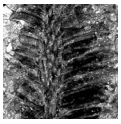
A new species of *Lepidostrobus* from the Early Westphalian of South Joggins, Nova Scotia, Canada

BARRY A. THOMAS, JIŘÍ BEK & STANISLAV OPLUŠTIL



A new species *Lepidostrobus dawsonii* sp. nov., from Langsettian-Duckmantian strata at Joggins section, Nova Scotia, Canada is proposed based on palaeobotanical and palynological study. The new species represents gently tapering, narrow and nearly cylindrical cone fragments the base and apical parts of which are missing. *In situ* spores are trilete, cingulizonate and of the *Lycospora uber*-type. This is the first description of a lycopsid fructifications and its *in situ* spores from the Canadian Carboniferous. Morphology of the cones and spores resembles those of the Czech species *Lepidostrobus thomasii* Bek & Opluštil from the Intra-Sudetic Basin, which is of the same age but represents a less robust and more cylindrical cone. • Key words: Lycopsids, *in situ* spores, *Lepidostrobus*, *Lycospora,* Pennsylvanian.

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Barry A. Thomas, Aberystwyth University, Aberystwyth, Ceredigion, SY23 3AL, UK; bat@aber.ac.uk • Jiří Bek, Institute of Geology v.v.i., Academy of Sciences, Rozvojová 269, 165 00 Prague 6, Czech Republic; mrbean@gli.cas.cz • Stanislav Opluštil, Faculty of Sciences, Charles University, Albertov 6, 128 43 Prague 1, Czech Republic; oplustil@natur.cuni.cz

Reproductive organs of arborescent lycopsids are usually found as fragments or rarely as the entire cone specimens. Scarce are those organically connected to branches of their parent plants. Some types of cones (*e.g.* sigillarian) have never been found attached to the parent plant; others (*e.g. Lepidocarpon*-type) are usually found disintegrated into very small fragments, such as sporophylls *etc*. Arborescent lycopsid cones of the *Lepidostrobus*-type are commonly found in Carboniferous plant assemblages and many have been studied (*e.g.* Brongniart 1828–1838; Binney 1870–1875; Crookall 1964, 1966; Němejc 1954; Chaloner *in* Boureau *et al*. 1967; Thomas 1965, 1978; Bek & Opluštil 2004, 2006). The generic and specific classification of cones of the *Lepidostrobus/Flemingites*-types sometimes can be difficult or even impossible especially if they are poorly preserved compression specimens. Therefore, a very important criterion is the study of *in situ* spores, *i.e*. spores isolated directly from reproductive organs of plants. The importance of combining macrofossils and palynological approaches to study of lycopsid cone holotype in order to determine affinity accurately was demonstrated by Brack-Hanes & Thomas (1983), who revised the genera *Lepidostrobus* (Brongniart) Brack-Hanes & Thomas and *Flemingites* (Binney) Brack-Hanes & Thomas. The records of *in situ* spores of arborescent lycopsid fructifications are not abundant (Felix 1954; Abbott 1963; Chaloner *in* Boureau *et al*. 1967; Balbach 1967; Brack 1970; Brack-Hanes & Thomas 1983; Thomas 1978, 1988; Willard 1989a, b) but today descriptions, classifications and illustrations of *in situ* spores are accepted as parts of diagnoses, and descriptions of fructifications or parent plants. Significant progress in the study of lycopsid fructifications and their *in situ* spores have been made recently by Czech palaeobotanists and palynologists (Bek *et al*. 2001, 2008, 2009a, b; Drábková *et al*. 2005; Libertín & Bek 2005), including study *Lepidostrobus strobili* (Bek & Opluštil 1998, 2004, 2006; Opluštil & Bek 2009).

North American specimens have been described from the USA but not, as yet, from Canada. There are records and descriptions of Canadian lycopsid cones by Bunbury (1847), Bell (*e.g.* 1938, 1940, 1962, 1966), Dawson (1866) and Zodrow & McCandlish (1980), but this is the first one to be described in detail with its *in situ* spores.

