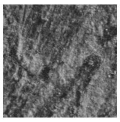
Porostrobus nathorstii (Leary & Mickle) emend. and its spores from the Namurian of Illinois, USA

JIŘÍ BEK & RICHARD L. LEARY



The type collection of the Carboniferous selaginellalean lycopsid cone species *Porostrobus nathorstii* (Leary & Mickle) emend. was palynologically re-examined for *in situ* microspores. Originally (Leary & Mickle 1989) this species was proposed as monosporangiate with only megaspores, but now microsporangia yielded microspores compared to the dispersed miospore genus *Cingulizonates* (Dybová & Jachowicz) Butterworth *et al*. All species of the genus *Porostrobus* Nathorst are, therefore, bisporangiate with *in situ* megaspores of the *Setosisporites*-type and microspores belong to the densospore group [genera *Densosporites* (Berry) Butterworth *et al*. and *Cingulizonates*]. The history of *Porostrobus* and *Bothrodendrostrobus* Hirmer cones is discussed with aspect of their possible relationship and ecological needs. • Key words: herbaceous lycopsids, *in situ* spores, *Porostrobus*, *Bothrodendrostrobus,* Carboniferous.

BEK, J. & LEARY, R.L. 2012. *Porostrobus nathorstii* (Leary & Mickle) emend. and its spores from the Namurian of Illinois, USA. *Bulletin of Geosciences 87(1)*, 45–52 (1 figure, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 27, 2011; accepted in revised form November 9, 2011; published online January 25, 2012; issued February 29, 2012.

Jiří Bek, Institute of Geology v.v.i., Academy of Sciences, Rozvojová 269, 165 00 Prague 6, Czech Republic; mrbean@gli.cas.cz • Richard L. Leary, Illinois State Museum, Springfield, Illinois 62706, USA; Leary@museum.state.ill.us

Carboniferous herbaceous lycopsids and their cones belong to a rarely reported group of fossil plants (Thomas 1997, 2005; Bek *et al.* 2001). Three groups of cones of Carboniferous herbaceous lycopsids can be distinguished on the basis of their *in situ* spores. All these fructifications are bisporangiate. The best known and the most often reported are cones of herbaceous forms of the genus *Selaginella* Palisot de Beauvoir. All these cones produced microspores of the genus *Cirratriradites* Wilson & Coe [mostly *C. saturni* (Ibrahim) Schopf *et al.*, see Bek *et al.* 2001] and megaspores compared with several species of the genus *Triangulatisporites* (Potonié & Kremp) Karczewska (Thomas 1997, Bek *et al.* 2001). The second group is represented by unnamed type of *Selaginella*-like plant (Drábková, pers. comm.) found in the Bolsovian of the Radnice Basin, Czech Republic. *In situ* megaspores correspond with the dispersed genus *Bentzisporites* Potonié & Kremp and microspores belong to the dispersed species *Lundbladispora gigantea* (Alpern) Doubinger.

The third group of Carboniferous fertile herbaceous lycopsids consists of the genera *Porostrobus* Nathorst and *Bothrodendrostrobus* Watson. Species of both genera produced megaspores of the *Setosisporites*-type and microspores of the densospore group (*e.g.* Balme 1995).

We re-examined the type collection of *Porostrobus nathorstii* Leary & Mickle stored in the Illinois State Museum, Springfield, USA from palynological view. The main goal was try to find *in situ* microspores, because all previously described *Porostrobus* species were bisporangiate and only *P. nathorstii* was defined as monosporangiate with only megaspores (Leary & Mickle 1989). This re-examination was successful and the species *P. nathorstii* could be emended based on newly macerated *in situ* microspores.

Material and methods

The Allied Quarry is on Vandruff Island, located in the Rock River between the cities of Rock Island and Milan, Illinois (SE 1/4 Sec. 14, T.17 N., R.2 W., Milan Quadrangle). Specimens were collected from sediments that fill a channel eroded in Devonian Cedar Valley Limestone (Leary 1981). The channel is 6 m deep, 8 to 30 m wide, steep-sided, and flat-bottomed. The meandering channel had been eroded by a river flowing roughly east to west and is exposed in several quarries in Rock Island and Henry counties, Illinois.

