

# Two new Carboniferous fertile sphenophylls and their spores from the Czech Republic

MILAN LIBERTÍN, JIŘÍ BEK, and JANA DRÁBKOVÁ



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Two new species of sphenophyllalean strobili with in situ spores are proposed from the Radnice Basin of the western and central Bohemian Carboniferous continental basins of the Czech Republic. *Bowmanites brasensis* sp. nov. from Břasy (Matylda Mine) and *B. pseudoaquensis* sp. nov. from Ovčín locality are determined mainly on the basis of their spores, which are about 100 µm in diameter. The thick-walled exine of the miospores is laevigate or sometimes very finely scabrate on the proximal contact area. Spores resemble the dispersed species *Punctatisporites obesus*. Cones of *B. brasensis* and *B. pseudoaquensis* are organically connected with stems having prominent blade leaves and represent a new group of sphenophyllalean strobili.

Key words: Sphenophyllales, *Bowmanites*, *Punctatisporites*, spores, Pennsylvanian, Carboniferous, Czech Republic.

Milan Libertín [milan\_libertin@nm.cz], National Museum, Václavské náměstí 64, 11821 Prague 1, Czech Republic; Jiří Bek [mrbean@gli.cas.cz], Laboratory of Palaeobiology and Palaeoecology, Institute of Geology v.v.i., Academy of Sciences, Rozvojová 269, 165 00 Prague 6, Czech Republic; Jana Drábková [drabkova@cgu.cz], Czech Geological Survey, Klárov 3, 118 21 Prague 1, Czech Republic.

## Introduction

The majority of Carboniferous sphenophylls and their spores are stratigraphically important fossils. Some also have palaeoecological importance and can be used in palaeoenvironmental reconstructions. Carboniferous sphenophylls have been classified based on sterile parts of plants (mainly leaves) for many years. Several authors have proposed a large number of sphenophyllalean species, even though heterophylly is widespread. The systematics of “leafy” sphenophyllalean taxa consists of several species that are probably synonymous. Most sphenophyllalean cones with different modes of preservation (petrifications and compressions) have been assigned only to the genus *Bowmanites*. The main criterion for their classification is the morphology/anatomy of the cones, the significance of their in situ spores having been ignored for many years. This contrasts with modern concepts of the classification of fossil reproductive organs where in situ spores are as important in taxonomic diagnoses and descriptions as their parent plants (e.g., Thomas 1970; Bek and Opluštil 2004, 2006). Authors following this concept have developed a new approach to the classification of Carboniferous sphenophyllalean fructifications based on a combination of morphological/anatomical features of the cones and their in situ spores (e.g., Bek 1998, 2004; Libertín and Bek 2003, 2006; Bek et al. in press). This new systematics represents a more natural classification and recognises seven groups (e.g., Libertín and Bek 2006) characterised by different cones and in situ spores. The current paper adds to our knowledge of a new group of sphenophyllalean plants. Studies of several specimens of compres-

sion strobili of *Bowmanites brasensis* sp. nov. and *B. pseudoaquensis* sp. nov. and slides with their in situ spores reveal a new type of sphenophyllalean spore.

*Institutional abbreviation.*—NMP, National Museum, Prague, Czech Republic; WBMP, West Bohemian Museum in Pilsen.

## History of research

Parent plants of *Punctatisporites obesus*-producing spores belong to the genus *Sphenophyllum* which was erected by Brongniart (1822) to formally accommodate fossil plants formerly included in *Sphenophyllites*. Presl (1838) was probably the first to describe a compression specimen of a sphenophyllalean cone, as *Rotularia marsileafolia*. Binney (1871) proposed the name *Bowmanites* for structureless fragments of sphenophyllalean cones, while Seward (1898) erected *Sphenophyllostachys* for cones of *Sphenophyllum*.

Sternberg (1823) described the sphenophyllalean plants *Rotularia* and *Volkmania* from the Carboniferous of the Czech Republic. Bek (1998) and Bek and Opluštil (1998) were the first to describe in situ sphenophyllalean spores from the Czech Republic. There are two approaches for the subdivision and classification of sphenophyllalean cones. The first divides them into three groups (*Jugati*, *Conferti*, and *Simplices*) based on the number and position of sporangia on each sporangiophore (Hoskins and Cross 1943). The second approach was suggested by Remy (1955), who

