Some Pennsylvanian arborescent lycopsid cones and their microspores from the British coalfields

Stanislav Opluštil & Jiří Bek

Six fructifications of arborescent lycopsids and their *in situ* spores from the Westphalian Coal Measures of the Pennine Basin and the Clackmannan Coalfield in Scotland, UK, were studied to improve our knowledge of their taxonomic characteristics and to provide a basis for the comparison of the floras of the British and Czech coalfields. The cones, which yielded *in situ* spores, were assigned to the genera *Lepidostrobus* (Brongniart) Brack-Hanes & Thomas, *Flemingites* (Carruthers) Brack-Hanes & Thomas and *Sigillariostrobus* Schimper. *Lepidostrobus* cones are represented by four species/specimens that can be subdivided into two groups based on their *in situ* spores. *L. boltonensis* n. sp., *L. huttonii* n. sp. and *L. spinosus* Kidston contain cingulizonate lycospores with relatively narrow cingulum and narrow zona which are comparable with the dispersed species *Lycospora subjuga* Bharadwaj, *L. brevijuga* Kosanke, *L. triangulata* Bharadwaj, *L. microgranulata* Bharadwaj or *L. contacta* Habib. The cone *L.* cf. *obovatus* yielded *in situ* lycospores with narrow cingulum and wide zona similar to those of the dispersed species *Lycospora loganii* (Wilson) Potonié & Kremp, *L. pellucida* (Wicher) Schopf, Wilson & Bentall, *L. micropapillata* (Wilson & Coe) Schopf, Wilson & Bentall, *L. micrograna* Hacquebard & Barss, *L. intermedia* (Wilson & Hoffmeister) Wilson & Hoffmeister, *L. pseudoannulata* Kosanke and *L. perforata* Bharadwaj & Venkatachala. The genus *Flemingites* is represented by *F.* cf. *russelianus* Binney. The *Flemingites* cone yields *in situ* microspores identified as the *Lycospora orbicula*-type. Sigillarian cones are rare and were represented by a single specimen of *Sigillariostrobus acicularis* n. sp. which contained *Crassispora kosankei*-type microspores. Only one of these British species (*Lepidodendron* cf. *obovatus*) is unequivocally present in the coalfields of central and western Bohemia. It is probable that *Flemingites* cf. *russelianus* also occurs in both areas. •
Key words: *Lepidostrobus*, *Flemingites*, *Sigillariostrobus*, *in situ* spores, *Lycospora*, *Crassispora.*

Opluštil, S. & Bek, J. 2009. Some Pennsylvanian arborescent lycopsid cones and their microspores from the British coalfields. *Bulletin of Geosciences 84(2)*, 203–226 (7 figures, 5 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 3, 2008; accepted in revised form January 26, 2009; published online March 27, 2009; issued June 30, 2009.

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Remains of arborescent lycopsids are among the most common fossils in the Late Palaeozoic coal deposits of the equatorial Amerosinian floral province (Opluštil & Cleal 2007; Thomas 1978, 2007). Because of their spectacular tree habit whole plants are rarely preserved. Typically, isolated organs or other fragments are found in the fossil record. Specimens showing the connection of particular organs and/or aspects of whole plant architecture are much less common. This is the main reason that our knowledge of the correlation of isolated organs to parent plants and the whole plant reconstruction of particular species remain quite incomplete, despite nearly two centuries of palaeobotanical research (Philips & DiMichele 1992, Bateman 1994). Individual organs found in isolation are given their own taxonomic names (Chaloner 1986, 1999; Meyen 1987; Forey *et al.* 2004; McNeill *et al.* 2006). Also, there is a range of morphological variablility among organ systems and preservation states that leads to further taxonomic complexity (Chaloner 1986). For example, several tens of species of the Pennsylvanian lycopsid genus *Sigillaria* Brongniart have been described based on bark impressions, but only a handful of cone species are known. Lepidodendrid cones illustrate an additional problem where the species often display gradations in their morphology and size. This variation results in very slight differences among species, frequent misinterpretations and a rich synonymy (Chaloner 1986). Progress in understanding the affinities of arborescent lycopsid fructifications requires careful examination of additional characteristics. The attachment of parts, such as the combination of the cone and the leafy stem on which it was borne, is especially important, but information of this sort