The exact stratigraphic age of the fossil-bearing shale is difficult to determine. The shale is underlain by upper Middle Devonian Cedar Valley Limestone. Pleistocene erosion has removed nearly all the overlying Pennsylvanian strata in the quarry, but at a few points clean white to buff sandstone is present above the fossil-bearing shale. This sandstone contains *Stigmaria* casts and, on this basis, has been correlated with the "Stigmarian Sandstone", or Babylon Sandstone. Across the Rock River from the quarry, the same sandstone is interlayered with shale, carbonaceous shale, and impure coals. Using palynomorphs, these strata have been dated as Caseyville, and probably lower Langsettian (R. Peppers, pers. comm.). Based on the spores recovered from the shale the Allied Quarry shale deposit is considered to be of mid Namurian age (R. Peppers, pers. comm.). Macrofossils also indicate a Namurian age (Leary 1981).

Specimens of fossil plants are stored in the Illinois State Museum, Springfield, as ISM 417032–417049. *In situ* micro- (isolated from paratype ISM 417034) and megaspores and their slides are stored in the Geological Institute v.v.i., Academy of Sciences, Prague, Czech Republic. The spores are classified according to the system of dispersed spores suggested by Dettmann (1963), and Smith & Butterworth (1967). *In situ* spores were compared directly with the original diagnoses (type specimens), descriptions and illustrations of dispersed spore species. Species determinations are based only on the original diagnoses, and not on the interpretations of subsequent authors. The terminology used for the descriptions of *in situ* spores is the same as that in the latest edition of the *Glossary of pollen and spore terminology* (Punt *et al*. 2007).

Systematic section

Class Lycopsida Scott, 1909
Order Selaginellales Prantl, 1874

Genus *Porostrobus* Nathorst, 1914

Type species. – *Porostrobus zeilleri* Nathorst, 1914.

Diagnosis. – See Leary & Mickle 1989, pp. 1639–1641.

***Porostrobus nathorstii* (Leary & Mickle, 1989) emend.**

Holotype. – Specimen ISM 417032, Geological Collection, Illinois State Museum, Springfield; Leary & Mickle 1989, fig. 3.

Paratypes. – ISM 417033–417043, Geological Collections, Illinois State Museum, Springfield; Leary & Mickle 1989, figs 4–6.

Collecting locality. – Shale deposits in the Allied Stone Company quarry, Milan, Rock Island County, Illinois (SE ¼ sec. 14, T. 17 N., R. 2 W., Milan Quadrangle).

Stratigraphy. – Caseyville Formation, Morrowan Series, Early Pennsylvanian.

Emended diagnosis (modified from Leary & Mickle 1989, p. 1639). – Bisporangiate cones up to 25 mm long and 7 mm in diameter (Fig. 1A, D, E, J), tapering slightly distally. Central axis up to 1 mm in diameter. Sporophylls lack a heel or keel, and possess a distal lamina up to 6 mm long. Tuft of leaves up to 20 mm long present at cone apex (Fig. 1A, B). Megasporangia containing a single megaspore tetrade (Fig. 1C–E, J) and microsporangia decreasing in size distally. Megaspores with prominent trilete arms; gulate; possessing branched hairs confined to an equatorial band. Trilete microspores with prominent equatorially thickened cingulum and thin radiated zona (Fig. 1F–I). Circular amb. Equatorial cingulum with thicker (darker) inner and lighter (outer) thinner portions. Inner body of the circular amb. Radial straight ridges from thicker to thinner part of cingulum and zona. The trilete mark is sometimes visible, reaching the diameter of the inner body.

