the Stephanian of the Czech Republic (Kounov Group of coals, Jedomělice locality, Kladno-Rakovník Basin). Żoldani (1966) mentioned the occurrence of this species in the Langsettian-Westphalian of Poland.

The dispersed *Valvisisporites* species (Bolsovian-Stephanian) from the Czech Republic were revised by Kalibová (1959) who recognised five species: *V. westphalensis*, *V. auritus*, *V. augustae*, *V. nitens* Kalibová and *V. cladnensis* Kalibová.

Lachkar (1965) described *Triletes saarensis* Lachkar and later he established (1968) the genus *Pseudovalvisisporites* Lachkar for megaspores of the *Valvisisporites*-type with small auriculae.

Loboziak (1965, p. 252) erected the genus *Expansisporites* to include the form previously described as *Valvisisporites westphalensis* which has a small vestibulum or gula-like extension. Loboziak and Soyez (1967) emended the generic diagnosis of *Expansisporites* and included another new species, *Expansisporites valvatus*; this latter form was previously descibed as *Triletes auritus* (Piérart, 1955; Dijkstra, 1955; Bonet and Dijkstra, 1956; Winslow 1959).

The genus *Triletisporites* was erected for trilete megaspores with relatively big tubercules on the distal surface and arcuate ridges, first described by Zerndt (1930) as *Triletes tuberculatus* Zerndt from the Stephanian of Libiaz, Poland. Zerndt (1937) included megaspores from the Bolsovian of the Czech Republic included in *T. tuberculatus*. Later, Bharadwaj (1957) emended the generic diagnosis of *Triletisporites* based on the occurrence of the cingulum (which was never mentioned previously).

Kalibová (1958) accepted Bharadwaj's concept of the genus *Triletisporites* and included into the species *T. bohemicus* Kalibová, which characteristic for the Bolsovian of the Bohemian Massif. This latter species is easily distinguishable from *Triletisporites tuberculatus* by the presence of wide laevigate cingulum.

5. Morphology and palaeoecology of plants

Polysporia/Chaloneria were obviously unbranched sub-arborescent lycopsids, because branched specimens have never been found. The whole plant was probably less than 2 m high. This subjective estimation is based on the thickness of compression specimen and reconstructions of other authors. The distal laminae were apparently shed from fertile zones because they are lacking in all specimens with preserved axes. The reconstruction of the whole plant of *Polysporia* is presented in Figure 1.

We tried to observe the arrangement of micro- and megasporophylls on some longest fragments of *P. robusta*, including a more than 40 cm long one. All are very poorly preserved and the recognition of micro- and megasporangia is almost impossible. For the same reason the recognition of a ligule in *Polysporia* was not possible; axes are usually not preserved.

It unknown which type of substrate *Polysporia* preferred in general. Some species (*P. robusta*) were found in the "Velká opuka" tuff horizon and never been found in roof shales. It thus seems, that *P. robusta* preferred peaty substrate.

Specimens of *P. drabekii* occur only in the sapropelitic coal from the Nýřany locality which is of lacustrine origin and occurs only within the Nýřany Member. The sapropelitic coal from the Nýřany locality is rich in lacustrine fauna fossils (fishes, stegocephales) which were described by Frič (1879-1891). All specimens of *P. drabekii* are preserved as clusters of mega- and microsporangia not connected with the parent plant. Sporangia of *P. drabekii* were probably transported for a short distance from surrounding area by river(s).

Other *Polysporia* species (*P. rothwellii* and *P. radvanicenis*) were found in roof shales, i.e. they grew in flood plains and apparently preferred clastic substrates.

The Euramerican late Westphalian extinction included all major arborescent lycopsids except sigillarians and sub-arborescent forms like *Omphalophloios*, *Spencerites* and *Polysporia*. *Polysporia* spores are palaeoecologically significant. Generally, in the Czech Republic, dispersed mio- and megaspores of *Polysporia* are more abundant within so-called transitional palynological phases (Smith, 1962). This means that they occur in higher percentage in assemblages intermediate between the lycospore phase dominated by arborescent lycopsids, *Lepidodendron* and *Lepidophloios* (i.e. *Lycospora*-producing plants) and the densospore phase showing a dominance of the sub-arborescent lycopsid *Omphalophloios* (i.e. a densospores-producing plant). In transitional or incursion phases lycospores and densospores are never dominant but sometimes the number of sphenophyll and selaginella spores can increase together with *Polysporia* spores. A similar feature was described by DiMichele et al. (1979) from the Pennsylvanian of the Baker and Herrin coals, USA. DiMichele et al. (1979) interpreted *Polysporia* as part of a low vegetation type and *Endosporites*-rich coals were considered to be deposited in large marshes. The opposite extreme of *Lepidophloios* can be *Polysporia* that is thought to be, in general, indicative of low water tables (or alternatively wet-dry conditions with emphasis on the drier side) of predominantly freshwater nature and probably moderate nutrient requirements. *Polysporia* could probably reproduce repeatedly under drier conditions (DiMichele et al., 1979).

The palaeoecological significance of *Polysporia* spores was confirmed by Bartram (1987), who recognised six palynological phases, based on the distribution of megaspores. This zonation shows an even more detailed pattern than the succession previously recognised using miospores. Bartram´s Phase 2 is interpreted as a transitional/incursion phase and is characterized by a dominance of the megaspores *Triangulatisporites* Potonié and Kremp (selaginellalean origin) and *Valvisisporites*.

6. Discussion

Polysporia and *Chaloneria* are both defined as free-sporing, heterosporous lycophytes with a rounded and/or lobed rooting base and ligulate leaves. Consistently produced leaf cushion are absent. Trilete megaspores have an equatorial extension of the exine in the form of separate auriculae or a continuous cingulum; trilete microspores have a pseudosaccus (Pigg and Rothwell, 1983b). Both genera had the same growth habit, i.e., unbranched, upright plants, they had the same type of leaves with stomata on the abaxial side, and an alternation of micro- a megasporangiate zones.

Abbott (1963) described *Lepidostrobopsis missouriensis* Abbott containing megaspores of the *Valvisisporites*-type, which therefore can be referred to *Polysporia*. Abbott (1963) transferred *Lepidostrobus mansfieldii* Lesquereux to *Lepidostrobopsis* Abbott based on the same megaspores of the *Valvisisporites auritus*-type. *Lepidostrobopsis* was proposed for *Valvisisporites*-producing female fructifications and male *Lycospora*-producing cones. The genus *Lepidostrobopsis* cannot longer be maintained, regarding our present knowledge on *Polysporia* and *Lepidostrobus*. First, *Valvisisporites*-producing megasporophylls are not organized in cones as was believed by Abbott, but they are directly attached to axes (together with microsporophylls), which are fertile in the apical region, and, secondly, *Lycospora* (Ibrahim) Schopf, Wilson and Bentall is not the microspore produced by the plant that has megasporangia with *Valvisisporites* megaspores.

Polysporia/Chaloneria is the oldest known member of the direct phylogenetic lineage *Polysporia-Viatscheslavia-Pleuromeia-Annalepis-Isoetes* beginning in the Late Devonian and continuing up to now (Bek et al., 2006). All these taxa share several morphological and palynological features and characteristics (Tryon and Lugardon, 1991; Grauvogel-Stamm, 1999; Lugardon et al., 1999, 2000; Grauvogel-Stamm and Lugardon, 2001, 2004; Pigg, 2001). The morphological similarities among the extant genus *Isoetes* L., the Triassic genera *Pleuromeia* Corda and *Annalepis* Fliche, the Permian to Triassic genus *Viatscheslavia* Zalessky and the Devonian and Carboniferous genus *Polysporia* are their rhizomorphs, their growth habit and their reproductive organs. Palynological similarities are based on the morphology of spores as seen in light and SEM microscopy and results of TEM observations. Some ultrastructural features of the spore exine, mainly of microspores, like the occurrence of proximal interradial papillae (laminated zones) and the type of exine layers indicate a close relationship of these genera (Pigg, 2001; Bek et al., 2006).

It seems that the size of megasporangia of *Polysporia* varies according to their degree of maturity. For example, a single megasporangium of *P. rothwellii* from the Slaný locality (Plate I, 7) is almost twice as large as megasporangia from clusters from the Schőller Mine (Plate I, 2). Also megaspores isolated from a megasporangium from the Slaný locality (average 964 μm) are larger than those macerated from megasporangia from the Schőller Mine (average only 700 μm). The ectexine of megaspores from the Slaný locality is thicker (15 μm) than the ectexine of megaspores from clusters of megasporangia from the Schőller Mine (8-10 μm). *In situ* megaspores macerated from *Polysporia radvanicensis* and dispersed megaspores from the same locality and the same stratigraphical level (described by Zerndt in 1937) are assigned to the same dispersed megaspore species *Valvisisporites auritus sensu* Bharadwaj, however, *in situ* megaspores are smaller than dispersed ones. It suggested that *in situ* megaspores can be relatively immature compared to fully mature dispersed specimens. Another evidence supporting the relatively immature stage of *in situ* spores isolated from *Polysporia radvanicensis* is the preservation its microspores. We never macerated complete specimens of microspores of the *Endosporites*-type but only single inner bodies.