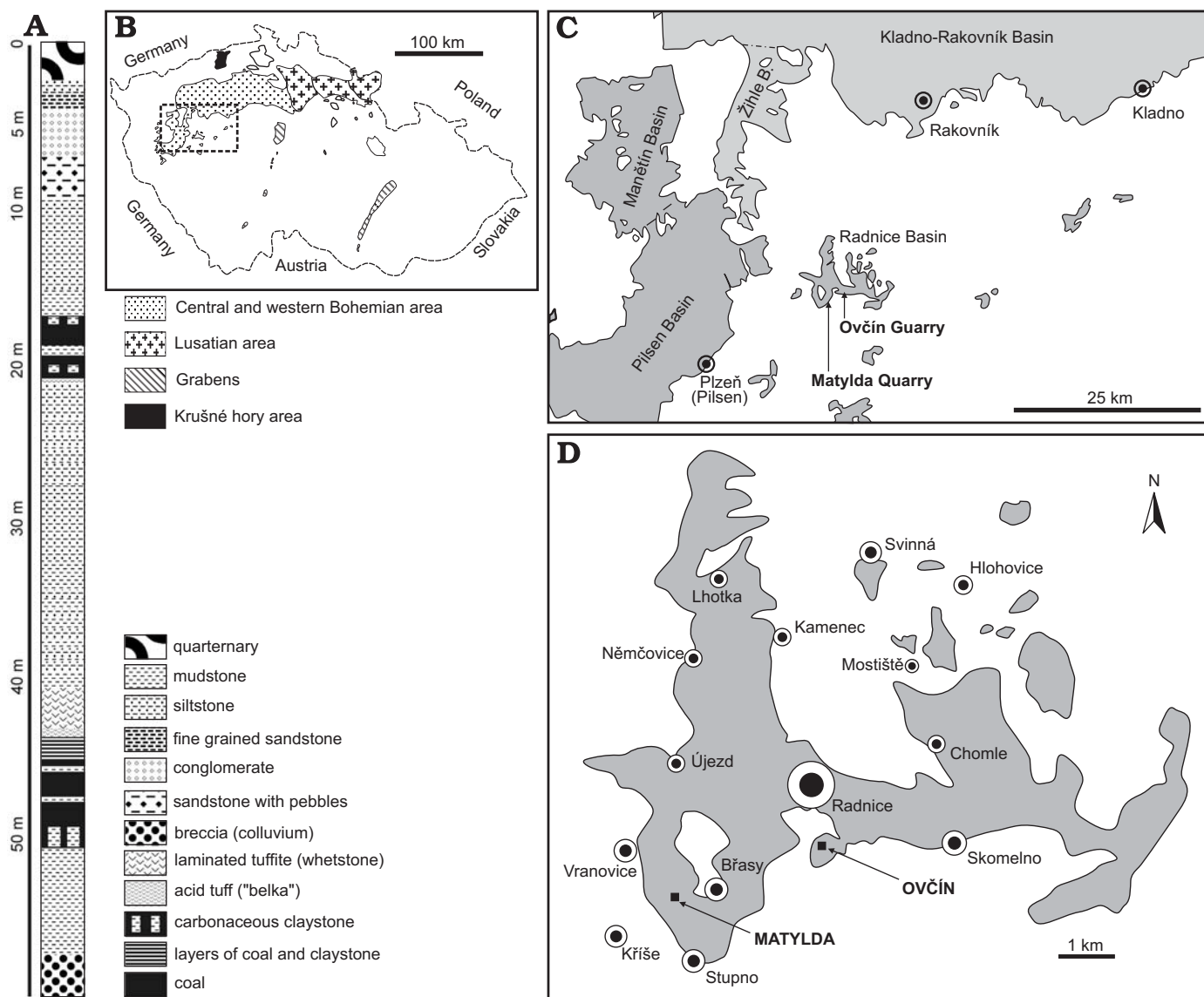


Fig. 1. A. Geological profile of the Radnice Basin. B. Sketch map of the Czech Republic. C. Position of the Radnice Basin among other basins of the central and western Bohemian continental basins of the Czech Republic. D. Sketch map of the Radnice Basin with localities mentioned in the text.

proposed four new cone genera of sphenophylls, *Koinostachys*, *Aspidiostachys*, *Tristachya*, and *Anastachys*, based on similar criteria with special attention to the number of sporangia. However, he also included some non-sphenophyllalean taxa (e.g., *Anastachys*). Both of these divisions united parent plants that produced monolete, trilete, and trilete operculate (vestisporae and *Pteroretis*) spores in one group or one genus.

## Localities, material, and methods

The specimens WBMP-F 82, NMP-E 6124 (1484 in Bek and Opluštil 1998), and NMP-E 6293 are from Ovčín opencast mine while specimens WBMP-F 03760, WBMP-F 01334, and WBMP-F 00188 came from Břasy, Matylda Mine (both Radnice Basin, Czech Republic). The geographic positions

of these localities are shown in Fig. 1. Digital photomicrographs and negatives of spores are stored in the Institute of Geology, Academy of Sciences v.v.i., Prague, whereas digital photographs of the cones and slides with spores are in the NMP. Spores were recovered by dissolving small portions of sporangia in 35 % hydrofluoric acid for 24 h and in nitric acid (40%) for 24–40 h, then cleared in KOH (5%) for 1 h. All spores were mounted in glycerine jelly for direct microscopic study. Some spores were examined with a CAMECA SX100 scanning electron microscope. Photomicrographs were taken using an Olympus C330s digital camera and a BX51 light microscope. The terms used for the descriptions of the in situ spores are the same as those in the latest edition of the *Glossary of pollen and spore terminology* (Punt et al. 2007). In situ spores were classified according to the system for dispersed spores suggested by Potonié and Kremp (1954, 1955), Dettmann (1963), and Smith and Butterworth (1967).

## Systematic palaeontology

Order Sphenophyllales Seward, 1898

Family Sphenophyllaceae H. Potonié, 1893

Genus *Bowmanites* Binney, 1871

*Type species: Bowmanites cambrensis* Binney, 1871

*Type locality:* Pontypool, South Wales, Bensham, Seam, Jarrow; Viséan.

*Bowmanites brasensis* sp. nov.

Figs. 2, 3.

*Etymology:* After Břasy, the type locality.

*Type material:* Holotype: NMP-E 6293; paratypes: WBMP-F 03760, WBMP-F 01334, and WBMP-F 00188.

*Type locality:* Břasy (Matylda Mine), Radnice Basin, Czech Republic.

*Type horizon:* Base of the Whetstone volcanic horizon, directly overlying the Lower Radnice Coal, Radnice Member, Radnice Basin, Kladno Formation, Lower Bolsovian, Pennsylvanian, Carboniferous.

*Material.*—Specimens NMP-E 6293, WBMP-F 03760, WBMP-F 01334 and WBMP-F 00188 from the Břasy (Matylda Mine) locality.

*Diagnosis.*—Monopodially branched sterile stems with internodes. Leaves divided into three or four lobes with sharp tips. Six leaves in whorls. Strobili borne terminally. Circular sporangia. The surface of sporangia grooved, terminal sporangia among the axis and sterile bracts. Trilete circular to subcircular spores. Rays of trilete mark three-quarters of the radius. Exine 3–6 µm thick.

*Description.*—Shoots are branched monopodially (Fig. 2C, E) and from 0.5 to 4 mm wide but thicker at the nodes. The internodes are 2–5 mm long. The narrow, elongate leaves can be divided into three or four segments, each with a prominent sharp tip (Fig. 2A, D). Leaves are arranged in verticills (Fig. 2E), up to six, deeply divided along single vein. The length of lobes is 2–5 mm. Reproductive organs are terminally borne (Figs. 2B, 3A). The strobili are 40–60 mm long and their width, including bracts, is 5–6 mm. The cone axis is relatively narrow, approximately 0.5 mm wide (Fig. 3D). Circular sporangia 1 mm in diameter (Figs. 2B, 3B–D) are connected to the cone axis by sporangiophores about 0.2 mm long (Fig. 3B, C). The surface of the sporangia is prominently grooved. Sporangioophores with terminal sporangia lie between the axis and sterile bracts (Fig. 3D). Sterile bracts are 4–5 mm long, hook-shaped, prominently deflected at the area with sporangiophores. Trilete spores are circular to subcircular 88(96)106 µm in diameter. Inner body 75(88)100 µm in diameter. The spores are three-dimensionally preserved (Fig. 3E–H). The outer exine layer, probably exospore, is almost always broken or is not preserved (Fig. 3E–H). Its thickness is 3–6 µm (Fig. 3I). Almost all spores are, therefore, preserved as isolated circular trilete inner bodies about 88 µm on average.