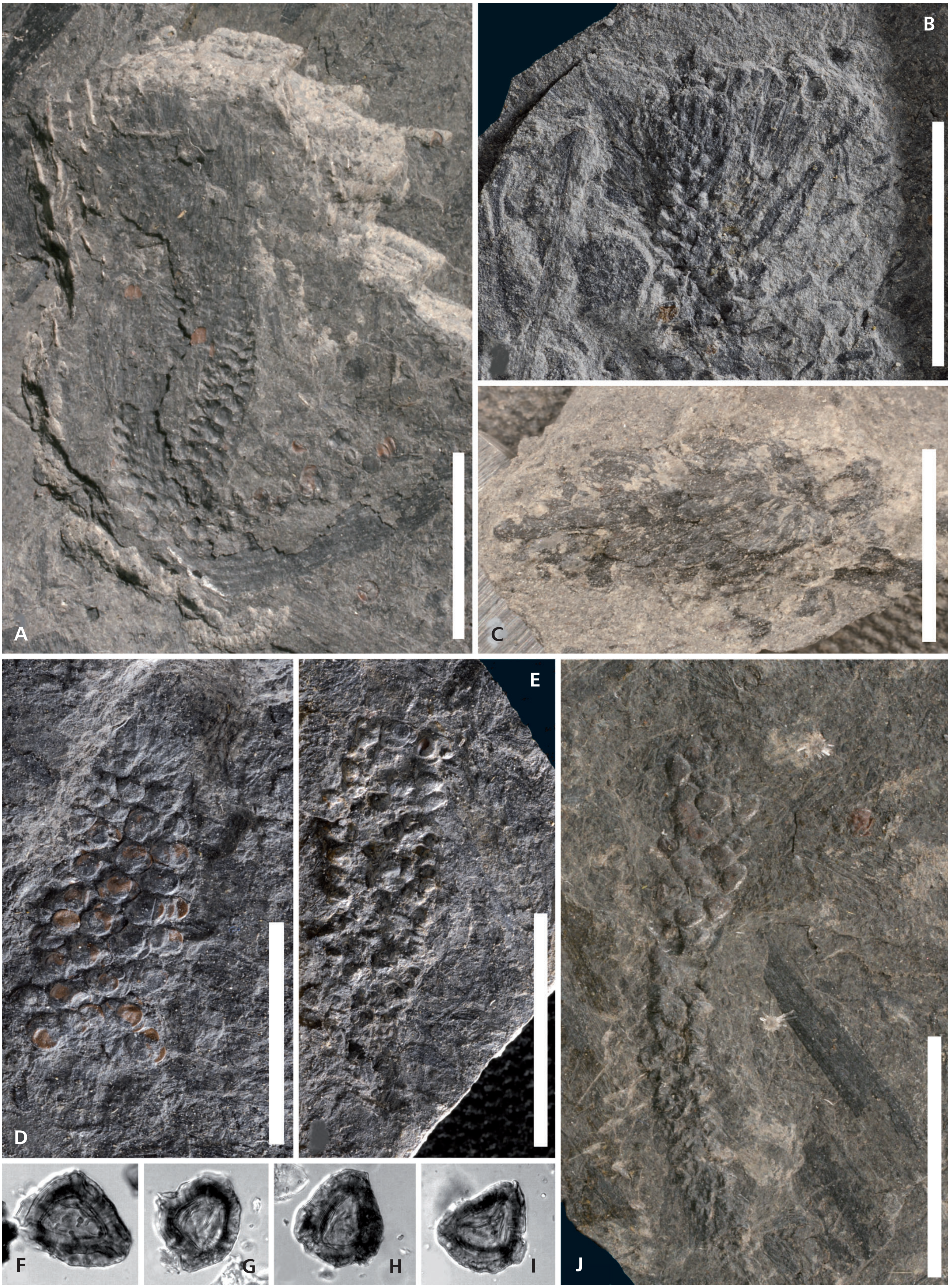
Remarks. – Megaspores can be compared with the dispersed spore species *Setosisporites praetextus* (Zerndt) Potonié & Kremp and microspores are comparable with the species *Cingulizonates bialatus* (Waltz) Smith & Butterworth.

Description of specimens. – See Leary & Mickle (1989, pp. 1640, 1643). *In situ* megaspores are 750–1,150 μm in diameter, microspores 35–52 μm in diameter. Hairs of megaspores are from 140 to 220 μm long.

History of the genera *Porostrobus, Bothrodendrostrobus* and *Bothrodendron*

The genus *Bothrodendron* Lindley & Hutton is based (Lindley & Hutton 1833) on compressions of large lycopsid

Figure 1. A – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417033. Two cones attached to a pedicle. Scale bar 1 cm. • B – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417036. Cone showing distal lamina of sporophyll. Scale bar 1 cm. • C – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417048. Part of the cone with sporangia. Scale bar 1 cm. • D – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417047. Cone arrangement of sporangia and tetrads. Scale bar 1 cm. • E – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417049. General view on the cone. Scale bar 1 cm. • F–I – *in situ* microspores isolated from *Porostrobus nathorstii* (Leary & Mickle) emend. (ISM 417034 – paratype) and compared to the dispersed miospore genus *Cingulizonates bialatus* (Waltz) Smith & Butterworth. All × 500. • J – *Porostrobus nathorstii* (Leary & Mickle) emend. ISM 417034. Axis and the cone. Scale bar 1 cm.


A
B
C
D
E
F
G
H
I
J

axes. But Lindley & Hutton (1833) also included in the genus anatomically preserved axes and cones without evidence that conclusively relates any of permineralized material to the compressions. The connection of cones and vegetative parts was never been demonstrated.