Another Carboniferous sub-arborescent lycopsid more-or-less comparable to *Polysporia* is the *Spencerisporites*-producing genus *Spencerites*, which has also been described from the Czech Republic (Drábková et al, 2001; Libertín et al, in press). Sporophylls of both plants are not arranged in cones but attached to vegetative axes. Both of them reached a comparable height, less than 2-2.5 m. These genera differ in the branching of the axis, because *Spencerites* had at least three orders of branches (Drábková et al., 2001) and *Polysporia* was probably unbranched. Another diference is, that *Spencerites* is eligulate and homosporous and evidently a represenative of a different evolutionary lineage than ligulate heterosporous genera *Polysporia* and *Omphalophloios*.

Another sub-arborescent lycopsid genus is *Omphalophloios* which also has sporophylls directly on vegetative axes like in *Polysporia* and *Spencerites*. *Omphalophloios* shares some features with *Spencerites* (branching) and *Polysporia* (heterospory, ligule). However, *Omphalophloios* differs from the other two sub-arborescent lycopsids in being much taller (up to 4-6 m), the small number of megaspores per sporangium (usually less than ten compared to hundreds of megaspores in *Polysporia*) and probably also by different nature of the roots.

Only five species of *Polysporia* (*P. mirabilis*, *P. doubingeri* and *P. robusta*) and *Chaloneria* (*Ch. periodica* and *Ch. cormosa*) were previously known. Most of the compression specimens of *Polysporia* were synonymised by Chaloner (1958). As a result of this study eight species of *Polysporia* (i.e. including three new species from the Czech Republic) are recognised.

A palynological study of the Bohemian *Polysporia* sporangia confirmed, that *in situ* spores are very significant for the definition and identification of *Polysporia* species. Therefore, the classification (and synonymy) of compression specimens of *Polysporia* should mainly be based on the detailed re-examination of *in situ* spores. The study of *in situ* spores of specimens of *Polysporia* provides evidence, that the diversity of *Polysporia* plants was much larger than previously assumed. In a relatively small area of the Czech Republic, at least four *Polysporia* species occurred, which are clearly distinguishable, particularly on the basis of in situ spores. It is questionable whether most of the other compression specimens of *Polysporia* (except for *P. doubingeri* and *P. robusta*) are really conspecific as has been suggested by Chaloner (1958). It is unlikely that the Pennsylvanian occurrences in the Czech Republic studied in this report represented a small area with exceptional conditions favouring a strong diversification of *Polysporia*. The problem might be, that Chaloner (1958) synonymised all species described from British Isles (assigned to *Lepidostrobus zea* and *Sigillariostrobus* sp. A *sensu* Kidston) and three species (referred to *Polysporia mirabilis*, *Lepidostrobus truncatus* and *Lepidophyllum truncatum*) known only from USA, although not all of them are from the same stratigraphic level. SEM and probably also TEM studies are neccessary for precise and definite synonymization of compression specimens of *Polysporia*..

During this study we visited the Kidston Collection of Carboniferous plants stored in the British Geological Survey, Keyworth, UK and examined some specimens from the same locality as types of *Lepidostrobus zea* originally described by Kidston as *Sigillariostrobus* and "Megasporangia" (Kidston 1897) and Chaloner (Plate XV, 1-3), as well as isolated *in situ* micro- (Plate XV, 5-7) and megaspores (Plate XV, 4, 8-10) for the comparisons with the material from the Czech Republic. Chaloner compared megaspores isolated from British specimens with the dispersed spore species *Valvisisporites auritus sensu* Potonié and Kremp. We re-examined these *in situ* megaspores using SEM (Plate XV, 4, 8-10) and in our opinion they should be identified as *Expansisporites valvatus*. It supports uncertainty concerning Chaloner´s synonymisation of all European and American *Polysporia* species, which was based on the observation of megaspores under reflected light and not based on SEM or even TEM, which are critical for precise determination and classification of *Polysporia* megaspores.

This study shows that a re-examination of all previously described *in situ Polysporia* megaspores from Europe and USA using SEM and TEM is needed to clear the still existing problems with regard to their classification, because palynology is the most important criterion how to distinguish compression *Polysporia* specimens.

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Dispersed *Endosporites*	Diameter of central body (µm)	Total diameter (µm)
Endosporites angulatus Wilson and Coe	75-85	145-175
Endosporites angustus Hacquebard	100-150	110-165
Endosporites breviradiatus Guennel	30-60	55-85
Endosporites circularis Guennel	4-10	36-46
Endosporites delicatus Singh	32-40	50-60
Endosporites formosus Kosanke	50-68	101-122
Endosporites globiformis (Ibrahim) Schopf, Wilson and Bentall	29-78	62-161
Endosporites magnificus (Horst) Potonié and Kremp		84-255
Endosporites ornatus Wilson and Coe	45-55	90-120
Endosporites pallidus Schemel	33-52	57-74
Endosporites parvus Guennel	20-25	30-45
Endosporites ? parvus sensu Staplin	16-20	24-35
Endosporites pellucidus Wilson and Coe	20-36	47-57
Endosporites plicatus Kosanke	59-68	78-99
Endosporites rarigranulatus Staplin	50-60	70-85
Endosporites triangularis Pi-Radondy and Doubinger	40-50	74-80
Endosporites uniformis Gupta and Boozer	46-80	59-88
Endosporites vesicatus Kosanke	40-58	70-148
Endosporites zonalis Kosanke	33-61	61-104
Wilsonia granulata Dybova and Jachowicz		115
Wilsonia punctata Dybova and Jachowicz		105

Tab. 1. List of selected Carboniferous *Endosporites* miospores and their size ranges.

	Characterization	Species
Group A	Central body more than a half of the whole diameter; occasional limbus	*Endosporites angulatus*, *E. breviradiatus*, *E. delicatus*, *E. ornatus*, *E.? parvus sensu* Staplin, *E. rotundus*, *E. triangularis*, *Wilsonia granulata*, *W. punctata*, *Zonotriletes punctulosus*
Group B	Thin endo- and exospore with folds; big central body	*Endosporites angustus*, *E. pallidus*
Group C	Three prominent apical papillae	*Endosporites plicatus*, *E. vesicatus*, *E. globiformis*
Group D	Small central body	*Endosporites formosus*, *E. pellucidus*

Tab. 2. Division of Carboniferous *Endosporites* species and their characteristics.

Parent fructification	Diameter of	Classification of	Diameter of	Classification of	References

	microspores (µm)	microspores	megaspores (µm)	megaspores	
Lepidostrobus zea	30-130	*Endosporites globiformis*	673-1024	*Valvisisporites auritus*	Chaloner, 1953
Polysporia mirabilis	30-175	*Endosporites globiformis*	520-1360	*Valvisisporites auritus*	Lesquereux, 1879, 1880, 1884; White, 1899; Chaloner, 1958
Lepidostrobopsis missouriensis	-	-	1000-1500	*Valvisisporites auritus*	Abbott, 1963
Lepidostrobopsis mansfeldii	-	-	-	*Valvisisporites*	Abbott, 1963
Lepidostrobus ovatus	-	-	-	*Valvisisporites auritus*	Drábek, 1967
Polysporia mirabilis	-	-	1090-1530	*Valvisisporites auritus*	Drábek, 1976b
Polysporia mirabilis	73-121	*Endosporites vesicatus*	-	-	Brack and Taylor, 1972
Polysporia robusta	37-95	*Endosporites*	1200	*Pseudovalvisisporites flavus* var. *sculptus*	Drábek, 1977
Polysporia mirabilis	67-140	*Endosporites globiformis=E. ornatus*	900-1560	*Valvisisporites auritus* var. *grandis*, *V. nigrozonalis*, *V. augustae*, *V. flavus*	DiMichele et al., 1979
Polysporia doubingeri		*Endosporites*		*Valvisisporites*	Grauvogel-Stamm and Langiaux, 1995
Chaloneria cormosa	48-87	*Endosporites ornatus*	430-670	*Valvisisporites auritus*, *Pseudovalvisisporites*	Pigg and Rothwell, 1983a
Chaloneria periodica	66-175	*Endosporites ornatus*	520-1360	*Valvisisporites auritus*	Pigg and Rothwell, 1983a
Chaloneria cormosa	-	-	430-670	*Valvisisporites*	Pigg and Rothwell, 1983b

Tab. 2. Palynological characteristics of *Polysporia/Chaloneria* plants.

Polysporia species from the Czech Republic	Macrofossils	Diameter of microsporangia (mm) L = lenght W= width	Classification and diameter of microspores (µm)	Diameter of megasporangia (mm) L = lenght W= width	Classification and diameter of megaspores (µm)
Polysporia rothwellii	Clusters of sporophylls	L: 20-22 W: 8-9	*Endosporites globiformis* 68(88)121	L: 12-16 W: 6-7	*Expansisporites westphalensis* 600(812)1100, 75 specimens
Polysporia radvanicensis	Fertile zone 115 mm long, 90 mm wide	L: 10-11 W: 6-7	-	L: 15-18 W: 5-6	*Valvisisporites auritus* 480(1010)1225, 78 specimens
Polysporia robusta	Fertile zones >140 mm long, max. 60mm wide	L: 12-16 W: 5-6	*Endosporites zonalis* 61(79)99	L: 6-7 W: 4-5	*Triletisporites bohemicus* 800(1245)1625, 100 specimens
Polysporia drabekii	Clusters of sporophylls and sporangia	L: 29 W: 8.3-11.8	*Endosporites* cf. *formosus* 58(81)97	L: 25-34 W: 8.9-14	*Valvisisporites auritus* 1090(1352)1530

Tab. 3. Characteristics of Czech *Polysporia* species.