DOI 10.3140/bull.geosci.1081

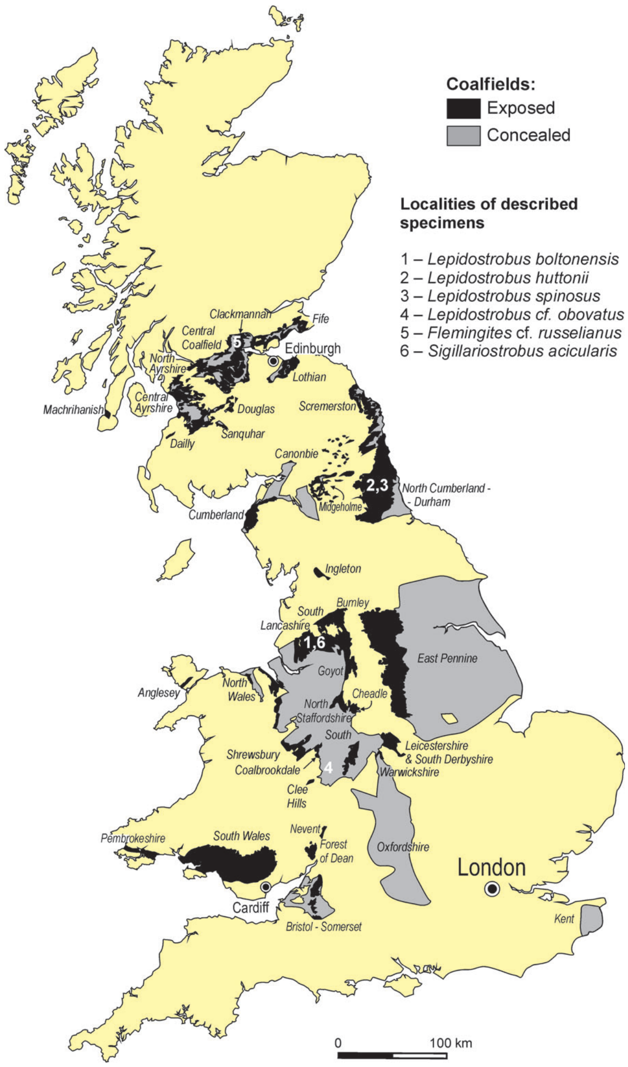

Figure 1. Carboniferous coalfields of Great Britain with location of specimens described herein. According to Chapman (1999).

is only rarely found. Another key source of additional information is the use of *in situ* spores released through the maceration of cones (Chaloner 1953a, 1953b, 1967; Thomas 1965, 1970, 1987; Thomas & Dytko 1980; Brack-Hanes & Thomas 1983; Thomas & Brack-Hanes 1991). This provides an important additional source of new taxonomic information from the cones themselves. Our primary aim here is to document the palynomorph content of selected well-preserved lycopsid cones from the British coalfields. We also review the evidence of cone morphology and, where known, the nature of the leafy foliage on which the cones were borne. This combination of morphological characteristics significantly improves our knowledge of particular species, facilitating comparisons with material elsewhere. We compare the British species with similar forms from the Czech coalfields to clarify their stratigraphic and geographic distribution. This study establishes the utility of this general approach. The large numbers of such cone specimens in museum collections around the world provides an invaluable source of materials for refining the taxonomic framework of tree lycopods and for developing a better understanding of their stratigraphic and geographic ranges.