Materials and methods

The principal study specimen bears a label in J.W. Dawson's handwriting stating it was recorded from South Joggins, Nova Scotia, Canada and to have been collected in 1888 (Fig. 1). The age of the specimen is therefore most

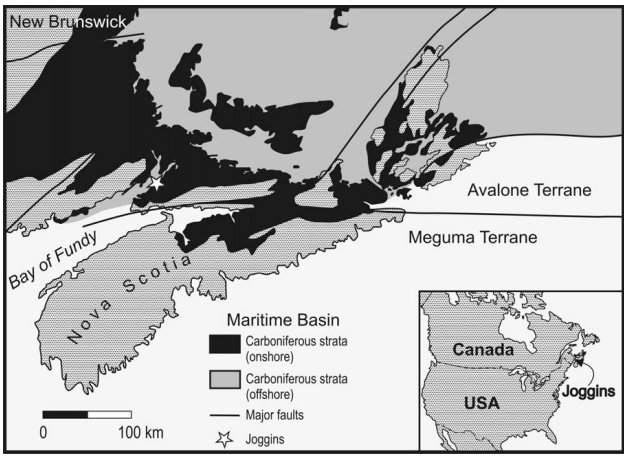

Figure 1. Distribution of Carboniferous strata of the Maritime Basin in eastern Canada and location of the Joggins section where the specimen of *L. dawsonii* sp. nov. was found. After Calder (1994).

likely to be Langsettian or Duckmantian. The holotype is deposited in the Kidston Collection of the British Geological Survey at Keyworth, England (No. 7318). This lycopsid cone is preserved as a longitudinally split compression on brown and grey fined grained sandstone. A second specimen, almost identical in appearance to the one in the British Geological Survey, was collected more recently by D. Reid and is now in the collections of the Joggins Fossil Centre, Joggins, Nova Scotia, Canada (No. NSM008 GF031.011). It is also a fragment of a cone approximately 55 mm long. Even though we have not prepared spores from this cone we believe it is sufficiently alike to be included the same species.

Portions of the cone were removed and macerated with concentrated nitric acid, followed by dilute ammonia solution. Some of the liberated microspores were mounted in glycerine jelly, while others were coated with gold for study with a CAMECA SX100 scanning electron microscope. Slides with *in situ* spores and digital photomicrographs are stored in the Geological Institute v.v.i., Academy of Sciences, Prague, Czech Republic. The terms used for the descriptions of spores are those of the 'Glossary of pollen and spore terminology' of Punt *et al*. (2007).

Systematic part

Class Lycopsida Scott, 1909
Order Lepidocarpales Thomas & Brack-Hanes, 1984

Genus *Lepidostrobus* (Brongniart) Brack-Hanes & Thomas, 1983

Type species. – *Lepidostrobus ornatus* Brongniart, 1828.

Lepidostrobus dawsonii sp. nov.

Figures 2, 3

Holotype. – Specimen No. 7318, Kidston's collection, British Geological Survey, UK.

Type locality. – South Joggins, Nova Scotia, Canada.

Type horizon. – Langsettian–Duckmantian.

Derivation of name. – In honour of J.W. Dawson, the noted palaeobotanist who found this specimen.

Material. – No. 7318, Kidston's collection, British Geological Survey, UK and No. NSM008 GF031.011, Joggins Fossil Centre, Joggins, Nova Scotia, Canada.

Diagnosis. – Cone at least 120 mm long, 24 mm wide basally but gradually tapering to 22 mm. Cone axis narrow, at least 3.6 mm wide. Sporophyll pedicels in vertices of *ca* 30°, basally *ca* 1.4 mm wide, orientated *ca* 5–15° up from the horizontal with an indistinct heel. Sporangia *ca* 2 mm high, attached along the pedicels. Trilete cingulizonate microspores, amb circular to subcircular. Proximal surface laevigate, distal sculpture finely scabrate, microgranulate to microverrucate.