Watson (1908) studied five cone specimens (coal-balls) and named them only as "the cones of *Bothrodendron*", but without any evidence about connection with *Bothrodendron* branches or trunks. But Hirmer (1927) referred Watson's specimens to *Bothrostrobus* Zalessky. Watson (1908) described *in situ* megaspores in megasporangia in the basal portions of the cones and microsporangia in the upper portions. Microsporangia are smaller than megasporangia. *In situ* megaspores are in four per megasporangium and possess typical hairs about 150 μm long. The only informations given about the *in situ* microspores was that they are about 27 μm in the diameter and possess an equatorial ridge. Watson (1908) wrongly attributed the cones to *Bothrodendron mundum* Williamson and stated that cones are different from those of arborescent lycopsids of the *Lepidostrobus*-type.

Hirmer (1927) named this type of cones for the first time as *Bothrostrobus mundus* Hirmer. Chaloner (1967) placed *Bothrostrobus olryi* Rénier (the type species of the genus) in synonymy with *Lepidostrobus* (Brongniart) Brack-Hanes & Thomas and recognised that cones reported by Watson (1908) cannot be referred to *Lepidostrobus*, *i.e*. to arborescent lycopsids. On the other hand, Chaloner (1967) realised that Watson's cones do not belong to *Bothrodendron mundum*. Therefore, Chaloner (1967) proposed the name *Bothrodendrostrobus watsonii* Chaloner for Watson's cones. It means that Watson's cones have been known by two different names, *Bothrostrobus mundus* and *Bothrodendrostrobus watsonii* but important is, that nothing was known about their parent plants. Generic name *Bothrodendrostrobus* was first used in the index of Hirmer (1927, p. 701) for some material that he named *Bothrostrobus* in the text. Later Chaloner (1967) validated the name *Bothrodendrostrobus* by supplying a description and designating the Watson's material as the type specimens.

Stubblefield & Rothwell (1981) described thirteen specimens of permineralized megagametophytes and embryos from the Langsettian of England, UK. They compared the megaspores with the dispersed spores species *Setosisporites praetextus* f. *minor* Chaloner. Stubblefield & Rothwell (1981, pp. 62, 68, 69) gave a brief review about the complicated position and classification of these cones and their parent plants and compared *Bothrodendrostrobus* with the extant genus *Isoetes* Linnaeus based on the embryogeny and stated that it is different from arborescent lycopsids of the *Lepidocarpon-Lepidophloios*-type. They also reinstalated the combination *Bothrodendrostrobus mundus* and proposed *B. watsonii* as synonymum of it. Important is that Stubblefield & Rothwell (1981) stated (based upon the embryological similarity known for *Bothrodendrostrobus* and the extant Isoetales), that parent plant of *Bothrodendrostrobus* was not an arborescent lycopsids with a stigmarian root system, but it have been a much smaller plant with cormose rooting-system like that of the Pennsylvanian genus *Paurodendron* Fry (Stubblefield & Rothwell 1981, p. 633).

Nathorst (1894, 1904) reported a small cone from the Mississippian of Spitzbergen as *Lepidostrobus zeilleri* Nathorst and he later (Nathorst 1914) erected the new genus *Porostrobus* for this species and described *in situ* microspores with prominent equatorial cingulum belonging to the densospore group. The *in situ* megaspores can be assigned to the dispersed species *Setosisporites hirsutus* var. *brevispinosa* (Zerndt) Potonié & Kremp (Chaloner 1967).

Emendation of the genus *Porostrobus* was proposed by Bharadwaj (1958) who re-investigated the original specimens of *P. zeilleri* Nathorst collected from the Mississippian of Lower Spitzbergen, assigned the *in situ* microspores to the genus *Densosporites* (Berry) Butterworth *et al*. and described the *in situ* megaspores as gulate with verrucate to granulate exine and developed contact area.

Chaloner (1958) described a new species *Selaginellites canonbiensis* Chaloner with *in situ* megaspores that he compared to the dispersed spore species *Setosisporites hirsutus* (Loose) Ibrahim and *in situ* microspores of the *Cingulizonates*-type. Later Chaloner (1962) realized similarity with *Porostrobus* and suggested the new combination *Porostrobus canonbiensis* (Chaloner) Chaloner.

The third fertile species of *Porostrobus* was described by Leary & Mickle (1989) as *P. nathorstii* when they also emended the genus. Leary & Mickle (1989) recovered only megaspores belonging to the dispersed species *Setosisporites praetextus* making *Porostrobus nathorstii* the only monosporangiate species of the genus within their original concept of the species.

Taxonomic and nomenclatoric problems with cones of the *Bothrodendrostrobus* and *Porostrobus*-type and their parent plants are still confusing and complicated (for anatomical details and detailed discussion see Bharadwaj 1958, pp. 71–74; Chaloner 1958, pp. 250, 251; Stubblefield & Rothwell 1981, p. 626; Leary & Mickle 1989, pp. 1643, 1644).