Overview of the study of the Pennsylvanian arborescent lycopsids of Great Britain

Palaeobotanical research in the Late Carboniferous has a very long tradition in the British Isles that dates back to the beginning of the 19th century, when the mining of coal served as a base for rapid industrial development. The purpose of this overview is not to provide a complete list of all the researchers, but to point out those who significantly contributed to our present-day knowledge of the Carboniferous lycopsids of Britain. In 1804, Parkinson figured as a "strobilus" a lepidodendrid cone from the Middle Coal Measures strata (Duckmantian) of Derbyshire, East Pennines, UK. This specimen, which is now stored in the collection of the Natural History Museum in London (No. V 16440), was later assigned by Brongniart (1828) to his *Lepidostrobus ornatus* Brongniart, representing the first described taxonomic fructification of Carboniferous arborescent lycopsids. Later, Lindley & Hutton (1831–1837) described several other species which they included in the genus *Lepidostrobus* and isolated sporophylls in *Lepidophyllum* Brongniart (now *Lepidostrobophyllum* Hirmer). In the second half of the 19th century, Binney (1870–1875) published several species from the British Coal Measures. Around the turn of the19th and 20th centuries, Kidston (*e.g.*, 1889, 1891, 1893), one of the most famous British palaeobotanists, described several new species and revised some existing taxa. Just a few years later, Arber (1922–1924) revised British lepidostrobuses and distinguished fourteen species, which he further subdivided into three subgenera; *Eulepidostrobus* Arber, *Ortholepidostrobus* Arber and *Sublepidostrobus* Arber, based on the size of distal laminae compared to that of the pedicel. Arber (1922–1924) also took into account whether the cones were homosporous or heterosporous, however, he used this character only at the specific level. He also realised the importance of parent plants, but he correlated some cone species to more than one parent plant, thus clearly illustrating the artificial character of this cone classification. Strobili borne on several different parent plant species can be grouped as a single cone species because of their similar morphology (Němejc 1954). A new approach in the study of the Carboniferous lycopsid fructifications was introduced by Chaloner (*e.g.*, 1953a, 1953b, 1967), who combined cone morphology with *in situ* spores. At the same time, Crookall (1964, 1966), in

Table 1. The diameter (d), cingulum (c) and zona widths (z), sculptures of proximal and distal surfaces of British *in situ* lycospores and their parent cones

cones	*in situ* lycospores				
	d (μm)	c (μm)	z (μm)	sculpture of proximal surface	sculpture of distal surface
Lepidostrobus boltonensis	29 (31.5) 35	2.6 (3.3) 4.2	1.2 (2.2) 2.5	laevigate, finely scabrate	microgranulate
Lepidostrobus spinosus	29 (33.8) 35	2.0 (2.7) 3.9	1.3 (2.2) 3.3	laevigate, finely scabrate	densely microgranulate
Lepidostrobus huttonii	28 (32.3) 35	2.5 (3.1) 3.8	1.2 (1.5) 2.1	finely microgranulate	densely microgranulate, granulate
Lepidostrobus cf. *obovatus*	38 (41.2) 43	1.6 (1.8) 2.0	3.0 (4.2) 5.6	finely microgranulate	densely microgranulate, granulate
Flemingites cf. *russelianus*	26 (32.6) 37	0.8 (1.3) 2.0	–	laevigate, finely scabrate	densely microspinate

his monograph, provided a thorough revision of Carboniferous lycopsids of the British Coal Measures. In the Pennine Basin he distinguished seventeen species of lepidodendrid fructifications and the same number of parent plants. He did not, however, study their *in situ* spores, and the species described are distinguished mostly on the basis of cone morphology, with the exception of a few species previously described by Chaloner (1953a, 1953b, 1967). The importance of *in situ* spores as a part of lycopsid cone diagnoses was than stressed by Thomas (1965, 1970, 1987), Thomas & Dytko (1980), Brack-Hanes & Thomas (1983) and Thomas & Brack-Hanes (1991) who studied cones and their spores from the British coalfields. The works of these authors as well as those of Chaloner can be considered as the basis for modern study of this complex plant group.