Description. – Both cones are split longitudinally revealing the axis and the sporangia in lateral view. Unfortunately they appear to have been abraded prior to fossilisation, presumably during transport and subsequent deposition. As a result, the cones have neither apex nor base and the distal parts, the laminae, of the sporophylls are also mostly missing (Fig. 2A). The remaining of the larger cone is approximately 120 mm in length and 24 mm in width at its base but gradually tapers upwards to a width of 22 mm. The cone axis appears to be comparatively narrow, but fragments revealed through missing sporangia show that it was at least 3.6 mm wide (Fig. 2B). The sporophyll pedicels are angled upwards from the axis at about 80–85° and scars of their bases on the pedicel show them to depart in verticals of about 30° (Fig. 2B–E). The pedicels are about 1.4 mm wide at their base and about 12 mm long. The length of sporangia, however, slightly decreases to the upper part of the fragment where they are only 9–10 mm long. Few of them appear to end with an indistinct heel (Fig. 2C, E). The sporangia appear to be attached along the pedicels and about 2 mm high. A few sporophyll laminae can be seen at the apical part of the cone and attached to isolated sporangia near the apical part of the cone. These isolated sporangia probably separated from the cone as it was settling into the sediment, similar to those illustrated by Thomas (1981). The only other plant debris on the surface of the rock is a piece of stem that is also badly worn and it is impossible to identify.