Explanation of plates

PLATE I

Polysporia rothwellii, sp. nov., E6016, National Museum, Prague, Kladno, Libušín (former Schöller) Mine, Kladno-Rakovník Basin.

Fig. 1. General view of the holotype.

Fig. 2. Details of megasporangium. Notice mass of megaspores visible on the surface.

Fig. 3. Detail of microsporangium. Notice smooth surface of microsporangium.

Fig. 4. Detail of the holotype showing mega- and microsporangia together. Notice different surface structures of micro- and megasporangia.

Fig. 5. Detail of a part of microsporangium with smooth surface in contrast to a part of megasporangium with megaspores visible on the surface.

Fig. 6. Detail of megasporangium with several megaspores.

Fig. 7. *Polysporia rothwellii*, sp. nov., ZS309, Czech Geological Survey, Prague, Slaný Mine, Kladno-Rakovník Basin. Detail of megasporangium. Notice mass of megaspores visible on the surface.

PLATE II

Polysporia rothwellii, sp. nov. *In situ* megaspores compared to the dispersed spore species *Expansisporites westphalensis* (Bharadwaj) Loboziak. All SEM.

Figs. 1, 4- 6, 9, 12. ZS309, Czech Geological Survey, Prague, Slaný Mine, Kladno-Rakovník Basin.

Figs. 2, 3, 7, 11. E6016, National Museum, Prague, Libušín (former Schöller) Mine, Kladno-Rakovník Basin.

Figs. 1-2. Proximal surfaces. Notice prominent rays of the trilete mark, cingulum, auriculae and gula-like extension in the polar proximal area.

Fig. 3. Detail of Fig. 2. Notice ubisch bodies and their imprints on the proximal surface of megaspore.

Figs. 4, 6. Lateral and semilateral views of megaspores with prominent labrum, cingulum and auriculae. Notice gula-like extension on the proximal pole.

Figs. 5, 7. Detail of the gula-like extension on the proximal pole in the lateral and polar compression.

Fig. 8. Detail of the surface of the gula and contact area. Notice the difference of the surface of gula and contact area.

Fig. 9-10. Distal surface of megaspores. Notice distinct auriculae.

Fig. 11. Detail of the distal surface of megaspore from Fig. 9. Notice ubisch bodies and their imprints.

PLATE III

Polysporia rothwellii, sp. nov. *In situ* megaspores compared to the dispersed spore species *Expansisporites westphalensis* (Bharadwaj) Loboziak.

Fig. 1. Transverse section of two megaspores isolated from specimen E6016 (holotype), National Museum, Prague, Kladno, Libušín (former Schöller) Mine, Kladno-Rakovník Basin. Notice two exine layers. Endexine partially detached from ectexine. SEM.

Fig. 2. Detail of transverse section. Notice the character of ectexine. SEM.

Fig. 3. Transverse section of megaspore isolated from specimen ZS309, Czech Geological Survey, Slaný Mine, Kladno-Rakovník basin. Notice two exine layers. Endexine detached from ectexine. Sporopollenin rods of ectexine spaced apart at exterior of megaspore wall. SEM.

Figs. 4-9. *In situ* microspores isolated from *Polysporia rothwellii* sp. nov. E6016 (holotype), National Museum, Prague, Kladno, Libušín (former Schöller) Mine, Kladno-Rakovník Basin and comparable to the dispersed spore species *Endosporites globiformis* (Ibrahim) Schopf, Wilson and Bentall. All × 500.

Figs. 4-5. Parts of microspores showing the pseudosaccus and central bodies. Notice dark peripheral zone of the inner body.

Fig. 6. Inner body with the trilete mark.

Figs. 7-9. Several complete specimens.

PLATE IV

Fig. 1. *Polysporia radvanicensis*, sp. nov. ZS322 (holotype), Czech Geological Survey, Prague, Czech Republic, Radvanice locality, Intra-Sudetic Basin. Notice megasporangia with

megaspores (lower part) and smooth microsporangia (middle and upper part) and their distinct boundary.

Fig. 2. Detail of Fig. 1 showing helically arranged microsporophylls.

Fig. 3. Detail of the contact of mega- and microsporangium (view from the axis). Mass of megaspores and microspores is visible.

Fig. 4. Detail of megasporangium showing mass of megaspores.

Fig. 5. View on the proximal surfaces of two megaspores. Notice less developed auriculae and cingulum. SEM.

Fig. 6. Lateral view showing well developed auriculae, elevated rays of the trilete mark and cingulum. SEM.

Fig. 7. Detail of Fig. 6 showing the proximal surface of auriculae. SEM.

PLATE V

Polysporia radvanicensis, sp. nov. ZS322 (holotype). Czech Geological Survey, Prague, Radvanice locality, Intra-Sudetic Basin.

Figs. 1-5. *In situ* megaspores compared to the dispersed spore species *Valvisisporites auritus* (Zerndt) Gastaldo *sensu* Bharadwaj. All SEM.

Fig. 1. Transverse section of megaspore demonstrated two-layered exine.

Fig. 2. Proximal surface of megaspore. Notice elevated rays of the trilete mark, auriculae and cingulum.

Fig. 3. Detail of proximal surface of megaspore showing two ubish bodies and their imprints.

Fig. 4. Distal surface of megaspore with auriculae.

Fig. 5. Detail of the surface of megaspore covered by plant tissues.

Figs. 6-7. Isolated inner bodies of microspores of the *Endosporites*-type. Notice the trilete mark and three apical papillae.

Fig. 8. Isolated inner body of microspore. SEM.

Fig. 9. Several isolated inner bodies of microspores. SEM.

PLATE VI

Polysporia drabekii, sp. nov., Nýřany locality, central and western Bohemian Carboniferous basins.

Fig. 1. E1805 (holotype), National Museum, Prague Nýřany locality, central and western Bohemian Carboniferous basins. General view showing six megasporangia together.

Fig. 2. E1605 (paratype), Nýřany locality, central and western Bohemian Carboniferous basins. Detail of microsporangium.

Fig. 3. *In situ* megaspore compared to the dispersed spore species *Valvisisporites auritus* (Zerndt) Gastaldo *sensu* Bharadwaj and isolated from specimen E1807, National Museum, Prague Nýřany locality, central and western Bohemian Carboniferous basins. Proximal surface, notice elevated rays of the trilete mark and auriculae. SEM.

Fig. 4. *In situ* megaspore compared to the dispersed spore species *Valvisisporites auritus* (Zerndt) Gastaldo *sensu* Bharadwaj and isolated from specimen E1807, National Museum, Prague Nýřany locality, central and western Bohemian Carboniferous basins. Lateral view showing prominent auriculae and cingulum. SEM.

Figs. 5-6, 8. *In situ* microspores *Endosporites* cf. *ornatus* in clusters and isolated from *Polysporia drabekii* sp. nov., E1605 (paratype), National Museum, Nýřany locality, central and western Bohemian Carboniferous basins. All × 500.

Fig. 7. Detail of megasporangium of specimen E1807, National Museum, Prague Nýřany locality, central and western Bohemian Carboniferous basins.

PLATE VII

Figs. 1-3. *In situ* megaspores isolated from *Polysporia drabekii*, sp. nov., E 1807, National Museum, Prague Nýřany locality, central and western Bohemian Carboniferous basins and compared to the dispersed spore species *Valvisisporites auritus* (Zerndt) Gastaldo *sensu* Bharadwaj. Upper and lower arrows show the positions of microsporophylls. Megasporophylls are between two arrows. All SEM.

Figs 1-2. Transverse section of megaspore showing two-layered exine and details of exine layers. SEM.

Fig. 3. Proximal view showing prominent auriculae and elevated rays of the trilete mark.

Figs. 4. *Polysporia robusta* Drábek. JD 0045. Czech Geological Survey, Prague. Prago Mine, Kladno-Rakovník Basin. The whole microsporangiate zone is preserved. Two lowermost and two uppermost sporangia are megasporangia.

Fig. 5. *Polysporia robusta* Drábek. E1467 (holotype), National Museum, Prague. Max Mine, near Kladno, Kladno-Rakovník Basin. General view on specimen E1467.

PLATE VIII

Fig. 1. *Polysporia robusta* Drábek. E1600. National Museum, Prague. Ronna Mine, Kladno-Rakovník Basin. General view.

Figs. 2-4, 7. *Polysporia robusta* Drábek. E5627. National Museum, Prague. Svinná, near Radnice, Radnice Basin.

Fig. 2. General view, notice the direction of sporophylls (upward) and that the end of the fertile zone is not the apex, but that sterile stem continues to the apex. Arrows show the positions of megaspores.

Fig. 3. Detail of Fig. 2 showing imprints of megaspores.