Generic concepts of the Carboniferous arborescent lycopsid fructifications

Since Brongniart (1828) established *Lepidostrobus* as the first Carboniferous arborescent lycopsid cone genus, many other genera, as well as opinions on their concepts, have appeared in the literature. These are discussed in detail by Brack-Hanes & Thomas (1983), Thomas & Brack-Hanes (1991), and Bek & Opluštil (2004, 2006). Current concepts of lycopsid cone genera are based not only on cone morphology, but also on whether they are seed-like or free sporing, monosporangiate or bisporangiate, and the types of spores they produced. Another important feature is the mode of preservation (*i.e.* adpression, permineralization), as independent generic names are usually used for each type of preservation (McNeill *et al.* 2006). Thus, the genus *Lepidostrobus* was restricted by Brack-Hanes & Thomas (1983) exclusively to monosporangiate, *Lycospora*-producing cones (excluded *Lycospora orbicula*-type), whereas bisporangiate lepidodendrid cones belong to the genus *Flemingites*. Anatomically preserved permineralized seed-like fructifications containing one megaspore tetrad with three abortive and one functional megaspore are classified as *Lepidocarpon* Scott if the megaspores are integumented or *Achlamydocarpon* (Schumacker-Lambry, 1966) if they are non-integumented. Compressed specimens are typically assigned to *Lepidocarpon*, whereas *Lepidocarpopsis* Abbott, introduced by Abbott (1963), could possibly be an equivalent to the petrified genus *Achlamydocarpon*. The classification of sigillarian cones is relatively straightforward. It was believed that these plants bore only monosporangiate cones producing either *Crassispora* (Bharadwaj) Sullivan microspores or *Laevigatisporites* Ibrahim or *Tuberculatisporites* Ibrahim megaspores. Both are classified as *Sigillariostrobus* if preserved flattened or *Mazocarpon* Benson if petrified. However, the recent discovery of new sigillarian cone *Nudasporestrobus* Feng *et al.* (Feng *et al.* 2008) from the Chinese Late Carboniferous which bears *Sublagenicula*-type megaspores reveals that even *Sigillaria* is an artificial taxon rather than monophylletic genus. Cones documented here belong to the genera *Lepidostrobus*, *Flemingites* and *Sigillariostrobus*.

Material and methods

All of the specimens described in this study are housed in the collection of the Natural History Museum in London, UK. The materials were examined by the authors during a research visit funded by the SYNTHESYS Programme in 2006. From more than 200 cones stored in this collection, sampling for palynomorphs was allowed on only fifteen examples. A small amount of coaly matter, representing very small fragments of sporangia, was removed from 15 specimens. Of these, only six yielded *in situ* spores after maceration. These are specimen numbers BMNH V.5888, BMNH V.12045A, BMNH 36465, BMNH 40587, BMNH V.65201b and BMNH V.65200.

Spores were recovered by dissolving small portions of the cones (separated from the cone species with a mounted needle) in nitric acid for 24–48 hours and KOH for 1–2 hours. Most of the released spores were then mounted in glycerine jelly for direct microscopic examination.

Microspores obtained from the studied cones were classified according to the system of dispersed spores suggested by Potonié & Kremp (1954, 1955), Dettmann (1963) and Smith & Butterworth (1967). *In situ* spores

Table 2. The diameter (d), cingulum (c) and zona (z) widths and sculptures of proximal and distal surfaces of selected Carboniferous adpressed *in situ* lycospores and their parent cones. View of selected *Flemingites* cones and their *in situ* micro- and megaspores