Ecology of *Porostrobus*/*Bothrodendrostrobus*

Leary & Mickle (1989) described *P. nathorstii* together with sphenophylls (*Sphenophyllum tenerrimum* Stur,

Table 1. Selected dimensions of *Bothrodendrostrobus* and *Porostrobus* cones, their stratigraphical positions and their *in situ* spores.

	Diameter (mm)	Length (mm)	Diameter of axis (mm)	*In situ* microspores	*In situ* megaspores	Stratigraphical position	References
Bothrodendrostrobus mundus	2–10	> 10	3	densospores	*Setosisporites praetextus* f. *minor*	Langsettian	Chaloner (1967)
Porostrobus zeilleri	6	> 20	1	*Densosporites*	*Setosisporites hirsutus* var. *brevispinosus*	Mississippian	Chaloner (1962)
Porostrobus canonbiensis	3.5	> 15	?	*Cingulizonates loricatus*		Westphalian	Bharadwaj (1958)
Porostrobus nathorsti	4–7	18–36	1	Not macerated	*Setosisporites praetextus*	Namurian	Leary & Mickle (1989)
Porostrobus nathorsti	4–7	18–36	1	*Cingulizonates*	*Setosisporites praetextus*	Namurian	Herein

S. sublaure Purkyňová*, S. cuneifolium* Sternberg), calamites [*Mesocalamites cistiformis* Stur, *Asterophyllites charaeformis* (Sternberg) Goeppert, *A. equisetiformis* Brongniart], *Sphenopteris preslesensis* Stockmans & Willière, *Alethopteris lonchitica* Schlotheim, *Gulpenia limburgensis* Gothan & Jongmans and *Palaeopteridium reussi* (Ettingshausen) Kidston. Lycopods are represented by *Lepidostrobus* cones, *Lepidocarpon* megasporophylls, *Lepidophylloides* leaves, *Stigmaria* and *Lepidodendron* axis. No vegetative structures unambiguously associated with *Porostrobus* cones have been found (Leary & Mickle 1989).

Cone specimens of *P. nathorstii* consist of two types. Some cones are essentially intact in that sporangium is found covering mature megaspore tetrads, and the distal sporophyll laminae and tuft are intact. Other cone specimens consist of little more than megaspore tetrads in the positions of sporangia in a cone, but the sporangium, laminae tissue, and axis are not preserved. No specimen has been observed that appeared to has dehisced sporangia. Based on these observations and indications that these cones were transported, it is possible to speculate that whole cones were shed from the parent plant intact (Leary & Mickle 1989).

Cones were found in sediments completely filled channels eroded in a nearly level limestone surface (Leary 1981). Isolated *S. praetextus* megaspores are concentrated in the highly fissile black shale at the top of the sequence. Parent cones are restricted to these upper black shales. Almost none of the channel sediments are bioturbated, indicating that plants did not grow in the channels, even when the channels filled with sediments (Leary & Mickle 1989). This observation suggests that cones and megaspores were transported prior to burial. Based on the associated flora, the *Porostrobus*-bearing plants probably grew in area adjacent to channels.

Leary & Trask (1985) interpreted plant assemblage of the Rock Island County as upland flora. This term has been used to designate distinctive nonswamp floras. The upland plants grew on soils derived from limestone bedrock, and many were stream banks and ultimately were deposited in stream channels with minimal transport. Generally upland flora includes a number of plant taxa which are unknown in coal swamp. The presence of a permanent body of water in the channels apparently permitted the growth on the drier sites in Rock Island of genera (*e.g. Lepidodendron* Sternberg and *Mesocalamites* Hirmer) common to coal swamp (Leary & Trask 1985).

The greatest similarity appears to be with the flora of the Czech part of the Upper Silesian Basin, Czech Republic (Šusta 1928, Purkyňová 1970). Here, Havlena (1970) recognised several microenvironments within Namurian hygrophile environment in addition to a major separation of the hygrophile and mesophile environments. The mesophile (*i.e.* upland) flora described by Havlena (1970) was present only as fragments whereas preservation of the plants in the Rock Island is excellent (Leary & Trask 1985).

It should be noted that *Porostrobus* and *Bothrodendrostrobus* were not the only densospores-producers because this type of microspores has also been recovered from a sub-arborescent lycopsid of the genus *Omphalophloios* White (*e.g.*, Wagner *et al.* 2003, Opluštil *et al.* 2010).