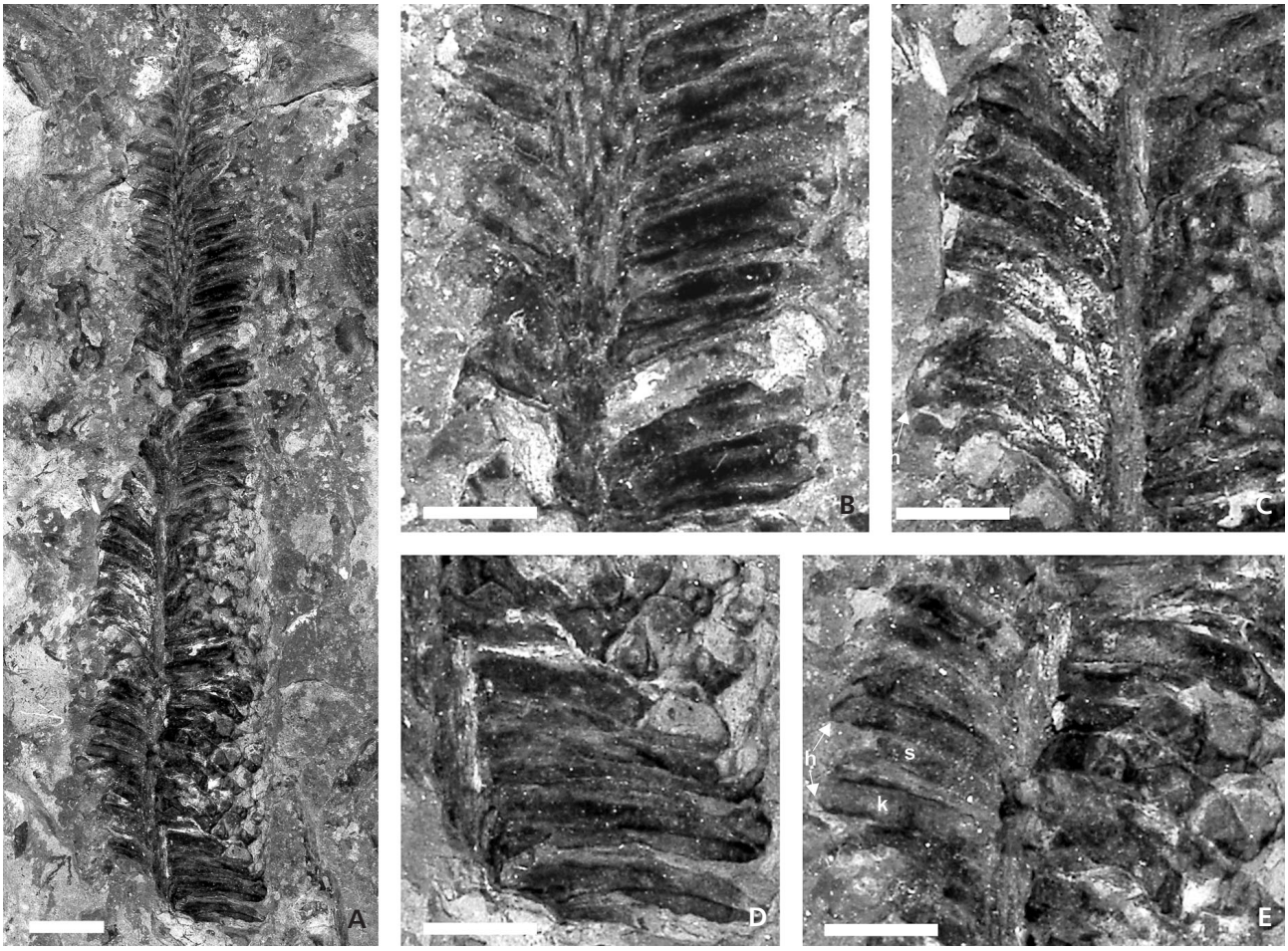

Figure 2. A – holotype of *Lepidostrobus dawsonii* sp. nov. preserved in very fine grained sandstone. Scale bar 10 mm. • B – detail of pedicels bearing sporangia and cone axis in upper part of the preserved cone fragment. Scale bar 5 mm. • C – detail of pedicels with sporangia from the middle part of cone. Scale bar 5 mm. • D, E – details of pedicels and cone axis in lower part of the cone fragment. k – keel, h – heel, s – sporangium. Scale bar 5 mm.

In situ microspores are all of the same type and differ only in diameter and width of cingulum and zona. The diameter is 31 (41.2) 46 μm. The laesurae is straight and simple, sometimes elevated (Fig. 3G). Microspores have an obvious cingulum 3–6 μm wide and a zona 2–6 μm wide (Fig. 3A–G). These spores are similar to the dispersed species *Lycospora uber* (Hoffmeister *et al*.) Staplin.

Comparison

Neither cone has any distinguishing feature that would permit us to refer them to a known species or to establish a new species. The *in situ* spores, however, are another matter, as their features are distinctive enough to characterise them and, therefore, the cone.

It is possible to divide *in situ* and dispersed lycospores into several morphological groups (Bek & Opluštil 2006). One cingulizonate with a relatively broad cingulum and zona, *i.e.* the same type as those from *L. dawsonii*, whereas others have a relatively narrow cingulum and zona, lack a zona, or possesses different sculpture. Thomas (1970), and Thomas & Dytko (1980) suggested that microsporangiate cones produced lycospores with a cingulum and zona, whereas bisporangiate cones contained lycospores with a narrow cingulum lacking a zona. The type of *Lepidostrobus*, *i.e*. *L. ornatus*, was later shown to contain microspores with a broad cingulum and zona so the genus was re-diagnosed to contain only microsporangiate cones with cingulizonate lycospores. Bisporangiate cones were assigned to the genus *Flemingites*. The Canadian cone, having cingulizonate lycospores of the microsporangiate type is therefore referred to *Lepidostrobus*.

Dispersed lycospores with a relatively broad cingulum and zona are included in *Lycospora noctuina* Butterworth & Williams, *L. nitida* Artüz, *L. paulula* Butterworth & Williams, *L. uzunmehmedii* Artüz, *L. tenuireticulatus* Artüz, *L. uber* and possibly *L. pellucida* (Wicher) Schopf *et al.* The spores of *L. dawsonii* fit roughly into the parameters of *Lycospora uber.* However, since they differ from the

Table 1. *Lepidostrobus* species that have yielded cingulizonate lycospores with a relatively broad cingulum and zona together with characteristics of their *in situ* spores.

Cone species	*In situ* spores						
	Lycospore species (as previously identified)	Diameter (μm)	Cingulum width (μm)	Zona width (μm)	Sculpture of proximal surface	Sculpture of distal surface	References
L. haslingdenensis	*L. noctuina*	24–44.5	0.6–4.8	1.8–4.2	Scabrate to finely granulate	Microspinate	Thomas & Dytko 1980
L. haslingdenensis	*L. noctuina*	30–39	4.5	5.8	Granulate	Verrucate to rugulate	Willard 1989b
L. cf. *haslingdenensis*	*L. uber*	30(39)45	2(2.57)3	2(4.39)6	Laevigate to finely scabrate	Microgranulate to microspinate	Bek & Opluštil 2006
L. kohoutii	*L. uzunmehmedii*	31(36.2)45	2(3.3)4	3(4.5)6	Laevigate to finely scabrate	Finely scabrate	Bek & Opluštil 2006
L. thomasii	*L.* cf. *uzunmehmedii*	27(35.4)45	1.5(2.86)4	1.5(3.88)5.4	Laevigate	Finely microgranulate	Bek & Opluštil 2004
L. dawsonii sp. nov.	*L.* cf. *uber*	31(41.2)46	3–6	2–6	Laevigate to scabrate	Microgranulate to microverrucate	Herein

original diagnosis given by Hoffmeister *et al*. (1955) in being slightly smaller in diameter and in having a slightly narrower cingulum and zona, they are best regarded as *Lycospora* cf. *L. uber*.