lycospore /parent cone	d (μm)	c (μm)	z (μm)	sculpture of proximal surface	sculpture of distal surface	reference
Lycospora perforata /*Lepidostrobus barnsleyensis*	14	2.5	3	microgranulate	laevigate	Thomas 1965
Lycospora sp./ *Lepidostrobus comosus*	17	5	2	microgranulate	microgranulate	Thomas 1965
Lycospora sp./ *Lepidostrobus* sp. C	16	2	2	microgranulate	microgranulate	Hagemann 1966
Lycospora sp./ *Lepidostrobus jacksonii*	18	2.5	2.5	microganulate	microgranulate, granulate	Thomas 1965
Lycospora/ *Lepidostrobus* sp. D	17	2	1.5	microgranulate	densely microgranulate	Hagemann 1966
Lycospora cf. *uber*/ *Lepidostrobus dawsonii*	20.5	4.5	4	laevigate	microgranulate, microverrucate	Thomas *et al.* unpublished
Lycospora noctuina/ *Lepidostrobus haslingdenensis*	16.45	2.25	2.9	granulate, microgranulate	verrucate, rugulate	Willard 1989b
Lycospora punctata/ *Lepidostrobus* cf. *squarrosus*	15·45	3.4	3.4	microgranulate	densely microgranulate	Willard 1989b
Lycospora rotunda/ *Lepidostrobus* sp. A	15.15	5.6	2.4	finely granulate	granulate, rugulate	Willard 1989b
Lycospora torquifer/ *Lepidostrobus praelongus*, *L. variabilis*	15.7	3.8	3.7	verrucate, rugulate, baculate	densely rugulate, baculate, verrucate	Willard 1989b
Lycospora noctuina/ *Lepidostrobus haslingdenensis*	17.13	2.7	3	scabrate, laevigate	microspinate	Thomas & Dytko 1980
Lycospora perforata/ *Lepidostrobus binneyanus*	13.5	2	4	microgranulate	laevigate	Thomas 1988
Lycospora granulata/ *Lepidostrobus ornatus*	14	2.5	3	granulate, microgranulate	densely granulate, microgranulate	Brack-Hanes & Thomas 1983
Lycospora punctata/ *Lepidostrobus stephanicus*	18	2.6	2.1	microspinate, microgranulate	densely microspinate, microgranulate	Bek & Opluštil 2004
Lycospora triangulata/ *Lepidostrobus nemejcii*	18	2.5	1.9	microverrucate, microgranulate	densely microverrucate, microgranulate	Bek & Opluštil 2004
Lycospora cf. *uzunmehmedii*/ *Lepidostrobus thomasii*	18	2.9	3.9	laevigate, finely scabrate	microgranulate	Bek & Opluštil 2004
Lycospora rotunda/ *Lepidostrobus ronnaensis*	19	3.9	3.8	laevigate, finely scabrate	Microverrucate, verrucate	Bek & Opluštil 2004
Lycospora loganii/ *Lepidostrobus obovatus*	18	2.7	2	microverrucate, verrucate	microverrucate	Bek & Opluštil 2004
Lepidostrobus kohoutii	18.1	3.3	4.5	laevigate, finely scabrate	microspinate, microgranulate	Bek & Opluštil 2006
Lepidostrobus cf. *haslingdenensis*	19.6	2.6	4.4	laevigate, finely scabrate	densely microspinate	Bek & Opluštil 2006
Lepidostrobus sp.A	22·3	2.2	2.6	microgranulate, granulate	densely microgranulate, granulate	Bek & Opluštil 2006
Lepidostrobus sp. B	22.5	2.6	2.7	microgranulate, granulate	densely microgranulate, granulate	Bek & Opluštil 2006
Lepidostrobus sp. C	16.3	2.7	2	microgranulate, granulate	microgranulate, granulate	Bek & Opluštil 2006
Lepidostrobus sp. D	18.5	2.6	2	microgranulate	densely microgranulate	Bek & Opluštil 2006

were compared directly with the original diagnoses (holotypes), descriptions and illustrations of dispersed species. Species determinations were based only on these original diagnoses, and not on the interpretations of subsequent authors. Comparisons were made with other lycospores isolated from various *Lepidostrobus* cones preserved as adpressions and petrifactions, whereas cones were compared only with adpression species.

Described cone specimens and palynological slides are housed in the Natural History Museum, London, UK. Digital photomicrographs of *in situ* spores are stored in the Institute of Geology v.v.i., Academy of Sciences of the Czech Republic, Prague and the Natural History Museum, London, UK. Digital photographs of cones are in the Faculty of Sciences, Charles University, Prague and Natural History Museum, London, UK.