Miospores of the densospore group [*i.e. Densosporites, Cristatisporites* (Potonié & Kremp) Butterworth *et al.* and *Cingulizonates*)] first appeared in Devonian strata although they are most abundant throughout the Pennsylvanian in most Euramerican coalfields. They are not very important from a stratigraphical view but they belong to ecologically significant spores. Smith (1962) assigned densospores-dominated parts of coal seams to the densospore phase which is interpreted as the ombrotrophic stage of mire development as is also supported by the high inertinite and very low mineral matter content (see also Butterworth 1964, Habib & Groth 1967). On the other hand, different authors (*e.g.* Littke 1987, Strehlau 1990, Opluštil *et al.* 1999) identified a densospore phase from coal seams which contained sedimentary partings or increased ash content and which evidently, did not develop into an ombrotrophic mire. Eble & Grady (1990) suggested an ecological link between densospores-producing plants and brackish conditions.

Stubblefield & Rothwell (1981) discussed the palaeoecological preference of the parent plants of *Bothrodendrostrobus* based on the dispersed occurrences of *Setosisporites* megaspores. They suggested that *Bothrodendrostrobus* may have grown in a swampy environment. Stubblefield & Rothwell (1981) found megagametophyte and embryos in isolated spores. It is, therefore, probable, that megagametophyte development, fertilization, and embryogeny in *Bothodendrostrobus* occured (like in the extant Isoetales) in an aqueous environment after the spores were released from sporangia (Stubblefield & Rothwell 1981, p. 632). The pores on the megaspore surface described by Stubblefield & Rothwell (1981), which were initially covered and later exposed, may be a mechanism for gaseous exchange or possibly for water regulation (Stubblefield & Rothwell 1981).

Piérart (1968) described two main assemblages of dispersed megaspores, "wet" with *Cystosporites* Schopf*, Triangulatisporites*, *Lagenicula* (Bennie & Kidston) Potonié & Kremp and *Tuberculatisporites* (Ibrahim) Potonié & Kremp and "less wet" with *Zonalesporites* (Ibrahim) Potonié & Kremp and *Setosisporites* (Ibrahim) Dybová-Jachowicz *et al*.

Similar results are described by Bartram (1987) who recognised five palynological phases based on megaspore record and petrological analysis. Generally drier Phase 3 is characteristic by the occurrence of *Spencerisporites radiatus* (Ibrahim) Bek *et al*., *Setosisporites hirsutus* (Loose) Ibrahim, *Lagenicula subpilosa* Ibrahim and *Zonalesporites*.

It means that *Setosisporites* and *Zonalesporites* megaspores (parent fructifications of both genera produced densospores) are often recorded together as dispersed. It suggests similar ecological needs of their parent plants.

The results of Piérart (1968), Bartram (1987), Leary & Trask (1985) and Leary & Mickle (1989) suggested, based on the study of compression specimens and dispersed megaspores, that *Porostrobus* could preferred less wet environment probably corresponding with ombrotrophic type stage of mire development.

Only Stubblefield & Rothwell (1981) described *Setosisporites* megaspores of the *Bothrodendrostrobus* origin (*i.e*. from permineralised cones) and stated that parent plants may have grown in swampy environment, similar to rheotrophic type stage of mire development.

It is possible that parent plants of compression specimens of *Porostrobus* cones preferred different ecological conditions (ombrotrophic-type of swamp) than permineralised (coal-balls) specimens of *Bothrodendrostrobus* (rheotrophic-type of swamp), although both cone genera produced the same spores.

Discussion

All cones of the genera *Bothrodendrostrobus* and *Porostrobus* have yielded the same types of micro- and megaspores that can be closely compared with the densospore group (microspores) and the spore genus *Setosisporites*.

Morphologically the simplest spore types, *i.e*. trilete, laevigate thin-walled (*e.g*. calamospores) or laevigate-microgranulate-microverrucate (*e.g*. genera *Leiotriletes* Naumova, *Granulatisporites* Ibrahim and *Apiculatisporis* Potonié & Kremp) miospores have been recovered from several plant species and genera, sometimes even from different plant groups (Balme 1995). This is not the case for microspores of the densospore group and megaspores of the genus *Setosisporites* as such morphologically more complicated spores were usually produced by the only parent plant genus (Balme 1995). This means that from a palynological point of view the two genera *Bothrodendrostrobus* and *Porostrobus* may be hypothetically synonymous. Additional circumstantial evidence is that the parent plants of both cones were herbaceous lycopsids. Chaloner (1958) originally named his specimen of *Porostrobus* as *Selaginellites* Zeiller and also Stubblefield & Rothwell (1981, p. 633) stated that *Bothrodendrostrobus* was not produced by arborescent lycopsids with stigmarian root system, but that it may have been a much smaller plant with cormose rooting system like *Paurodendron*, *i.e*. a *Selaginella*-like plant.