Fig. 4. Detail of Fig. 2 showing the end of the fertile zone and the begining of sterile stem. SEM.

Fig. 7. Detail of Fig. 2 showing the surface of fertile zone.

Figs. 5-6. *In situ* microspores of the *Endosporites zonalis*-type. Notice large inner body and limbus at the outer margin of pseudosaccus seen as a dark ring.

PLATE IX

Polysporia robusta Drábek.

Fig. 1. E2283. National Museum, Prague. Ronna Mine, near Kladno, Kladno-Rakovník Basin. Notice lanceolate sterile leaves.

Figs. 2-3, 5-6. *In situ* megaspores isolated from specimen JD0045, Czech Geological Survey, Prague and compared to the dispersed spore species *Triletisporites bohemicus* Kalibová. All SEM.

Figs 2. Proximal surface with prominent elevated rays of the trilete mark and folded zona.

Fig. 3. Proximal surface with prominent elevated rays of the trilete mark and folded zona. Notice small circular microspores of the *Endosporites zonalis*-type lying directly on surface of their megaspore.

Fig. 4. Detail of Fig. 3 showing *in situ* microspore of the *Endosporites zonalis*-type lying directly on the surface of in situ megaspore compared to the dispersed spore species *Triletisporites bohemicus* Kalibová. SEM.

Figs. 5-6. Distal surfaces of megaspores. Notice complex sculpture of several-times folded units.

PLATE X

Polysporia robusta Drábek. *In situ* megaspores compared to the dispersed spore species *Triletisporites bohemicus* Kalibová. All SEM.

Fig. 1. Detail of folded zona of megaspore isolated from specimen JD0045 Prago Mine, Czech Geological Survey, Prague.

Fig. 2. Detail of the proximal pole of megaspore isolated from specimen JD 0045 Prago Mine, Czech Geological Survey, Prague and showing the centre of trilete mark.

Fig. 3. Detail of exine of proximal surface of megaspore isolated from specimen JD0045 Prago Mine, Czech Geological Survey, Prague.

Fig. 4. Distal view showing irregular tubercules of megaspore isolated from specimen E1471, National Museum, Prague. Ronna Mine, Kladno.

Fig. 5. Proximal view showing sinuos and elevated rays of the trilete mark, well developed auriculae and folded zona of megaspores isolated from specimen F669. West-Bohemian Museum, Pilsen. Dubí, near Kladno,

Fig. 6. Detail of the sculpture of the distal surface of megaspore isolated specimen JD0045 Prago Mine, Czech Geological Survey, Prague.

Fig. 7. View on a part of proximal surface showing elevated and sinuos rays of the trilete mark, folded zona, a part of the distal surface and the sculpture of the proximal surface of central body of megaspore isolated from specimen JD0045 Prago Mine, Czech Geological Survey, Prague.

PLATE XI

Polysporia robusta Drábek. *In situ* megaspores compared to the dispersed spore species *Triletisporites bohemicus* Kalibová.

Figs. 1-5. F03718, West-Bohemian Museum, Pilsen, Kladno locality, Kladno-Rakovník Basin.

Figs. 1-2. Transverse sections of megaspore demonstrated two-layered exine and its relative thickness (a-apex, t-triradiate ridge, c-cingulum). The thickness of the distal exine is variable due to the occurrence of tubercules. All SEM.

Fig. 3. Detail of Fig. 2 showing the structure of megaspore exine. (Proximal part up). SEM.

Fig. 4. Detail of Fig. 1 showing the structure of exine on the distal side and surface of the tubercules. The endexine is partially tear off and wrinkled. Notice the negative reticulum of the tubercules. SEM.

Fig. 5. Distal side (polar view). Notice negative reticulum of the exine creates impression of „giraffe-like" colouring.

Fig. 6. Proximal side of megaspore (polar view) isolated from specimen F03712, Kladno locality, Kladno-Rakovník Basin. Notice the „giraffe-like" colouring.

PLATE XII

Polysporia mirabilis Newberry.

Fig. 1. 1273, Kidston's collection, British Geological Survey, Keyworth, UK, Barnsley Bed, Wooley Colliery, Darton, Yorkshire, UK. General view on several megasporangia.

Fig. 2. Detail of Fig. 1 showing one megasporangium with mass of megaspores visible on its surface.

Fig. 3. 1573. Kidston's collection, British Geological Survey, Keyworth, UK, Major Coal, Springhill No. 3 Pit, Crosshouse, Ayrshire, UK. Several microsporangia (left) and fragment of *Sigillaria* stem (right).

Figs. 4, 8-10. *In situ* megaspores isolated from specimen 1273, Kidston's collection, British Geological Survey, Keyworth, UK, Barnsley Bed, Wooley Colliery, Darton, Yorkshire, UK and compared to the dispersed spore species *Expansisporites valvatus* Loboziak and Soyez.

Fig. 4. Proximal surface with elevated rays of the trilete mark and less developed auriculae. SEM.

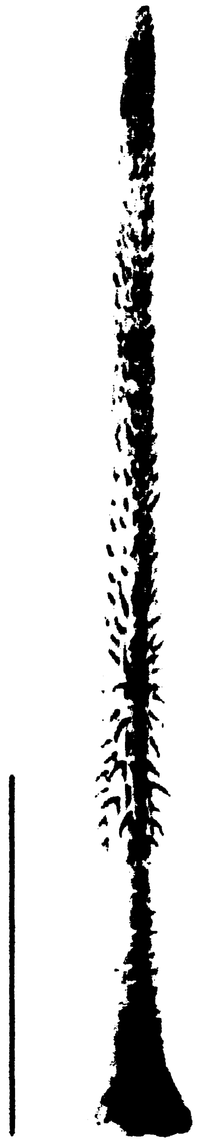
Figs. 5-7. Microspores of the *Endosporites globiformis*-type isolated from specimen 1573. Kidston's collection, British Geological Survey, Keyworth, UK, Major Coal, Springhill No. 3 Pit, Crosshouse, Ayrshire, UK. Notice relatively small inner body.

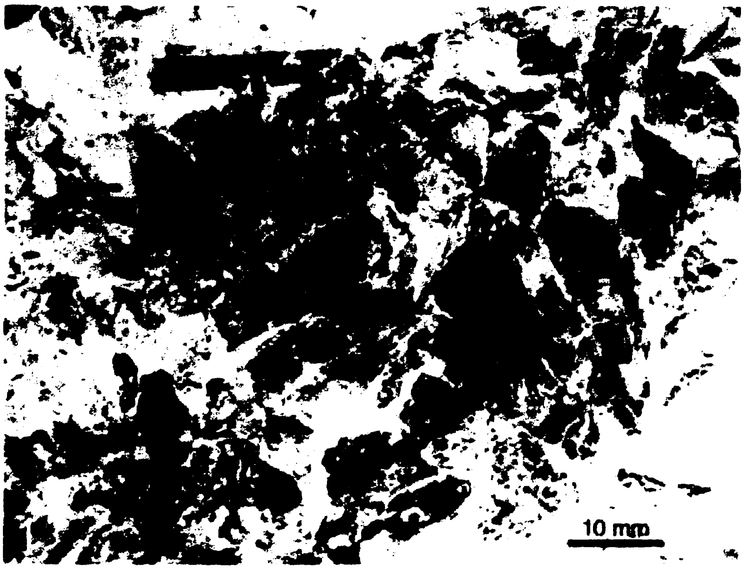
Fig. 7. Tetrad of microspores of the *Endosporites globiformis*-type isolated from specimen 1573.

Figs. 8-10. Proximal surface of megaspore showing elevated rays of the trilete mark, gula-like extension, cingulum and less developed auriculae. All SEM.

Fig. 9. Lateral view showing less developed auriculae and elevated rays of the trilete mark.

Fig. 10. Detail of Fig. 8 showing proximal pole. Notice gula-like extension.