Table 3. The diameter (d), cingulum (c) and zona (z) widths and sculptures of proximal and distal surfaces of selected permineralized (coal-balls) *in situ* lycospores and their parent cones

lycospore /parent cone	d (μm)	c (μm)	z (μm)	sculpture of proximal surface	sculpture of distal surface	reference
Lycospora sp./*Lepidostrobus oldhamius* (associated with *Lepidophloios harcourtii*)	17	4	6	laevigate	microspinate, microgranulate	Willard 1989a
Lycospora cf. *perforata/ Lepidostrobus fayettevillense*	23	3	4	laevigate, finely microgranulate	densely microgranulate	Taylor & Eggert 1968
Lycospora sp./ *Lepidostrobus coulterii*	13	1.5	2.5	microgranulate	densely microgranulate	Balbach 1966
Lycospora sp./ *Lepidostrobus minor*	13	2	3	microgranulate	microgranulate	Leisman & Rivers 1974

Measurements and the type of sculptures of proximal and distal surfaces of Bohemian *in situ* lycospores are given in Table 1. It was possible to compare our results only with papers where a good description or precise measurements of *in situ* spores have been made. Therefore, we used only data reported by the following authors for comparisons: Thomas (1965, 1970, 1987, 1988), Willard (1989b), Thomas & Dytko (1980), Brack-Hanes & Thomas (1983), Hagemann (1966) and Bek & Opluštil (1998, 2004, 2006) from adpressed specimens and from permineralized specimens (coal-balls) published by Felix (1954), Balbach (1966), Taylor & Eggert (1968), Leisman & Rivers (1974) and Willard (1989a). Data from these *in situ* lycospores are given in Table 2 (adpressed specimens) and Table 3 (permineralized specimens). A review of sigillarian *in situ* micro- and megaspores is on Table 4.

Systematic palaeontology

The cones that provided spores can be subdivided into genera *Lepidostrobus*, *Flemingites* and *Sigillariostrobus*. The genus *Lepidostrobus* is represented by specimens Nos BMNH V.12045A, BMNH 36465, BMNH 40587 and BMNH V.65201b. Specimen BMNH V.5888 belongs to the genus *Flemingites,* and specimen No. BMNH V.65200 is a representative of the genus *Sigillariostrobus*. Specimens classified as *Lepidostrobus* can be subdivided into two groups based on their *in situ* spores and their cone morphology. The first group represents rather small cylindrical to oval cones (Nos BMNH V.12045A, BMNH 36465 and BMNH 40587), the *in situ* spores of which can be compared with dispersed species *Lycospora subjuga*, *L. brevijuga*, *L. triangulata*, *L. microgranulata* and *L. contacta*. These spores are characterised by relatively narrow cingulum and narrow zona. The second group is represented only by specimen No. BMNH V.65201b which provided lycospores with narrow cingulum and wide zona compared with the dispersed species *Lycospora loganii*, *L. pellucida*, *L. micropapillata*, *L. microgranna*, *L. intermedia*, *L. pseudoanullata* and *L. perforata*. Morphology of this cone differs from those of the first group.

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

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

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

***Lepidostrobus boltonensis* sp. nov.**
Figure 2

Material. – Specimen BMNH V.12045A.

Locality. – Chequerbent Pit, Bolton, South Lancashire Coalfield.

Stratigraphy. – Lower Coal Measures (Langsettian), Roof of the Royal Arley Coal.

Etymology. – According to Bolton, the type locality in South Lancashire.

Diagnosis. – Cone cylindrical or only very slightly tapering with blunt apex and base, more than 72 mm long and 21–22 mm wide including distal laminae. Cone axis 2 to 2.2 mm in diameter, with sporophylls attached in helix of about 30° and at an angle between 70° near the apex and 90° at and near the base. Pedicels between 4 and 9 mm long, laminae triangular, with entire margins slightly concave, about 5 to 6 mm long and slightly bent to the cone apex, adpressed to the cone. Sporangia oval, 4–9 mm long and about 1.5 to 2 mm high, microsporangiate. Microspores subtriangular to subcircular trilete with narrow cingulum and zona. Proximal and distal surfaces irregularly scabrate, finely or densely microgranulate, microverrucate or microspinate.