*Discussion.*—All the spores are closely similar and are comparable to the dispersed species *Punctatisporites obesus*.

*Stratigraphic and geographic range.*—Radnice Member,

Lower Bolsovian, Carboniferous, the Radnice Basin, Czech Republic.

*Bowmanites pseudoaquensis* sp. nov.

Figs. 4–6.

1998 *Sphenophyllostachys aquensis* (Remy) Boureau 1964; Bek 1998: 87–90, pl. 83.

1998 *Sphenophyllostachys aquensis* (Remy) Boureau 1964; Bek and Opluštil 1998: 149–150, pl. 4: 8–10.

*Etymology:* The morphology of the holotype closely resembles cones of *Sphenophyllostachys aquensis*.

*Holotype:* NMP-E 6124.

*Type locality:* Ovčín opencast mine, near Radnice, Radnice Basin, Czech Republic.

*Type horizon:* Base of the Whetstone volcanic horizon, directly overlying the Lower Radnice Coal, Radnice Member, Kladno Formation, the Radnice Basin, lower Bolsovian, Pennsylvanian; Carboniferous.

*Material.*—Holotype (NMP-E 6124), and specimen NMP-E 6293 from Ovčín opencast mine, Radnice Basin.

*Diagnosis.*—Twelve lanceolate leaves per whorl. Tips of leaves pointed. Circular sporangia, sterile bracts arch-like bend apically. Subcircular to circular trilete spores. Thick-walled exine laevigate to finely scabrate.

*Description.*—Stems are monopodially branched, 1–2 mm wide with internodes 2–8 mm long and 1–3 mm wide (Fig. 6A, B, D). Leaves are 4–8 mm with narrow lanceolate margins (Fig. 6C) and arranged in whorls (Fig. 4A, B<sub>2</sub>). Cones are 200 mm long and 4–5 mm wide and possess an apex with sterile leaves. Circular sporangia are about 1.5–2 mm in diameter (Figs. 4A<sub>3</sub>, 5A, G, 6E). Sporangia occur between the axis of the cone and sterile bract on reduced sporangiophores (Fig. 5A, G). The surface of sporangia is finely rugose. Sterile bracts are hook-shaped; the apical margins are slightly wider at the end with rounded tips. Sterile stems are 1.0–2.5 mm in diameter.

Trilete spores are 110(121)150 µm in diameter (Fig. 5B–F). Circular to subcircular amb, simple laesurae, 1/2–2/3 of the radius. Exine laevigate to finely scabrate at the proximal contact area, 5–9 µm thick (Fig. 5B–F).

*Remarks.*—All the spores are closely similar and can be identified as *Punctatisporites* cf. *obesus* because the sculpture of the exine is sometimes very finely scabrate (Fig. 5E, F) and not laevigate as given in original diagnosis of *P. obesus* (Potonié and Kremp 1954).

*Stratigraphic and geographic range.*—Radnice Member, Kladno Formation, Lower Bolsovian, Radnice Basin, Czech Republic.

## Discussion of the spores

*Dispersed Punctatisporites.*—The dispersed spore genus *Punctatisporites* consists of several different spore types. Some species possess a relatively thin (e.g., *P. minutus*) or thicker exine (e.g., *P. breviornatus*). The exine of some spe-