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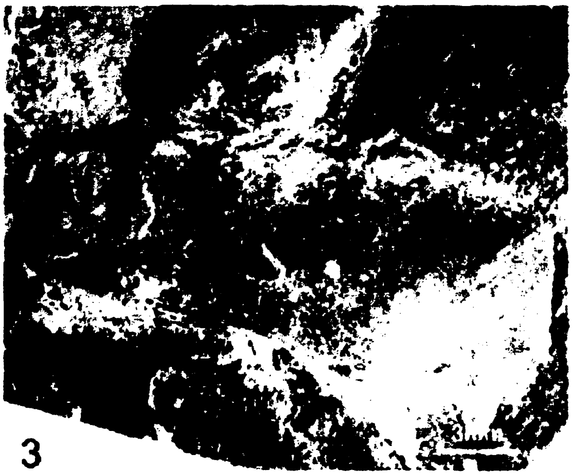
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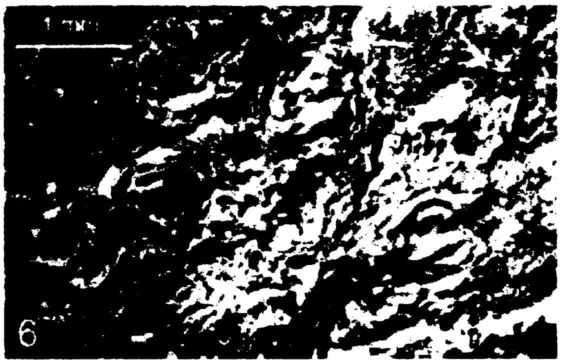
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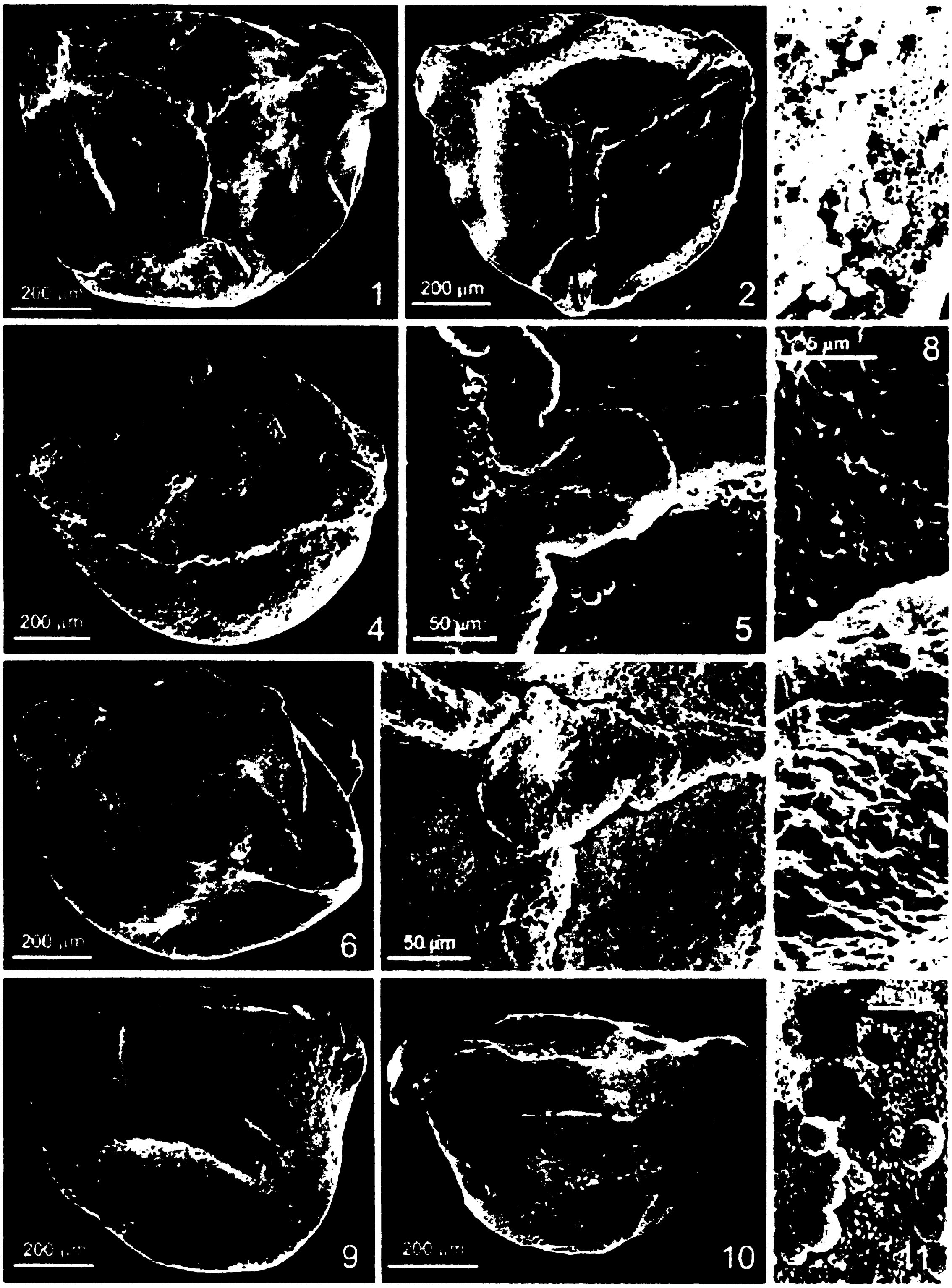
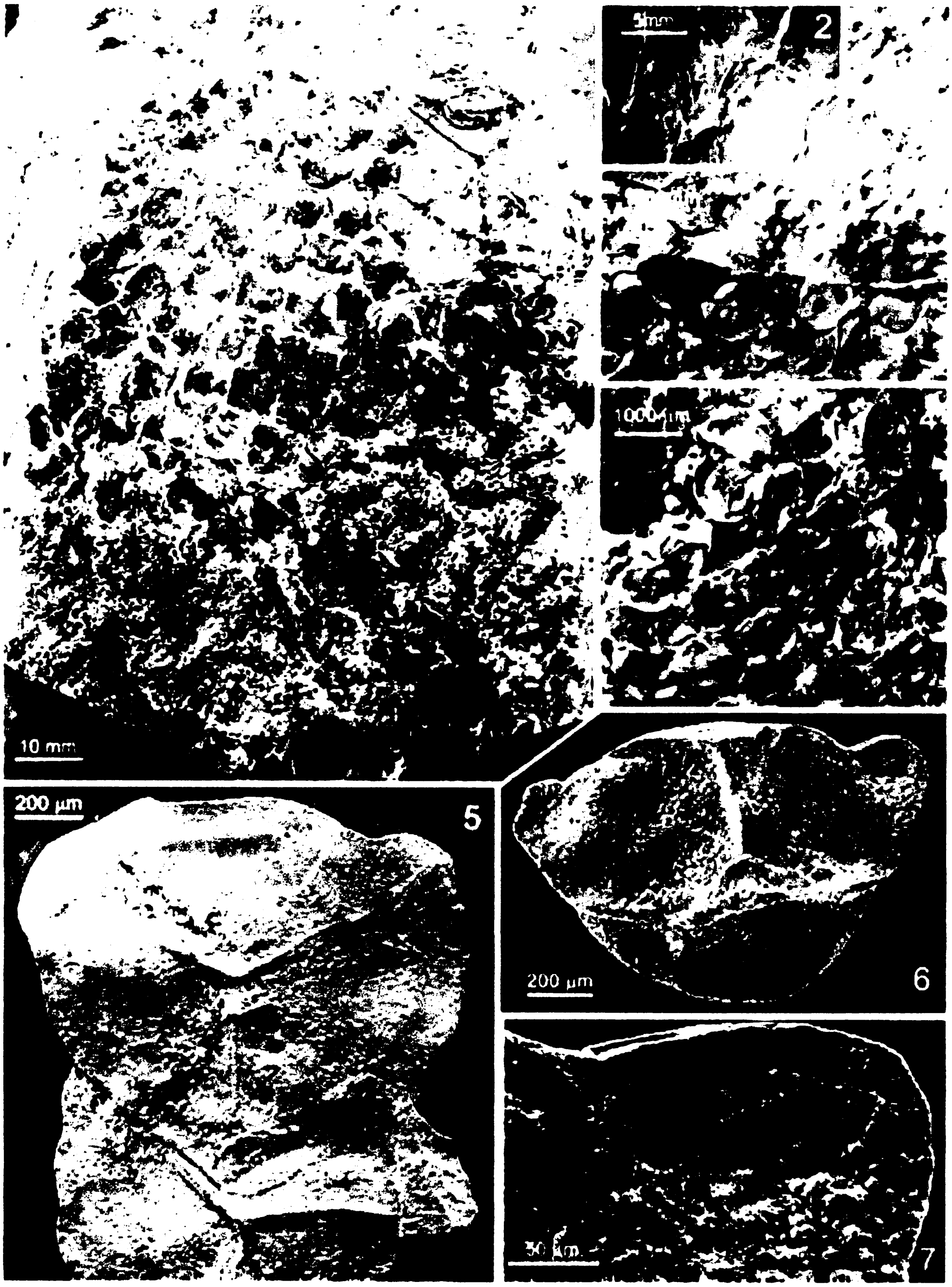
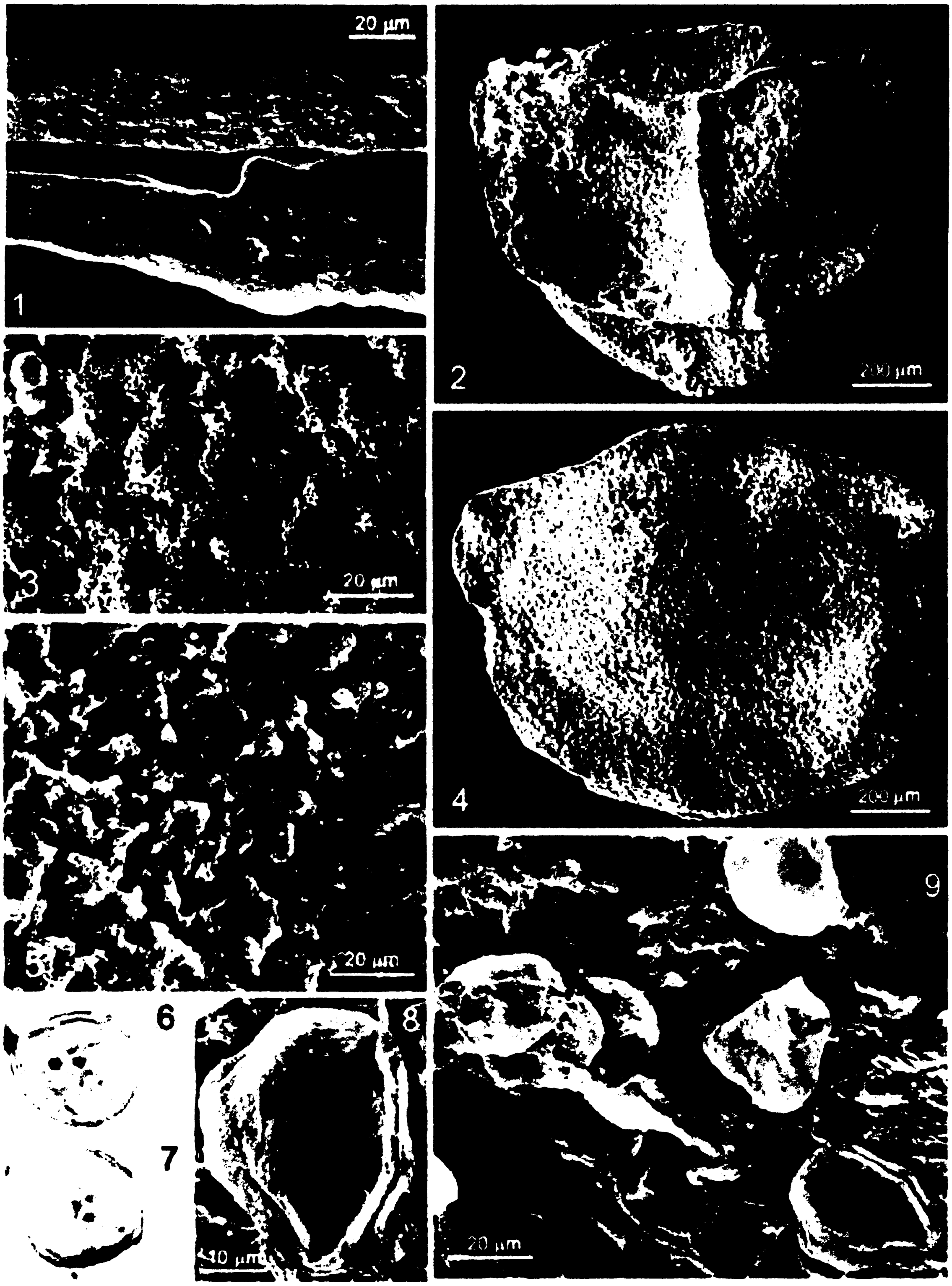
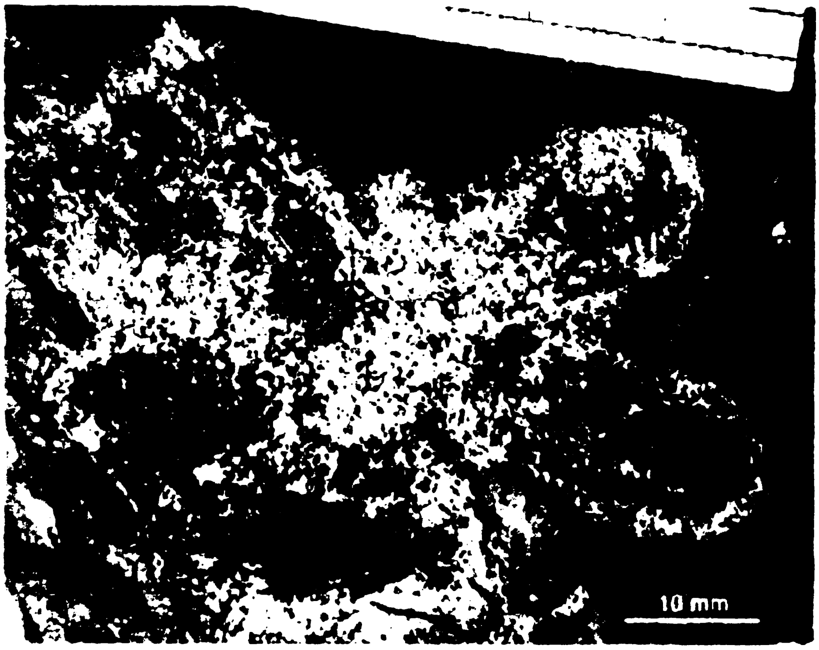
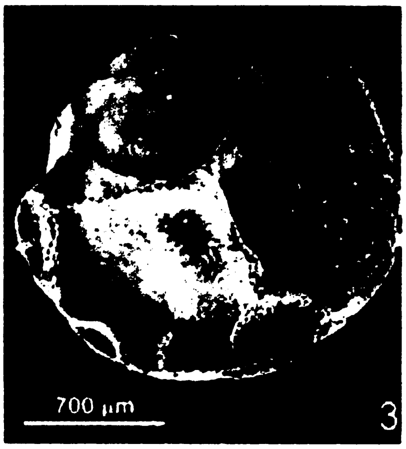