We cannot be sure about the synonymity of *Porostrobus* and *Bothrodendrostrobus* because all specimens of *Porostrobus* are preserved as compressions while all *Bothrodendrostrobus* specimens are from coal-balls. We know some anatomical data from *Bothrodendrostrobus* cones but they cannot be observed on *Porostrobus* specimens. Also morphological informations described on *Porostrobus* cones cannot be proved for specimens of *Bothrodendrostrobus*. Maybe both genera represent different modes of the preservation (like *Sigillariostrobus* Hirmer and *Mazocarpon* Benson), but we still have no direct evidence for such a conclusion.

Acknowledgement

We acknowledge financial support from the Grant Agency of the Czech Republic (IAA301110701) and the Research Program (AVOZ30130516) of the Institute of Geology v.v.i., Academy of Sciences, Prague. Special thanks to M. Libertín from the National Museum, Prague, Czech Republic and E. Schroeder from the Illinois State Museum, Springfield, USA for excellent photographs of plant specimens. We are obliged to B.A. Thomas from the University of Aberystwyth, UK and S. Opluštil from the Faculty of Sciences, Charles University, Prague, Czech Republic for reviews, helpful comments and suggestions.

References

BALME, B.A. 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology 87*, 81– 323. DOI 10.1016/0034-6667(95)93235-X

BARTRAM, K.M. 1987. Lycopod succession in coals: an example from the Low Burnley Seam (Westphalian B), Yorkshire, England, 187–199. *In* SCOTT, A.C. (ed.) *Coal and Coal-bearing strata: Recent advances. Geological Society, Special Publications 32*.

BEK, J., OPLUŠTIL, S. & DRÁBKOVÁ, J. 2001. Two species of *Selaginella* cones and their spores from the Bohemian Carboniferous continental basis of the Czech Republic. *Review of Palaeobotany and Palynology 114*, 57–81. DOI 10.1016/S0034-6667(00)00069-5

BHARADWAJ, D.A. 1958. On *Porostrobus zeilleri* Nathorst and its spores with remarks on the systematic position of *P. benholdi* Bode and phylogeny of *Densosporites* Berry. *The Palaeobotanist 7*, 67–75.

BUTTERWORTH, M.A. 1964. Die vertliegung der *Densosporites sphaerotriangularis* in Westphalian B der westpenninschen steinkohlenfelder Englands. *Fortschritte in der Geologie von Rheinland und Westphalen 12*, 3173–330.

CHALONER, W.G. 1958. A Carboniferous *Selaginellites* with *Densosporites* microspores. *Palaeontology 1*, 245–253.

CHALONER, W.G. 1962. A *Sporangiostrobus* with *Densosporites* microspores. *Palaeontology 5*, 73–85.

CHALONER, W.G. 1967. Lycophyta, 437–802. *In* BOUREAU, E. (ed.) *Traité de Paléobotanique. Tome II.* Masson et Cie, Paris.

DETTMANN, M.E. 1963. Upper Mesozoic microfloras from southeastern Australia. *Proceedings of the Royal Society of Victoria 77,* 1–148.

EBLE, C.F. & GRADY, W.C. 1990. Paleoecological interpretation of a Middle Pennsylvanian coal bed from the central Appalachian Basin, U.S.A. *International Journal of Coal Geology 16*, 255–286. DOI 10.1016/0166-5162(90)90054-3

HABIB, B. & GROTH, P.K.H. 1967. Paleoecology of migrating Carboniferous peat habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology 3*, 185–195. DOI 10.1016/0031-0182(67)90013-2

HAVLENA, V. 1970. Ecology and mode of deposition of the macroflora in cyclothems of the Ostrava Formation (Namurian A). *Věstník Ústředního ústavu geologického 45*, 291–294.

HIRMER, M. 1927. *Handbuch der Pälaobotanik. Band I: Thallophyta, Bryophyta, Pteridophyta*. 724 pp. R. Oldenburg Verlag, München & Berlin.

LEARY, R. 1981. Early Pennsylvanian geology and paleobotany of the Rock Island County, Illinois area. Part 1: Geology. *Illinois State Museum, Report of Investigation*, 37.

LEARY, R. & MICKLE, J.E. 1989. *Porostrobus nathorstii*, sp. nov.: a new species of lycopsid cone from the early Pennsylvanian of Illinois. *American Journal of Botany 76*, 1638–1645. DOI 10.2307/2444401

LEARY, R.L. & TRASK, C.B. 1985. Early Pennsylvanian paleotopography and depositional environments, Rock Island County, Illinois. *Illinois State Geological Survey Guidebook 18*, 1–42.