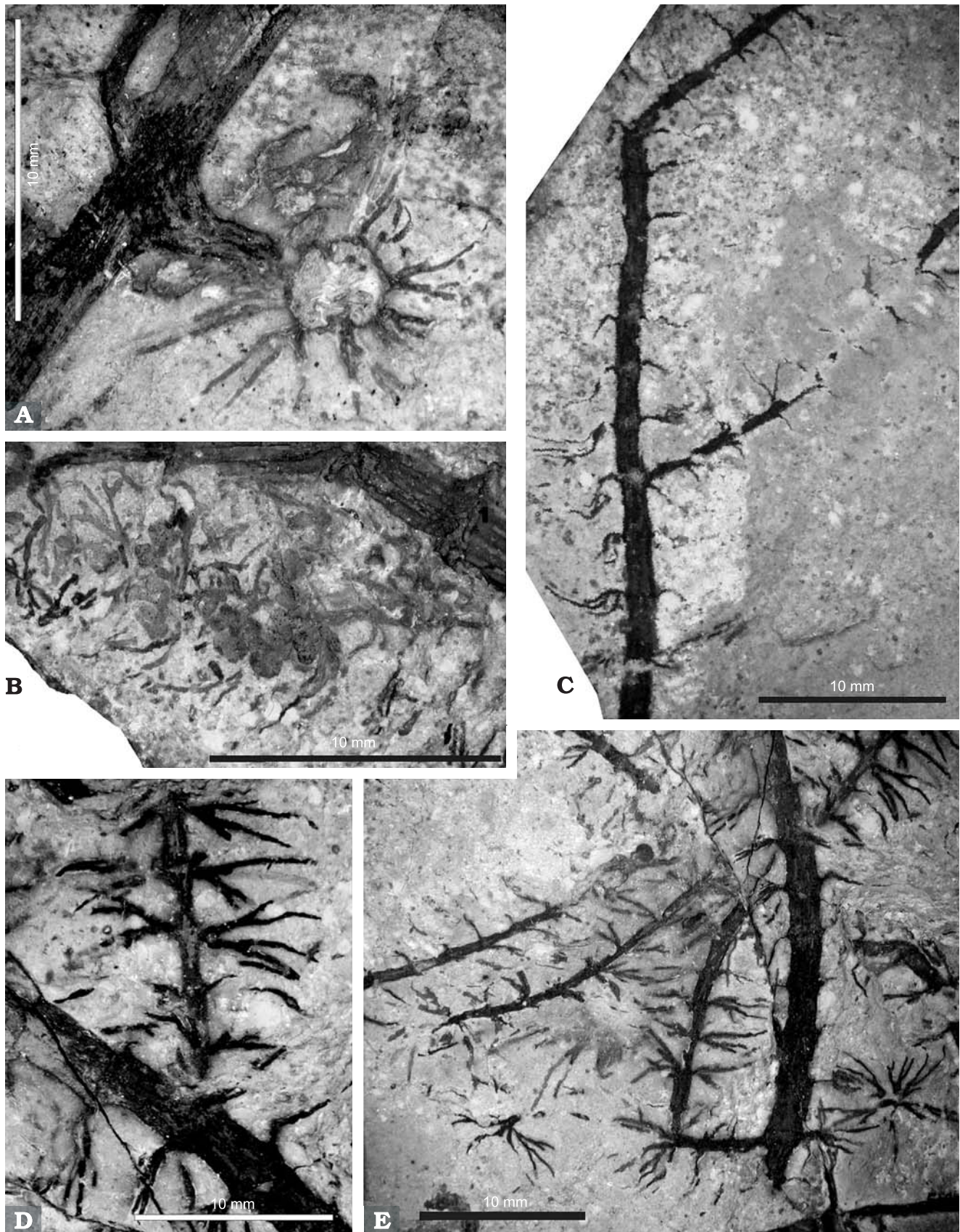


Fig. 2. Carboniferous (Bolsovian) fertile sphenophyll *Bowmanites brasensis* sp. nov., NMP-E 6352, Matylda Mine, Břasy, Radnice Basin, Kladno Formation, Radnice Member. A. Stem with leaves divided twice and three times. B. Cone and stem. C. Monopodially branched stem with leaves. D. Detail of twice divided leaves. E. Monopodially branched stem with leaves arranged in verticils.



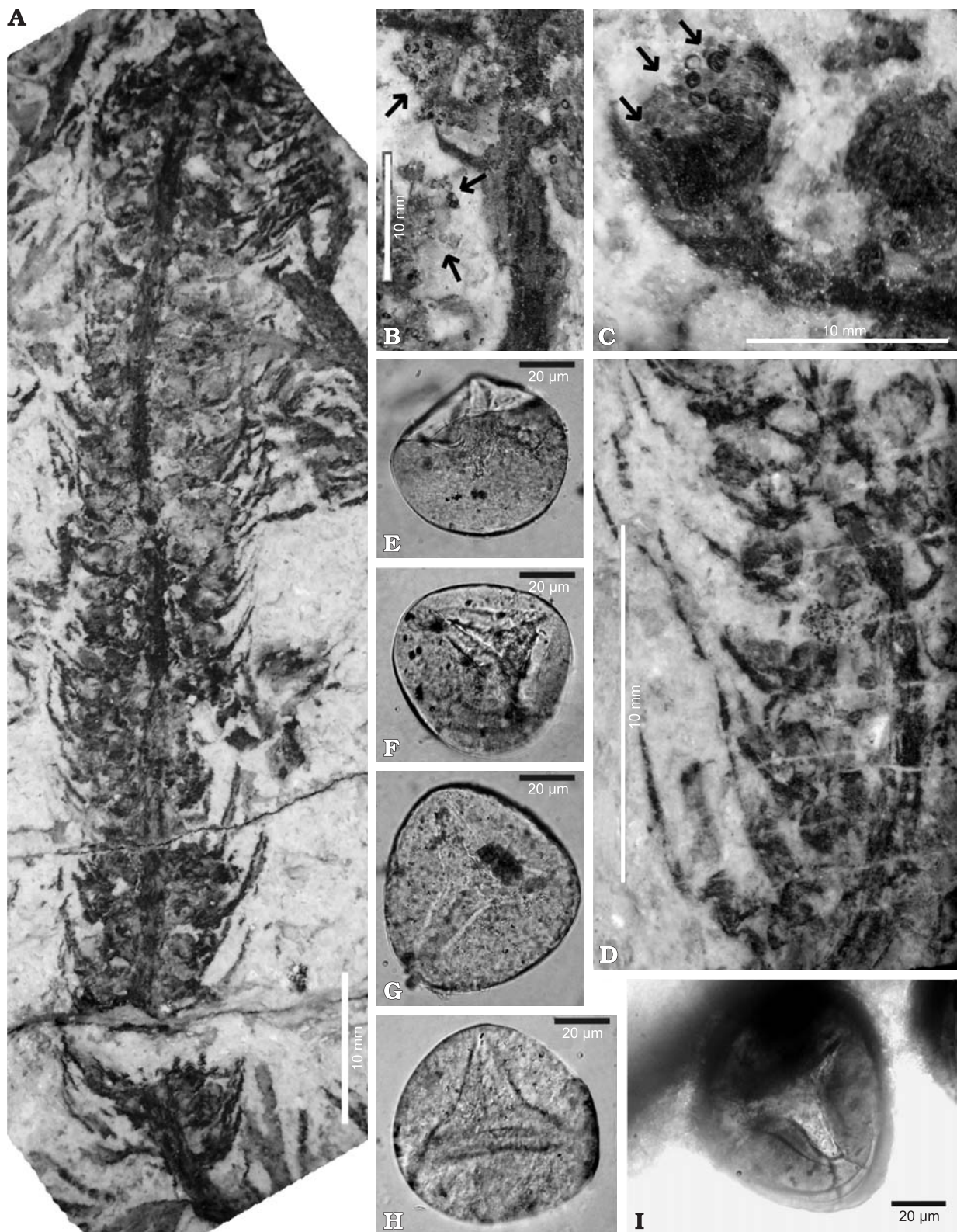


Fig. 3. Carboniferous (Bolsovian) fertile sphenophyll *Bowmanites brasensis* sp. nov., WBMP-F 03760 Matylda Mine, Břasy, Radnice Basin, Kladno Formation, Radnice Member. **A.** General view of the cone. **B.** Detail showing the position of sporangia with in situ spores (arrows) on the sporangiophore. **C.** Detail of in situ spores (arrows) in sporangia. Note the length of the sporangiophore. **D.** Position of sporangia between sterile bracts and the axis of a cone. **E.** Central body of a spore of *Punctatisporites obesus*-type; lateral view. **F, G.** Central bodies of spores of *Punctatisporites obesus*-type. Note the trilete mark and labrum. **H.** Central body of a spore of *Punctatisporites obesus*-type; distal view. **I.** Spore with exospore assigned to the dispersed species *Punctatisporites obesus* (Loose) Potonié and Kremp, 1954; proximal view.