200 µm
1
200 µm
2
5 µm
8
200 µm
4
50 µm
5
200 µm
6
50 µm
200 µm
9
200 µm
10
11

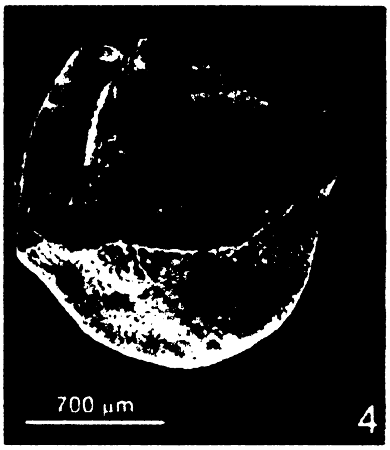

1
100 µm
2
3
2 µm
4
5
6
7
8
9


1 mm
2
1000 µm
10 mm
200 µm
5
200 µm
6
50 µm
7


20 µm
1
2
200 µm
3
20 µm
4
200 µm
5
20 µm
6
7
8
10 µm
9
20 µm







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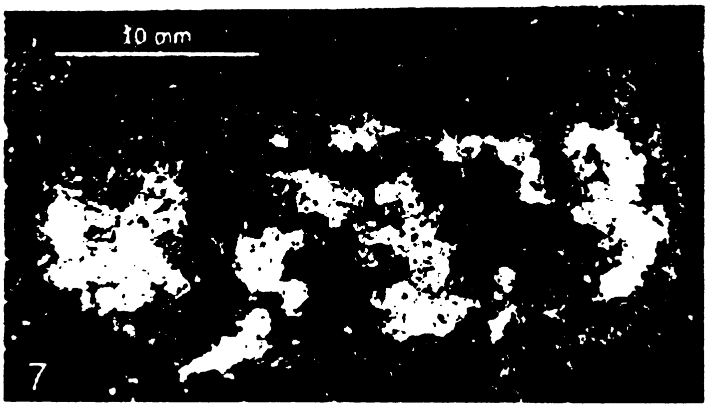
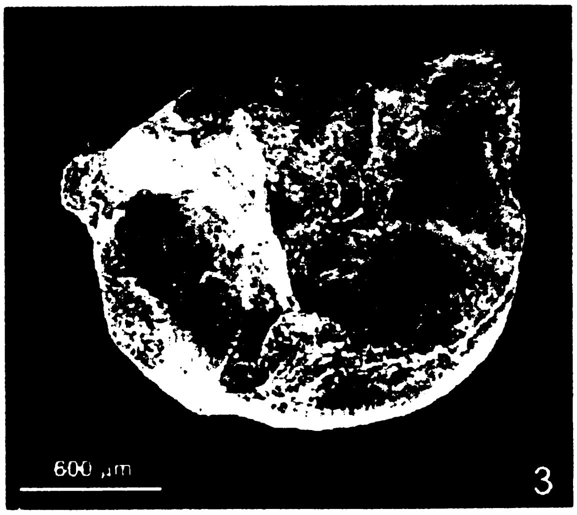