This type of *in situ* lycospore with relatively broad cingulum and zona has rarely been reported from *Lepidostrobus* cones. Thomas & Dytko (1980) isolated similar lycospores from compression specimens of *Lepidostrobus haslingdenensis* Thomas & Dytko from the uppermost Namurian of the Millstone Grit Series of Great Britain. These lycospores differ from those described here in having a differently sculptured distal surface and a narrower cingulum and zona. Thomas & Dytko (1980) compared them with the dispersed species *Lycospora noctuina.* Willard (1989b) described similar lycospores from compressed specimens that she also referred to as *Lepidostrobus haslingdenensis* from the Namurian B/C of Illinois, USA and compared them with the same dispersed species as Thomas & Dytko (1980), *i.e. Lycospora noctuina.* However, the British and American *in situ* lycospores differ from are another in the sculpture of both surfaces. The distal surfaces of the British spores are densely microspinate, while the American ones possess microverrucate to rugulate sculpture (Willard 1989b). The proximal surfaces of the British spores are scabrate while the American ones have microgranulate exines. Although both sets of *in situ* spores were closely compared with the same dispersed species, *Lycospora noctuina,* we now interpret as belonging to different natural species. The American spores recovered by Willard (1989b) correspond more closely with the original diagnosis of this species, as the densely microspinate distal surface of the British lycospores is not mentioned in original diagnosis of *L. noctuina* (Butterworth & Williams 1958, p. 376).

Three similar morphological types of *in situ* lycospores als have been described from three compressed species of *Lepidostrobus* cones from the Carboniferous of the Czech Republic. Lycospores isolated from a specimen of *Lepidostrobus* cf. *L. haslingdenensis* by Bek & Opluštil (2006) from the Bolsovian of the Kladno-Rakovník Basin are compared with the dispersed species *Lycospora uber*. These lycospores have more densely microgranulate sculpture on the distal surface than the *Lepidostrobus dawsonii* spores although both lycospores correspond well in all other characteristics. Also, *L.* cf. *haslingdenensis* is most probably a different and generally larger type of cone. Lycospores isolated from *Lepidostrobus kohoutii* Bek & Opluštil (Bek & Opluštil 2006) from the Bolsovian of the Kladno-Rakovník Basin were compared with the dispersed species *Lycospora uzunmehmedii* Artüz. They differ mainly in perforations of the zona and its width.

The greatest similarity is seen between *Lepidostrobus dawsonii* and *L. thomasii* Bek & Opluštil (Bek & Opluštil 2004) from the Langsettian/lower Duckmantian of the Intra-Sudetic Basin, Czech Republic. Cones of both species are relatively long and narrow, more (in case of *L. thomasii*) or less (*L. dawsonii*) cylindrical. Furthermore both species are found in strata of the same age. *In situ* spores of *L. thomasii,* named as *Lycospora* cf. *L. uzunmehmedii,* are similar in some respects to those of our Canadian cone. The main difference between the two species is in the slightly tapering character of the cone of *L. dawsonii*, whereas the largest known fragment of *L. thomasii,* about 300 mm long, is a cylindrical cone about 18–20 mm wide. Also, pedicels of *L. thomasii* are generally smaller, only 6–7 mm long compared to 10–12 mm in *L. dawsonii*. The axis of these cone species is of comparable width, varying between 3 and 4 mm. The length of