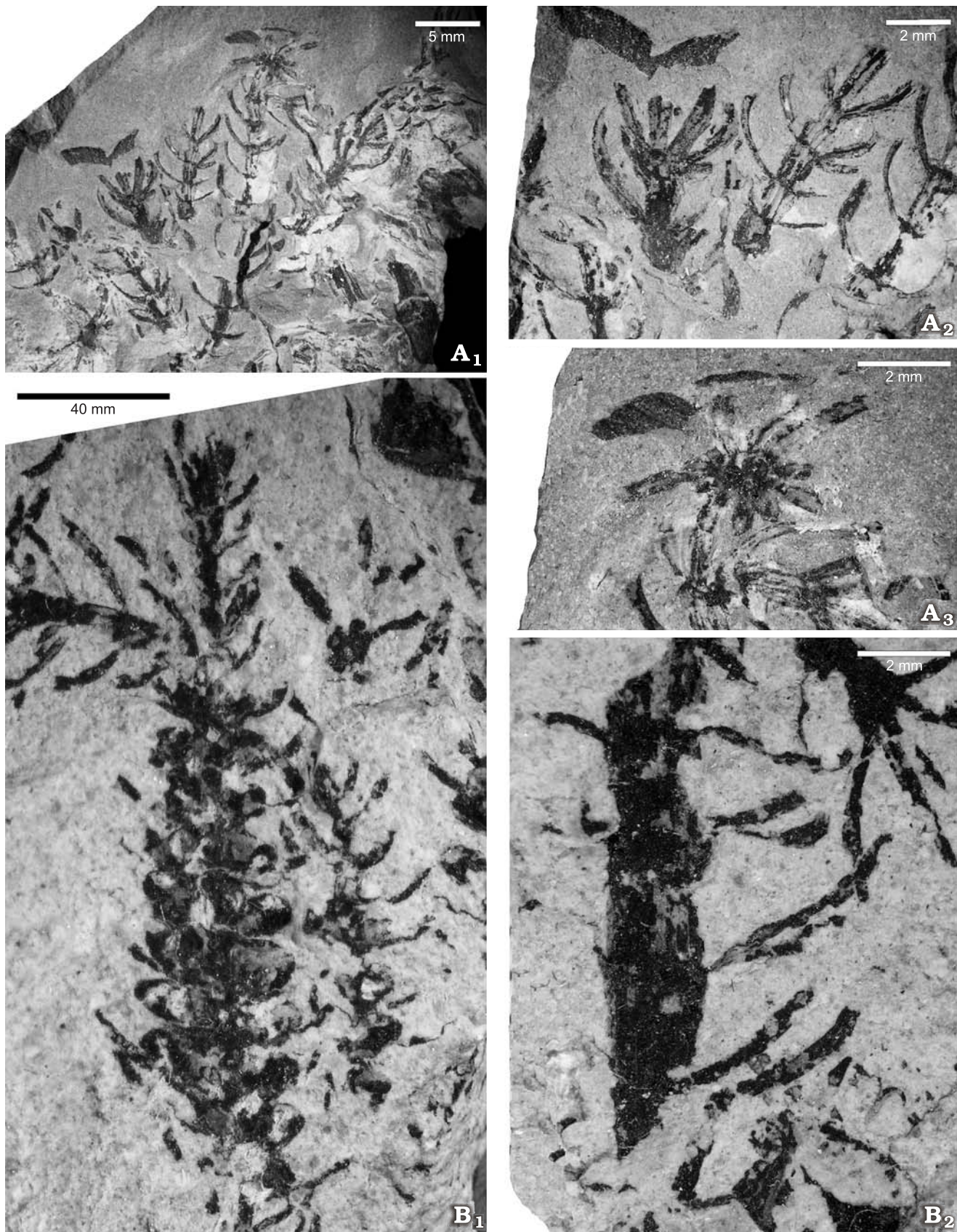


Fig. 4. Carboniferous (Bolsovian) fertile sphenophyll *Bowmanites pseudoaquensis* sp. nov., Ovčín opencast mine, Radnice Basin, Kladno Formation, Radnice Member. **A.** NMP-E 6123, general view of sterile stems with leaves arranged in verticils (A<sub>1</sub>); detail showing lanceolate leaves (A<sub>2</sub>); detail of nine lanceolate leaves arranged in verticils (A<sub>3</sub>). **B.** NMP-E 6124; cone with sterile apex (B<sub>1</sub>); detail of leafy stem (B<sub>2</sub>).