8


1
200 μm


600 μm
3

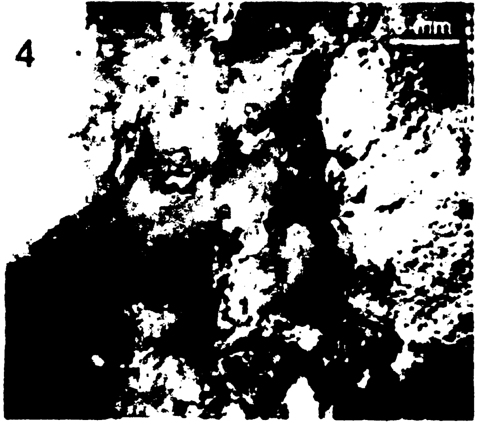

4

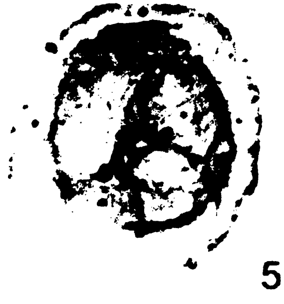

20 mm
5


1
10 mm


20 mm

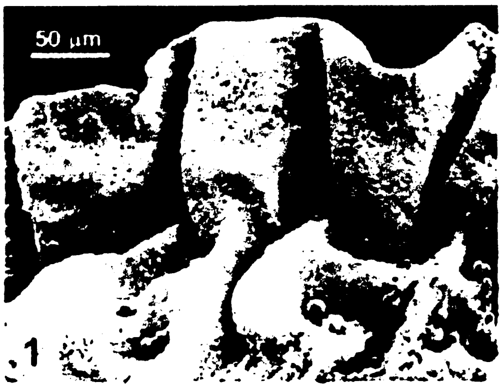

1000 µm

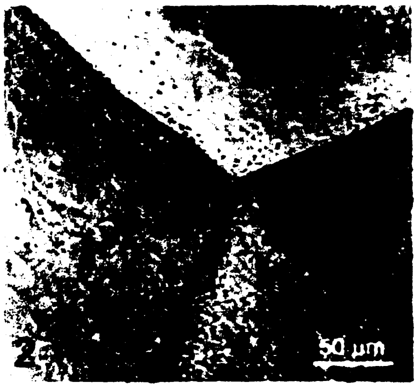

4
mm


5

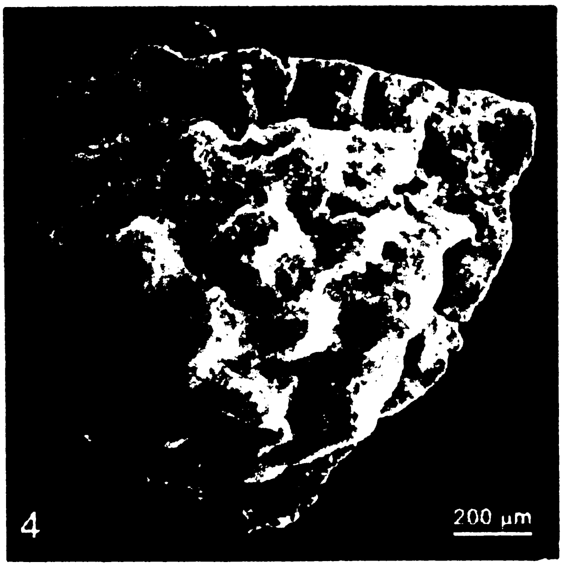

6

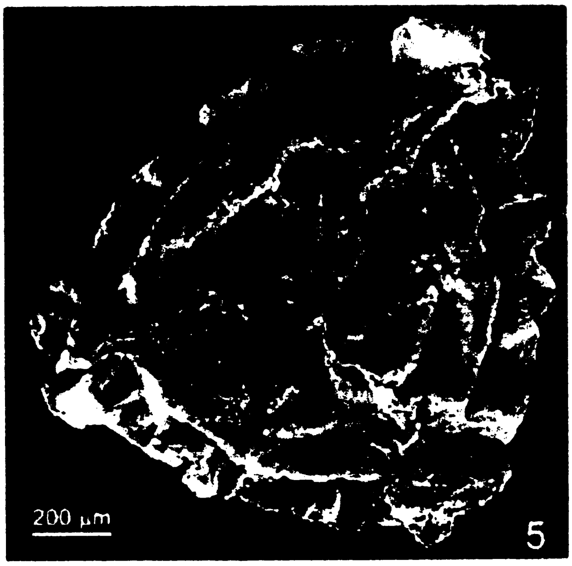

mm
7


50 µm
1

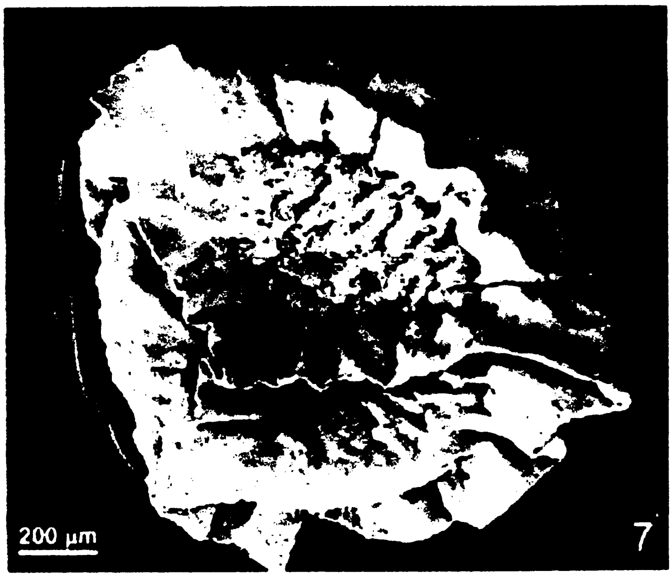

2
50 µm

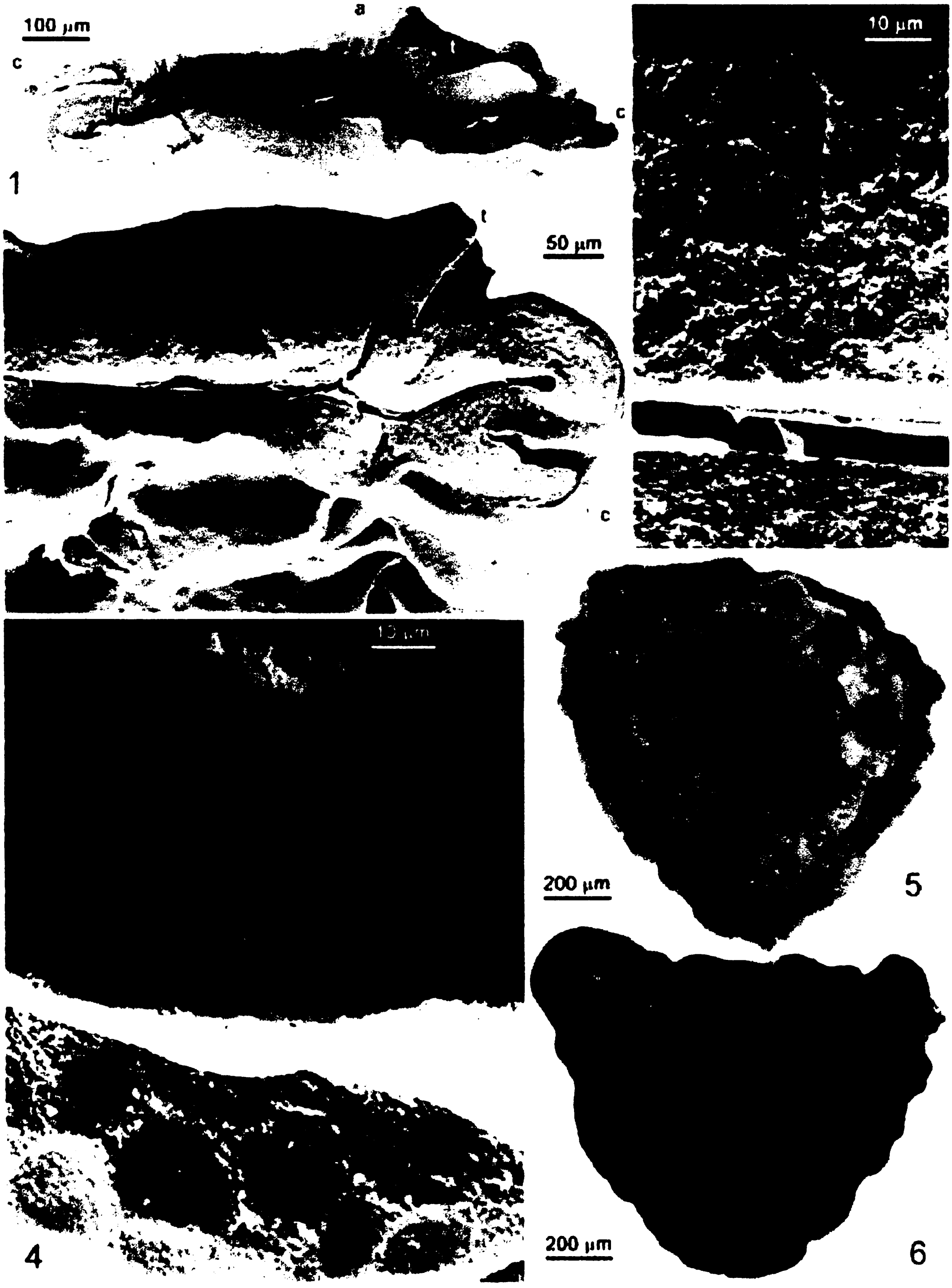

3
20 µm

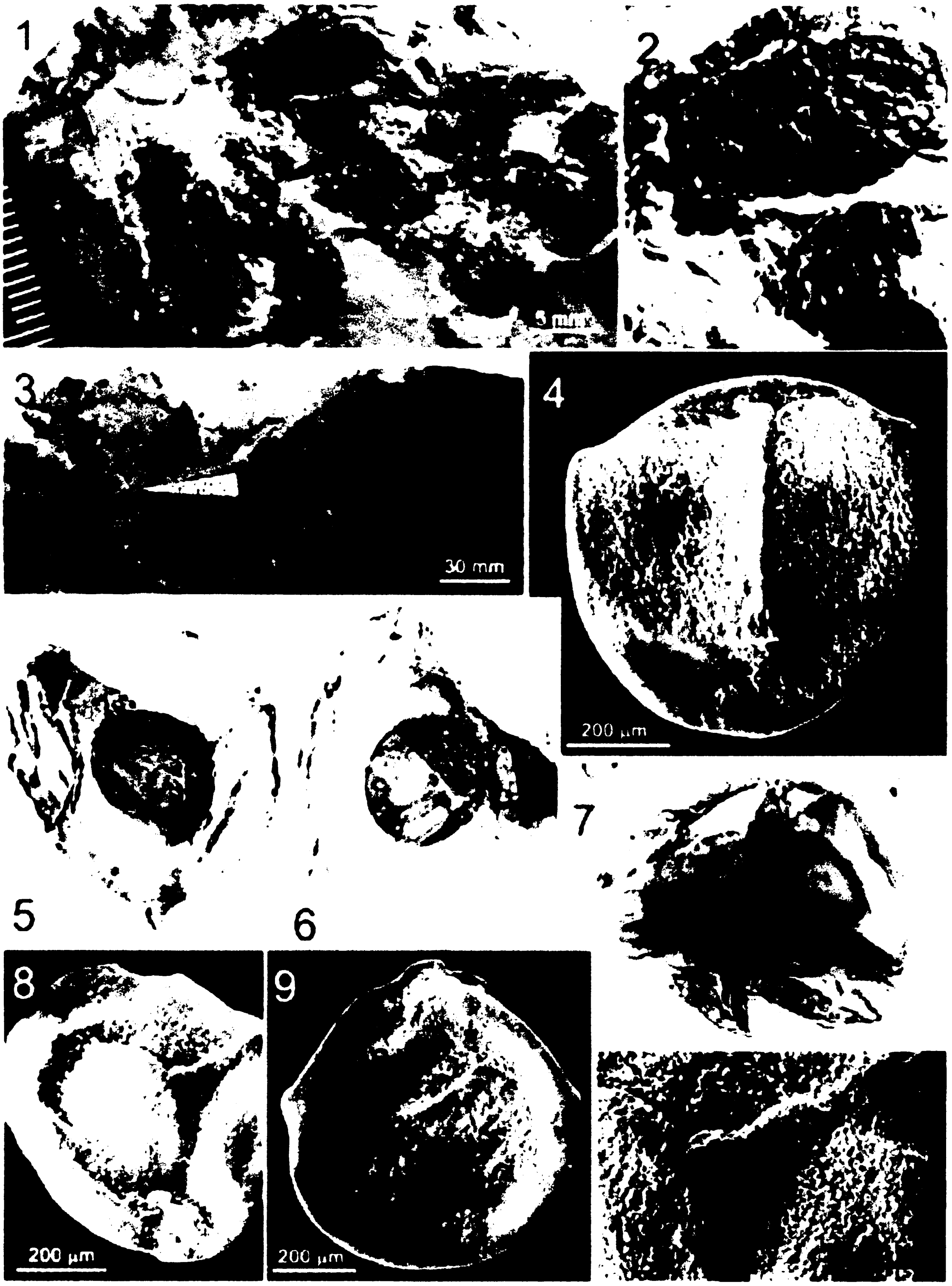

4
200 µm


200 µm
5


60 µ


200 µm
7


100 µm
a
c
t
c
1
t
50 µm
c
10 µm
10 µm
200 µm
5
4
200 µm
6


1
5 mm
2
3
30 mm
4
200 µm
5
6
7
8
200 µm
9
200 µm

Dispersed *Endosporites*	Diameter of central body (μm)	Total diameter (μm)
Endosporites angulatus Wilson and Coe	75-85	145-175
Endosporites angustus Hacquebard	100-150	110-165
Endosporites breviradiatus Guennel	30-60	55-85
Endosporites circularis Guennel	4-10	36-46
Endosporites delicatus Singh	32-40	50-60
Endosporites formosus Kosanke	50-68	101-122
Endosporites globiformis (Ibrahim) Schopf, Wilson and Bentall	29-78	62-161
Endosporites magnificus (Horst) Potonié and Kremp		84-255
Endosporites ornatus Wilson and Coe	45-55	90-120
Endosporites pallidus Schemel	33-52	57-74
Endosporites parvus Guennel	20-25	30-45
Endosporites ? parvus sensu Staplin	16-20	24-35
Endosporites pellucidus Wilson and Coe	20-36	47-57
Endosporites plicatus Kosanke	59-68	78-99
Endosporites rarigranulatus Staplin	50-60	70-85
Endosporites triangularis Pi-Radondy and Doubinger	40-50	74-80
Endosporites uniformis Gupta and Boozer	46-80	59-88
Endosporites vesicatus Kosanke	40-58	70-148
Endosporites zonalis Kosanke	33-61	61-104
Wilsonia granulata Dybova and Jachowicz		115
Wilsonia punctata Dybova and Jachowicz		105

Tab. 1. List of selected Carboniferous *Endosporites* miospores and their size ranges.

	Characterization	Species
Group A	Central body more than a half of the whole diameter; occasional limbus	*Endosporites angulatus*, *E. breviradiatus*, *E. delicatus*, *E. ornatus*, *E.? parvus sensu* Staplin, *E. rotundus*, *E. triangularis*, *Wilsonia granulata*, *W. punctata*, *Zonotriletes punctulosus*
Group B	Thin endo- and exospore with folds; big central body	*Endosporites angustus*, *E. pallidus*
Group C	Three prominent apical papillae	*Endosporites plicatus*, *E. vesicatus*, *E. globiformis*
Group D	Small central body	*Endosporites formosus*, *E. pellucidus*

Tab. 2. Division of Carboniferous *Endosporites* species and their characteristics.