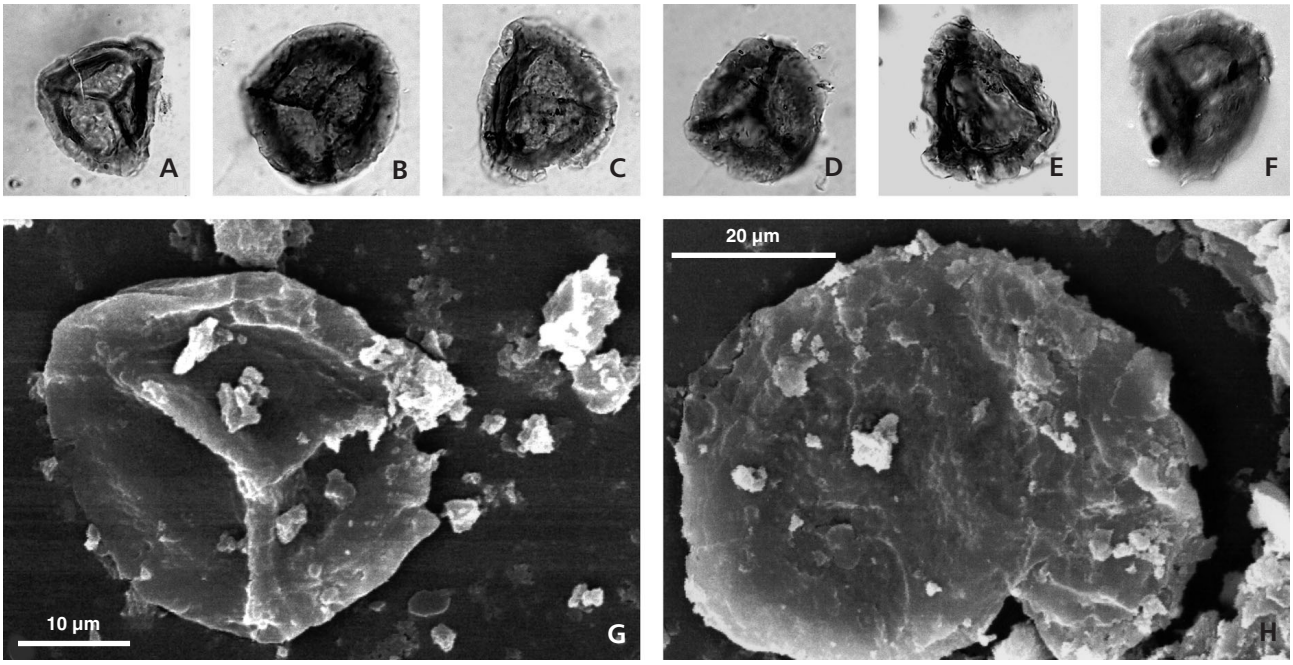

Figure 3. A, B, D, F –– *in situ* spores of the *Lycospora uber*-type. Proximal views. All × 500. • C, E – in situ spore of the *Lycospora uber*-type. Distal view. × 500. • G – *in situ* spore of the *Lycospora uber*-type. Proximal view. Notice laevigate sculpture of the proximal surface and elevated rays of the trilete mark. SEM. • H – *in situ* spores of the *Lycospora uber*-type. Distal view. Notice finely scabrate sculpture of the distal surface. SEM.

cones is not useful because only fragments of each species are preserved. Nevertheless, it seems that *L. dawsonii* represents a slightly more robust, less cylindrical cone than *L. thomasii*. However, both could be born on similar type of lepidodendrid lycopsid. The cones of *L. thomasii* are often associated with remains of *Lepidophloios* sp. (Bek & Opluštil 2004).

No similar lycospores have been reported from petrified, *i.e.* coal-ball specimens of *Lepidostrobus.*

Conclusion

Comparison of these lepidodendrid cone fragments from the Joggins section in eastern Maritime Canada indicates that they are similar to other *Lepidostrobus* species from Euramerican coalfields. In detail, however, there are differences either in morphology and/or type of *in situ* microspores, which warrants placing these specimens as a new *Lepidostrobus* species (*L. dawsonii*). This is the first *Lepidostrobus* cone species from the Canadian Carboniferous the diagnosis of which is based on cone morphology and *in situ* spores.

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References

ABBOTT, M.L. 1963. Lycopod fructifications from the Upper Freeport (No.7) coal in southeastern Ohio. *Palaeontographica, Abteilung B 112*, 93–118.