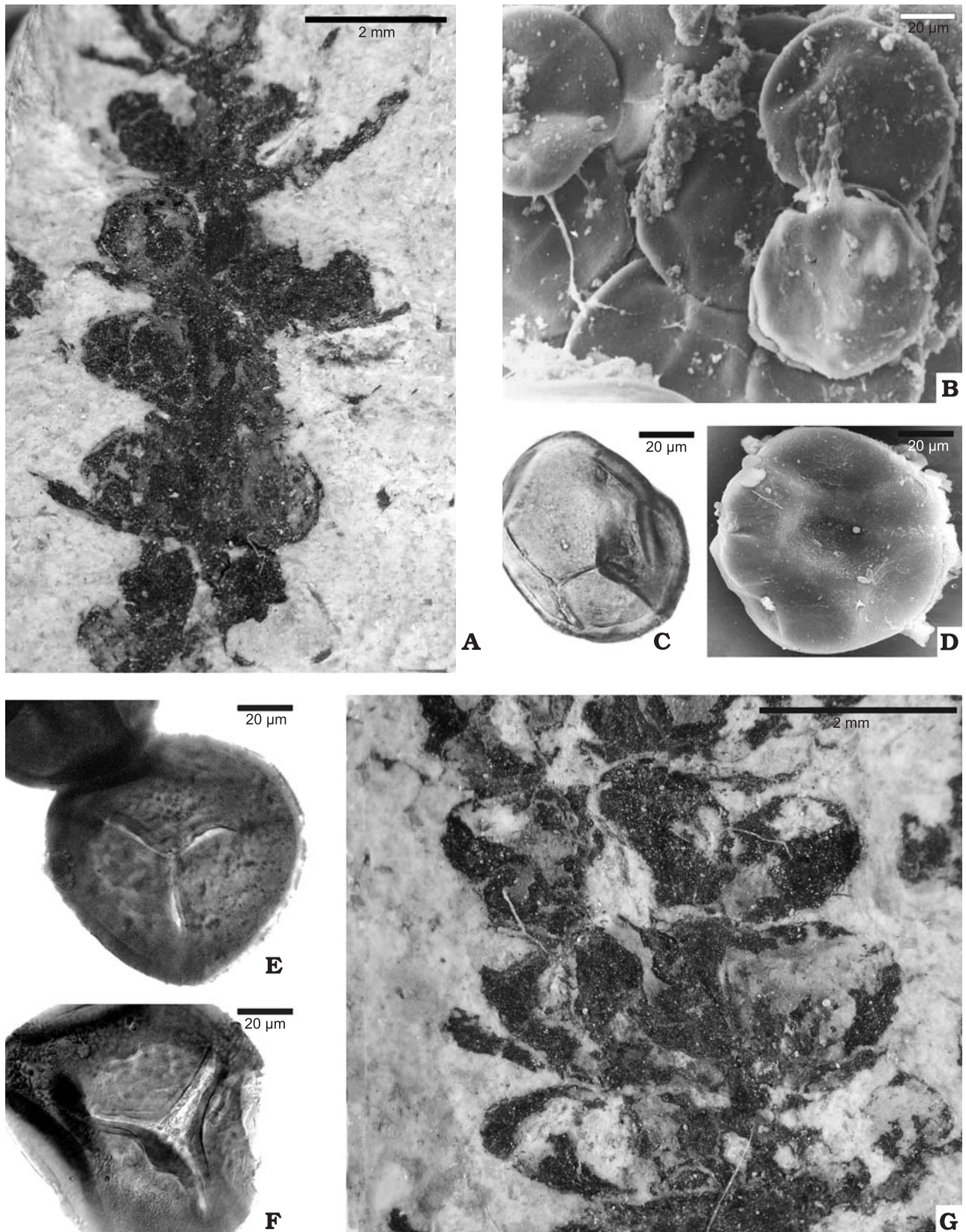


Fig. 5. Carboniferous (Bolsovian) fertile sphenophyll *Bowmanites pseudoaquensis* sp. nov., NMP-E 6124, Ovčín opencast mine, Radnice Basin, Kladno Formation, Radnice Member (A, G) and their spores of *Punctatisporites obesus*-type (B–F). A. Detail showing the position of sporangia. Note that one sporangium occurs per sporangiophore between the sterile bract and the axis of a cone. B, D. Spores of *Punctatisporites obesus*-type; distal surfaces, SEM micrographs. C, E, F. Spore of *Punctatisporites obesus*-type. Proximal views. Note finely scabrate sculpture on the proximal surface (E, F) and slightly developed labrum. G. Detail of sub-terminally located sporangium on shortened sporangiophore.



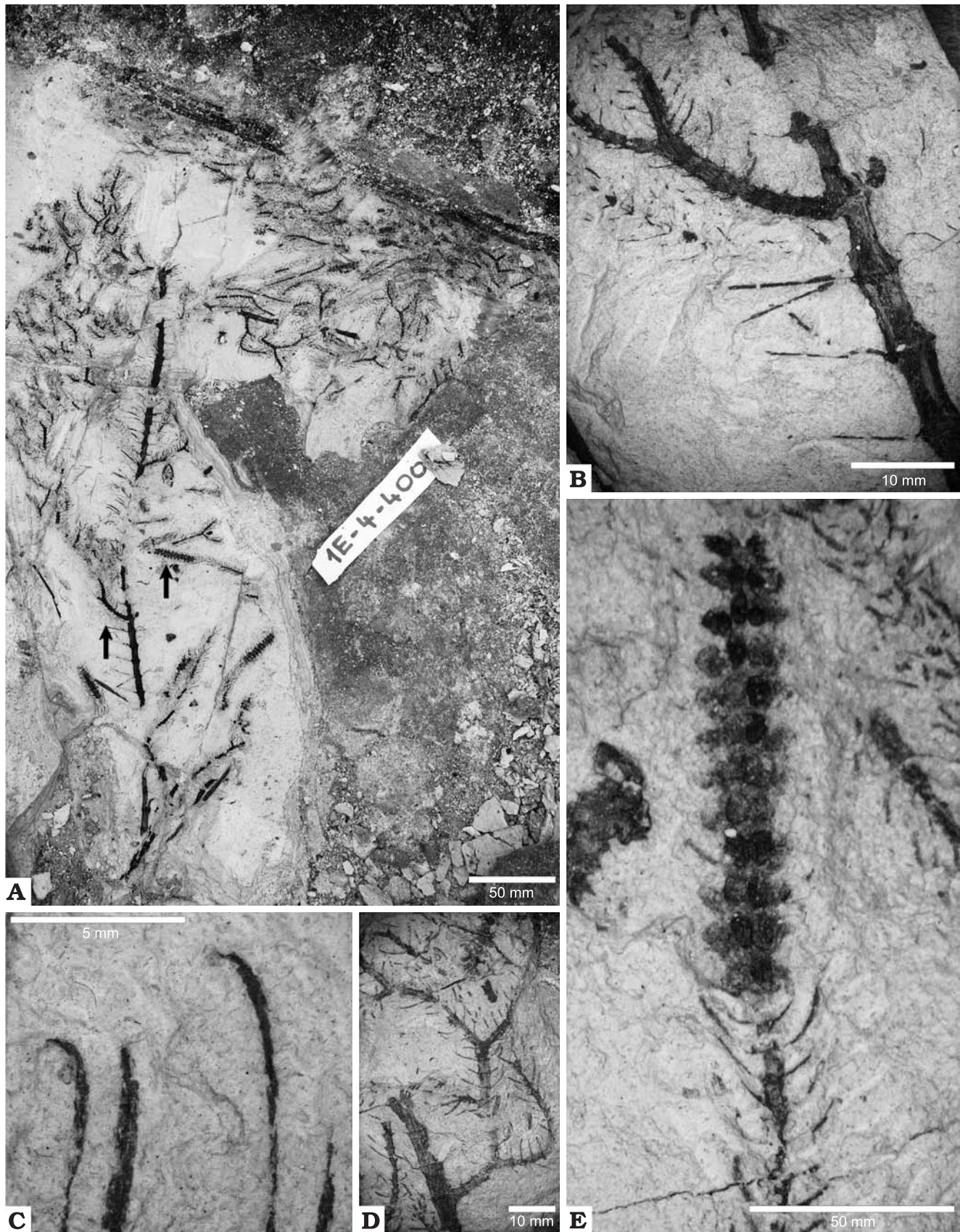


Fig. 6. Carboniferous (Bolsovian) fertile sphenophyll *Bowmanites pseudoaquensis* sp. nov., NMP-E 6358, holotype, Ovčín opencast mine, Radnice Basin, Kladno Formation, Radnice Member. **A.** General view of the holotype showing sterile axis, leaves and several cones. **B.** Leaves on the central axis. **C.** Detail of the leaf tips. **D.** Leaves on the central axis. **E.** Terminal position of the cone.