Parent fructification	Diameter of microspores (μm)	Classification of microspores	Diameter of megaspores (μm)	Classification of megaspores	References
Lepidostrobus zea	30-130	*Endosporites globiformis*	673-1024	*Valvisisporites auritus*	Chaloner, 1953
Polysporia mirabilis	30-175	*Endosporites globiformis*	520-1360	*Valvisisporites auritus*	Lesquereux, 1879, 1880, 1884; White, 1899; Chaloner, 1958
Lepidostrobopsis missouriensis	-	-	1000-1500	*Valvisisporites auritus*	Abbott, 1963
Lepidostrobopsis mansfeldii	-	-	-	*Valvisisporites*	Abbott, 1963
Lepidostrobus ovatus	-	-	-	*Valvisisporites auritus*	Drábek, 1967
Polysporia mirabilis	-	-	1090-1530	*Valvisisporites auritus*	Drábek, 1976b
Polysporia mirabilis	73-121	*Endosporites vesicatus*	-	-	Brack and Taylor, 1972
Polysporia robusta	37-95	*Endosporites*	1200	*Pseudovalvisisporites flavus* var. *sculptus*	Drábek, 1977
Polysporia mirabilis	67-140	*Endosporites globiformis=E. ornatus*	900-1560	*Valvisisporites auritus* var. *grandis*, *V. nigrozonalis*, *V. augustae*, *V. flavus*	DiMichele et al., 1979
Polysporia doubingeri		*Endosporites*		*Valvisisporites*	Grauvogel-Stamm and Langiaux, 1995
Chaloneria cormosa	48-87	*Endosporites ornatus*	430-670	*Valvisisporites auritus*, *Pseudovalvisisporites*	Pigg and Rothwell, 1983a
Chaloneria periodica	66-175	*Endosporites ornatus*	520-1360	*Valvisisporites auritus*	Pigg and Rothwell, 1983a
Chaloneria cormosa	-	-	430-670	*Valvisisporites*	Pigg and Rothwell, 1983b

Tab. 2. Palynological characteristics of *Polysporia/Chaloneria* plants.

Polysporia species from the Czech Republic	Macrofossils	Diameter of microsporangia (mm) L = lenght W= width	Classification and diameter of microspores (µm)	Diameter of megasporangia (mm) L = lenght W= width	Classification and diameter of megaspores (µm)
Polysporia rothwellii	Clusters of sporophylls	L: 20-22 W: 8-9	*Endosporites globiformis* 68(88)121	L: 12-16 W: 6-7	*Expansisporites westphalensis* 600(812)1100, 75 specimens
Polysporia radvanicensis	Fertile zone 115 mm long, 90 mm wide	L: 10-11 W: 6-7	-	L: 15-18 W: 5-6	*Valvisisporites auritus* 480(1010)1225, 78 specimens
Polysporia robusta	Fertile zones >140 mm long, max. 60mm wide	L: 12-16 W: 5-6	*Endosporites zonalis* 61(79)99	L: 6-7 W: 4-5	*Triletisporites bohemicus* 800(1245)1625, 100 specimens
Polysporia drabekii	Clusters of sporophylls and sporangia	L: 29 W: 8.3-11.8	*Endosporites* cf. *formosus* 58(81)97	L: 25-34 W: 8.9-14	*Valvisisporites auritus* 1090(1352)1530

Tab. 3. Characteristics of Czech *Polysporia* species.