LINDLEY, J. & HUTTON, W. 1833. *The fossil flora of Great Britain I.* 218 pp. J. Ridgway, London.

LITTKE, R. 1987. Petrology and genesis of Upper Carboniferous seams from the Ruhr region, West Germany. *International Journal of Coal Geology 7*, 147–184. DOI 10.1016/0166-5162(87)90047-4

NATHORST, A.G. 1894. Zur fossilien Flora der Polander. I. Zur paläozoischen Flora der Arktischen Zone. *Kongliga Svenska Vetenskaps-Akademiens Handlingar 26*, 1–80.

NATHORST, A.G. 1904. Sur la flore fossile regions antarctiques. *Compte Rendu de la Academie des Sciences Paris 138*, 1447–1450.

NATHORST, A.G. 1914. *Zur fossilien Flora der Polarlander I(4): Nachträge zur paläozoischen Flora Spitzbergens*. 110 pp. Norstedt & Söner, Stockholm.

OPLUŠTIL, S., BEK, J. & SCHULTKA, S. 2010. Re-examination of the genus *Omphalophloios* White, 1893 from Upper Silesian Basin. *Bulletin of Geosciences 85(1),* 123–136.

OPLUŠTIL, S., SÝKOROVÁ, I. & BEK, J. 1999. Sedimentology, coal petrology and palynology of the Radnice Member in the S-E part of the Kladno-Rakovník Basin, Central Bohemia (Bolsovian). *Acta Universitatis Carolinae, Geologica 43*, 599–623.

PIÉRART, P. 1968. Les associations de microspores et de megaspores dans une couche (couche 70 de Beeringen) du Westphalien A superieur de la Campine (Belgique). *Review of Palaeobotany and Palynology 7*, 275–283. DOI 10.1016/0034-6667(68)90033-X

PUNT, W., HOEN, P.P., BLACKMORE, S., NILSSON, S. & LE THOMAS, A. 2007. Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology 143*, 1–81. DOI 10.1016/j.revpalbo.2006.06.008

PRANTL, K.A.E. 1874. *Lehrbuch der Botanik*. 498 pp. W. Engelmann, Leipzig.

PURKYŇOVÁ, E. 1970. Die Unternamurflora des Beckens von Horní Slezsko (ČSSR). [The lower Namurian flora of the Upper Silesian Basin, Czechoslovakia.] *Paläontologische Abhandlunge Paläobotanik, Abteilung B 3(2)*, 129–268.

SCOTT, D.H. 1909. *Studies in Fossil Botany, 2nd edition.* 552 pp. A. & C. Blafl Ltd., London.

SMITH, A.H.V. 1962. The palaeoecology of Carboniferous peats based on the miospores and petrography of bituminous coals. *Proceedings of the Yorkshire Geological Society 33*, 423–474. DOI 10.1144/pygs.33.4.423

SMITH, A.H.V. & BUTTERWORTH, M.A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology 1,* 1–324.

STREHLAU, K. 1990. Facies and genesis of Carboniferous coal seams of Northwest Germany. *International Journal of Coal Geology 15*, 245–292. DOI 10.1016/0166-5162(90)90068-A

STUBBLEFIELD, S.P. & ROTHWELL, G.W. 1981. Embryogeny and reproductive biology of *Bothrodendrostrobus mundus* (Lycopsida). *American Journal of Botany 68(5)*, 625–634. DOI 10.2307/2442789

Šusta, V. 1928. Stratigrafie des Ostrau-Karviner Steinkohlenreviers im lichte der Paläontologie. *Der Köhlenbergau des Ostrau-Karviner Steinkohlenreviers I*, 385–484.

Thomas, B.A. 1997. Upper Carboniferous herbaceous lycopsids. *Review of Palaeobotany and Palynology 95*, 129–153. DOI 10.1016/S0034-6667(96)00032-2

Thomas, B.A. 2005. A reinvestigation of *Selaginella* species from the Asturian of the Zwickau coalfield, Germany and their assignment to the new sub-genus *Hexaphyllum*. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 156(3)*, 1–12. DOI 10.1127/1860-1804/2005/0156-0403

Wagner, R.H., Brousmiche-Delcambre, C. & Coquel, R. 2003. Una Pompeya Paleobotanica: historia de una marisma carbonifera sepultada por cenizas volcanicas, 448–475. *In* Nuche, R. (ed.) *Separata de Patrimonio Geológico de Castilla-La Mancha*. Enresa, Madrid.

Watson, D.M.S. 1908. The cone of *Bothrodendron mundum. Memoires of the Manchester Literary and Philosophical Society 52*, 1–15.