cies is laevigate (e.g., *P. calvus*), microgranulate (e.g., *P. irrasus*), vermiculate (e.g., *P. vermiculatus*), echinate-spinate (e.g., *P. decorus*), infrareticulate (*P. nervatus*), setate (*P. setulosus*) or possesses a ridge (*P. sinuatus*). The smallest spores of *Punctatisporites* are only about 14 µm in diameter, while the largest can reach 140 µm in diameter. *Punctatisporites* was proposed by Ibrahim (1933) and emended by Potonié and Kremp (1954) for spores with a variable exine sculpture (laevigate, punctate, microreticulate or microgranulate). For example, Guennel (1958) considered that all species with a sculptured exine (like *P. punctatus*, the type species of the genus) should be separated taxonomically. *Punctatisporites* today consists of several miospore morphotypes and it is evident that the genus is highly heterogenous and represents an artificial taxon. This presumption is supported by the extremely long stratigraphic ranges of the morphologically simplest spores. The first rare records of spores of this type are from the Silurian, more frequently occurring in the Devonian and becoming more abundant in the Carboniferous (Bek 1998).

Some dispersed *Punctatisporites* species are more or less similar to *P. obesus*, like *P. limbatus*, *P. labiatus*, *P. pseudobesus*, *P. edgarensis*, or *P. bifurcatus*. *Laevigatisporites laevigatus* and the Permian genus *Callumispora* may be also be similar.

**In situ *Punctatisporites*.**—In situ spores of the *Punctatisporites*-type have been described from fructifications of plant species of different stratigraphic ages and taxonomic positions. The oldest in situ record of similar simple spores was published by Hoeg (1967) from a Devonian member of the Trimerophytophytina. Boureau (1964) mentioned in situ spores of the *Calamospora*–*Punctatisporites*-type from a sphenopsid cone (*Cheirostrobos pettycurensis*). The most abundant *Punctatisporites*-producing plants were ferns and fern-like plants, mainly genera like *Corynepteris*, *Stauropteris*, *Pecopteris*, *Scolecopteris*, *Asterotheca*, and *Radstockia* (Balme 1995; Bek 1998). Similar in situ spores are reported also from parent plants of Triassic–Jurassic (Potonié 1962), Cretaceous (Krassilov 1982) and even Eocene (Balme 1995) age. Dispersed species of *Punctatisporites* are far more numerous than those reported in situ. Some spores of the *Punctatisporites*-type may even represent ontogenetic stages of marattialean microspores of the *Cyclogranisporites*–*Verrucosisporites*-type (Zodrow et al. 2006).

## Results

The strobili of *Bowmanites brasensis* and *B. pseudoaquensis* are morphologically similar to *Sphenophyllostachys aquensis* Remy, 1955 (see Table 1) but differ mainly in their spore contents. In situ spores isolated from the type specimen of *S. aquensis* by Remy (1955) are laevigate, thin-walled and correspond with the dispersed genus *Calamospora*, while in situ spores of *B. brasensis* and *B. pseudoaquensis* are thick-walled and are assigned to a different spore genus, *Punctatisporites*.

In situ spores of both of the new Bohemian species correspond to the dispersed species *Punctatisporites obesus*. In situ spores isolated from the specimen assigned to *B. pseudoaquensis* (former *S. aquensis*) by Bek and Opluštil (1998) differ slightly in total diameter (120 µm on average) compared with spores of *Bowmanites brasensis*. It is evident that the Bohemian specimens, early wrongly assigned to *S. aquensis* by Bek and Opluštil (1998), differ from the holotype of *S. aquensis* and represent a new species.

The cone morphologies of *Bowmanites pseudoaquensis*, *B. brasensis*, and *S. aquensis* are only roughly similar. Sterile bracts of *Bowmanites brasensis* are distinctly dichotomously divided, but bracts of *B. pseudoaquensis* and *S. aquensis* are simple and lanceolate. The angle between the axis of the cone and bracts of *S. aquensis* is larger than in *B. pseudoaquensis*. Bracts of *S. aquensis* possess a prominent S-like shape, while bracts of *B. pseudoaquensis* are straighter and those of *B. brasensis* curve apically two-thirds of their length from the point of attachment. Sporangioophores of *B. pseudoaquensis* and *S. aquensis* are relatively short, undivided and their sporangia are borne terminally. Sporangioophores of *B. brasensis* are relatively long (2 mm) and bear sub-terminal sporangia (Fig. 3C). *Sphenophyllostachys aquensis* is reported (Remy 1955) from the Duckmantian of Germany (Schacht Adolf locality) whereas Bohemian specimens are from the Bolsavian (Whetstone horizon) of the Radnice Basin.

There is no evidence of heterophylly comparable to that reported in *Sphenophyllum tenerrimum* and *S. myriophyllum*. The general habit is similar to *S. trichomatosum*, but *B. brasensis* does not possess trichome bases of the stem.

Similar laevigate, thick-walled spores have never been reported in situ from any Carboniferous fructifications.

Table 1. Comparison of measurements of *Bowmanites brasensis* sp. nov., *Bowmanites pseudoaquensis* sp. nov., and *Sphenophyllostachys aquensis* Remy, 1955.

Measurements of strobili	<i>Bowmanites brasensis</i> sp. nov.	<i>Bowmanites pseudoaquensis</i> sp. nov.	<i>Sphenophyllostachys aquensis</i> Remy, 1955
Length (mm)	40–60	25–30	30–35
Width (mm)	5–6	4–5	6
Axis diameter (mm)	0.7	0.5	?
Bracts per whorl	?	12	6
Length of bracts (mm)	4–5	3–3.3	3–4
Sporangium (mm)	1	1.5–2	?
Length of sporangiophore (mm)	0.2	?	?

Division of *Punctatisporites* spores into natural groups would be facilitated by a good knowledge of their parent plants and/or an accurate grouping of morphologically similar spore types into a few new independent spore groups/genera (according to their sculpture, diameter and exine thickness). This is needed because *Punctatisporites* is probably the most variable Carboniferous dispersed spore genus known.