BALBACH, M.K. 1967. Paleozoic lycopsid fructifications. III Conspecificity of British and North American *Lepidostrobus* petrifactions. *American Journal of Botany 54*, 867–875. DOI 10.2307/2440908

BEK, J., OPLUŠTIL, S. & DRÁBKOVÁ, J. 2001. Two species of *Selaginella* cones and their spores from the Bohemian Carboniferous continental basins of the Czech Republic. *Review of Paleobotany and Palynology 114(1),* 57–81. DOI 10.1016/S0034-6667(00)00069-5

BEK, J., DRÁBKOVÁ, J., DAŠKOVÁ, J. & LIBERTÍN, M. 2008. 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 152*, 176–199. DOI 10.1016/j.revpalbo.2008.05.002

BEK, J., LIBERTÍN, M. & DRÁBKOVÁ, J. 2009a. *Selaginella labutae* sp. nov., a new compression herbaceous lycopsid and its spores from the Kladno-Rakovník Basin, Bolsovian of the Czech Republic. *Review of Palaeobotany and Palynology 155*, 101–115. DOI 10.1016/j.revpalbo.2007.12.010

BEK, J., LIBERTÍN, M. & DRÁBKOVÁ, J. 2009b. *Spencerites*

leismanii sp. nov., a new sub-arborescent compression lycopsid and its spores from the Pennsylvanian of the Czech Republic. *Review of Palaeobotany and Palynology 155*, 116–132. DOI 10.1016/j.revpalbo.2007.12.007

BEK, J. & OPLUŠTIL, S. 1998. Some lycopsid, sphenopsid and pteropsid fructifications and their miospores from the Upper Carboniferous of the Bohemian Massif. *Palaeontographica, Abteilung B 248*, 127–161.

BEK, J. & OPLUŠTIL, S. 2004. Six rare *Lepidostrobus* cones from the Pennsylvanian of the Czech Republic and their bearing on the classification of lycospores. *Review of Palaeobotany and Palynology 131*, 49–89. DOI 10.1016/j.revpalbo.2004.02.008

BEK, J. & OPLUŠTIL, S. 2006. 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 139*, 211–226. DOI 10.1016/j.revpalbo.2006.01.003

BELL, W.A. 1938. Fossil flora of Sydney Coalfield, Nova Scotia. *Geological Survey of Canada, Memoir 215*, 1–334.

BELL, W.A. 1940. The Pictou Coalfield, Nova Scotia. *Geological Survey of Canada, Memoir 225*, 1–161.

BELL, W.A. 1962. Flora of the Pennsylvanian Pictou Group of New Brunswick. *Geological Survey of Canada, Bulletin 87*, 1–71.

BELL, W.A. 1966. Illustrations of Canadian fossils: Carboniferous Plants of eastern Canada. *Geological Survey of Canada, Paper 66-11*, 1–76.

BINNEY, E.W. 1870–1875. *Observations on the structure of fossil plants found in the Carboniferous strata*. 147 pp. Palaeontological Society, London.

BRACK, S.D. 1970. On a new structurally preserved arborescent lycopsid fructification from the lower Pennsylvannian of North America. *American Journal of Botany 57*, 317–330. DOI 10.2307/2485310

BRACK-HANES, S.D. & THOMAS, B.A. 1983. A re-examination of *Lepidostrobus* Brongniart. *Botanical Journal of Linnaean Society 86*, 125–13. DOI 10.1111/j.1095-8339.1983.tb00720.x

BRONGNIART, A. 1828–1838. *Historie des végétaux fossiles, ou recherches botaniques et géologiques sur les Végétaux renfermés dans les diverses couches du globe*. 1 – 488 pp.; 2 – 72 pp. G. Dufour & Ed. d'Ocagne, Paris & Amsterdam.

BUNBURY, C.J.F. 1837. On fossil plants from the Coal Formations of Cape Breton. *Quartenary Journal of Geological Society London 3*, 423–437.

BUTTERWORTH, M.A. & WILLIAMS, R.W. 1958. Small spore floras of coals in the Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland. *Transactions of Royal Society of Edinburgh 63*, 353–392.

CALDER, J.H. 1994. The impact of climate change, tectonism and hydrology on the formation of Carboniferous tropical intramontane mires: the Springhill coalfield, Cumberland basin, Nova Scotia. *Palaeogeography, Palaeoclimatology, Palaeoecology 106*, 323–351. DOI 10.1016/0031-0182(94)90017-5

CHALONER, W.G. 1967. Lycophyta, 435–802. *In* BOUREAU, E. (ed.) *Traité de Paléobotanique, II, Bryophyta, Psilophyta, Lycophyta*. Masson, Paris.