It is possible to divide Carboniferous sphenophylls into seven groups based on their in situ spore types and different morphologies and anatomies of the cones (Libertín and Bek 2006). Spores isolated from *Bowmanites brasensis* and *B. pseudoaquensis* do not correspond with any members of these groups and represent a new group of Carboniferous sphenophyllalean plants. Their special position is based mainly on their in situ spores. This suggests that the previous classifications of sphenophyllalean cones given by Hoskins and Cross (1943) and Remy (1955) need basic revision because these classifications group together plants that produce different spores (e.g., monolete versus trilete) and overlook the significance of in situ spores. We are currently working on a new classification of Carboniferous fertile specimens of sphenophylls. This revision will be based not only on the morphology of the cones, but also on their in situ spores, underlining the necessity of collaboration between palaeobotanists and palynologists.

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## References

- Balme, B.A. 1995. Fossil *in situ* spores and pollen grains: An annotated catalogue. *Review of Palaeobotany and Palynology* 87: 81–323.
- Bek, J. 1998. *Spore Populations of Some Plants of Groups Lycophyta, Sphenophyta, Pteridophyta and Progymnospermophyta from Carboniferous Limnic Basins of the Czech Republic*. 505 pp. Unpublished Ph.D. thesis. Institute of Geology, Academy of Science, Prague.
- Bek, J. 2004. Carboniferous sphenophyllalean spores and their parent plants. *Abstracts of 2004 Central European Meeting IGCP 469*, 9. Freiberg.
- Bek, J., Libertin, M., Owens, B., McLean, D., and Oliwkiewicz-Mikłasińska, M. (in press). The first compression *Pteroretis*-producing cones, Pennsylvanian of the Czech Republic. *Review of Palaeobotany and Palynology*.
- Bek, J. and Opluštil, S. 1998. Some lycopsid, sphenopsid and pteropsid fructifications and their miospores from the Upper Carboniferous basins of the Bohemian Massif. *Palaeontographica B* 248: 127–161.
- Bek, J. and Opluštil, S. 2004. Palaeoecological constraints of some *Lepidostrobus* cones and their parent plants from the Late Palaeozoic continental basins of the Czech Republic. *Review of Palaeobotany and Palynology* 131: 49–89.
- Bek, J. and Opluštil, S. 2006. Six rare *Lepidostrobus* species from the Pennsylvanian of the Czech Republic and their bearing on the classification of lycosporites. *Review of Palaeobotany and Palynology* 139: 211–236.
- Binney, E.W. 1871. Observations on the structure of the fossil plant found in the Carboniferous strata, Part 2. *Lepidostrobus* and some allied cones. *Monograph of the Palaeontographical Society* 1871: 33–62.
- Boureau, E. 1964. *Traité de Paléobotanique, III, Sphenophyta, Noeggerathiphyta*. 544 pp. Masson et Cie, Paris.
- Brongniart, A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. *Mémoires du Muséum National d'Histoire Naturelle* 8: 203–348.
- Dettmann, M.E. 1963. Upper Mesozoic microfloras from south-eastern Australia. *Proceedings of Royal Society of Victoria* 77: 1–148.
- Guennel, G.K. 1958. Miospore analysis of the Pottsville coals of Indiana. *Bulletin of Indiana Department of Conservation, Geological Survey* 13: 1–101.
- Hoeg, O.A. 1967. Psilophyta, In: E. Boureau (ed.), *Traité de Paléobotanique, II, Bryophyta, Psilophyta, Lycophyta*, 362–399. Masson et Cie, Paris.
- Hoskins, J.H. and Cross, A.T. 1943. Monograph of the Paleozoic cone genus *Bowmanites* (*Sphenophyllales*). *American Midland Naturalist* 30: 47–148.
- Ibrahim, A.C. 1933. *Spore forms of the Ägir Horizon of the Ruhr Basin*. 46 pp. Triltsch. Würzburg.
- Krassilov, V.A. 1982. Early Cretaceous flora of Mongolia. *Palaeontographica B* 181: 1–43.
- Libertín, M. and Bek, J. 2003. The revision of sphenophyllalean cones and their spores from the Pennsylvanian continental basin of the Czech Republic. *Abstracts of the XVth International Congress on Carboniferous and Permian Stratigraphy*, 335. Leiden.
- Libertín, M. and Bek, J. 2006. Proposal of the new classification of Palaeozoic sphenophyllalean cones. *Abstracts of the XIIth European Palaeobotany Palynology Conference*, 82. Prague.
- Potonié, H. 1893. Über die Sphenophyllaceen. *Naturwissenschaften Wochenschriften* 8: 219–220.
- Potonié, R. 1962. Synopsis der Sporae in situ. *Beihafte der Geologische Jahrbuch* 52: 1–204.
- Potonié, R. and Kremp, G. 1954. Die Gattungen der Palaözoischen *Sporae dispersae* und ihre Stratigraphie. *Geologische Jahrbuch* 69: 111–193.
- Potonié, R. and Kremp, G. 1955. Die *Sporae dispersae* des Ruhrkarbons ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. Teil I. *Palaeontographica B* 98: 1–136.
- Presl, K. 1838. *Versuch einer geognostischen botanischen Darstellung der Flore der Vorwelt. Vol. 2, 7/8*. 39 pp. Tentamen, Leipzig.
- Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., and LeThomas, A. 2007. Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology* 143: 1–81.
- Remy, W. 1955. Untersuchungen von kohlig erhaltenen fertilen und strilen Sphenophyllen und Formen unsicherer systematischer Stellung. *Abhandlungen Deutschen Akademie Wissenschaften zu Berlin, Klasse für Chemie und Biologie* 1: 5–40.
- Seward, A.C. 1898. *Fossil Plants. Vol. 1*. 245 pp. Cambridge University Press, London.
- Smith, A.H.V. and Butterworth, M.A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology* 1: 1–324.
- Sternberg, K. 1823. *Versuch einer geognostischen botanischen Darstellung der Flore der Vorwelt*. 39 pp. Tentamen, Leipzig.
- Thomas, B.A. 1970. A new specimen of *Lepidostrobus binneyanus* from the Westphalian Bof Yorkshire. *Pollen et Spores* 12: 217–234.
- Zodrow, E.L., Šimůnek, Z., Cleal, Ch.J., Bek, J., and Pšenička, J. 2006. Taxonomic revision of the Palaeozoic marattialean fern *Acitheca* Schimper. *Review of Palaeobotany and Palynology* 138: 239–280.