CROOKALL, R. 1964. Fossil plants of the Carboniferous rocks of Great Britain. Memoirs of the Geological Survey of Great Britain. *Palaeontology IV(3),* 217–354.

CROOKALL, R. 1966. Fossil plants of the Carboniferous rocks of Great Britain. Memoirs of the Geological Survey of Great Britain. *Palaeontology IV(4),* 355–572.

DAWSON, J.W. 1866. On the conditions of the deposition of coal, more especially illustrated by the coal-formation of Nova Scotia and New Brunswick. *Quartenary Journal of Geological Society London 22*, 95–169.

DRÁBKOVÁ, J., BEK, J. & OPLUŠTIL, S. 2005. The first compression fossils of *Spencerites* (Scott) emend., and its isospores, from the Bolsovian (Pennsylvanian) of the Kladno-Rakovník and Radnice basins, Czech Republic. *Review of Palaeobotany and Palynology 130*, 59–88. DOI 10.1016/j.revpalbo.2004.01.004

FELIX, C.J. 1954. Some American arborescent lycopod fructifications. *Annals of Missouri Botanical Garden 41*, 351–394. DOI 10.2307/2394684

HOFFMEISTER, S.L., STAPLIN, F.L. & MALLOY, R.E. 1955. Mississippian plant spores arom ahe Hardinsburg Formation af Illinois and Ketucky. *Journal of Palentolology 29*, 372–399.

LIBERTÍN, M. & BEK, J. 2005. *Huttonia spicata* (Sternberg) emend. and its spores, the Radnice Basin (Bolsovian), Carboniferous continental basins of the Czech Republic. *Review of Palaeobotany and Palynology 128*, 247–261. DOI 10.1016/S0034-6667(03)00136-2

NĚMEJC, F. 1954. Taxonomical studies on the strobili of the *Lepidodendraceae* of the coal district of Central Bohemia. *Sborník Národního Musea 10 B*, 1–84.

OPLUŠTIL, S. & BEK, J. 2009. Some Pennsylvanian arborescent lycopsid cones and their microspores from the British coalfields. *Bulletin of Geosciences 84(2),* 203–226. DOI 10.3140/bull.geosci.1081

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

SCOTT, D.H. 1909. *Studies in Fossil Botany, 2nd edition*. 221 pp. Adam and Charles Black, London.

THOMAS, B.A. 1965. *Some studies on Carboniferous lycopods*. PhD thesis, Reading University.

THOMAS, B.A. 1970. A new specimen of *Lepidostrobus binneyanus* from the Westphalian B of Yorkshire. *Pollen et Spores 12*, 217–234.

THOMAS, B.A. 1978. New British records of Carboniferous lycopod cones. *Geological Journal 13*, 11–14.

THOMAS, B.A. 1981.Structural adaptations shown by the Lepidocarpaceae. *Review of Palaeobotany and Palynology 32*, 377–388. DOI 10.1016/0034-6667(81)90019-1

THOMAS, B.A. 1988. The fine structure of the Carboniferous lycophyte microspore *Lycospora perforata* Bharadwaj and Venkatachala. *Pollen et Spores 30*, 81–88.

THOMAS, B.A. & BRACK-HANES, S.D. 1984. A new approach to family groupings in the lycophytes. *Taxon 33*, 247–255. DOI 10.2307/1221165

THOMAS, B.A. & DYTKO, A. 1980. *Lepidostrobus haslingdenensis*: A new species from the Lancashire Millstone Grit. *Geological Journal 15*, 137–142.

WILLARD, D.A. 1989a. Source plants for Carboniferous microspores: *Lycospora* from permineralized *Lepidostrobus*. *American Journal of Botany 76*, 820–826. DOI 10.2307/2444538

WILLARD, D.A. 1989b. *Lycospora* from Carboniferous *Lepidostrobus* compressions. *American Journal of Botany 76*, 1429–1440. DOI 10.2307/2444429

ZODROW, E.K. & MCCANDLISH, K. 1980. *Upper Carboniferous fossil flora of Nova Scotia*. 275 pp. Nova Scotia Museum, Halifax.