Description. – Cone: This specimen consists of a mudstone slab containing remains of three isolated cones, which are all of the same size and morphology and apparently belong to the same species (Fig. 2A). They are preserved as adpressions split mostly along the cone surface but locally also along the cone axis. Arrangement of pedicels and axis width are overprinted and can be partly observed.

The most complete specimen is a 72 mm long cone that lacks a base (Fig. 2A, D). The other specimens comprise a 66 mm long cone fragment with detached apex and a 40 mm long fragment of the middle part of a cone without apex and base. All of the specimens represent cylindrical cones of the same width, which vary only a little between 21 and 22 mm due to distal laminae spreading. Cones start to taper about 12 mm in front of the apiculate apex (Fig. 2D). Similarly, the cones taper to a truncate or slightly cordate base. The length of the complete cone is estimated to be about 90 mm, with an estimated length/width ratio of 4.5. The axis is 2 to 2.2 mm wide throughout its whole length (Fig. 2A–D). The pedicels are attached to the cone axes at an angle that varies from perpendicular insertion at and near the base to 70°–80° near the middle part of the cone length. This angle further decreases to about 65° near the apex where the cone starts to taper. Pedicels are 8–9 mm long, but in the apical and basal parts decrease to as little as 4–5 mm. Their morphology is not clearly seen because they are covered by imbricated laminae and only the outline is overprinted on the cone surface. The outline indicates that they are slightly triangular in lateral view (Fig. 2E). The pedicels appear to be densely spaced; however, it is not possible to directly measure the distance due to preservation. Sporangia are oval and have the same length as pedicels, between 1.5 and 2 mm high. The laminae are short, triangular, 5–6 mm long, gently bent upward and adpressed to the cone body.

Spores: Subtriangular to subcircular trilete microspores 29 (31.5) 35 µm in diameter. The laesurae is simple, extending to the outer margin of the central body. Cingulum 2.6 (3.3) 4.2 µm wide developed as a dark thickened ring on the outer margin of the central body. Zona may be sometimes perforated and usually is laevigate to finely scabrate, 1.2 (2.2) 2.5 µm wide. Proximal and distal surfaces are irregularly scabrate, finely or densely microgranulate, microverrucate or microspinate (Fig. 2F, G). The number of sculpture elements is higher on the distal than on the proximal surface.

Parent plant: The specimen described here contains only isolated cones that do not provide any information about the parent plant. There is no other similar cone in the collection of the Natural History Museum in London that could be assigned to this species or could have provided any information on the parent plant.

Comparisons and discussion. – *In situ* spores isolated from the largest cone fragment belong to the subgroup of cinguli-zonate lycospores with relatively narrow cingulum and narrow zona (Bek & Opluštil 2006) and can be correlated to the dispersed miospore species *Lycospora subjuga*, *L. brevijuga*, *L. triangulata*, *L. microgranulata* or *L. contacta*.

Similar spores were isolated by Bek & Opluštil (2004, 2006) also from *Lepidostrobus nemejcii* Bek & Opluštil, *L.* sp. C and *L.* sp. D from the Late Palaeozoic continental basins of the Czech Republic. However, all of these species differ in cone morphology and cone size. *L. nemejcii* is a large cylindrical cone, several tens of centimetres long and 90 mm wide. Remaining species are rather poorly known, and would not be reliable for comparison with *L. boltonensis*. However, some morphological features (cone axis, cone width or laminae shape, *etc*.) indicate that they are rather different species. A similar type of *in situ* lycospore was described by Hagemann (1966) from the cone adpression of *L.* sp. D from the Westphalian of the Campine Basin, Belgium. This specimen is an 84 mm long fragment of the middle part of a cylindrical cone that is 20 to 25 mm wide, depending on whether the laminae are included or not. Laminae are relatively short, lanceolate, and with apparently concave margins on their upper triangular part, and are different from those of *L. boltonensis* described here. Another difference seems to be the much thicker axis of the Belgian specimen. The ratio between pedicel length and axis width is 3.4 for *L. boltonensis* but only 0.95 for the Belgian cone, which, again, indicates that these cones belong to different species. *In situ* lycospores isolated from permineralized (coal-balls) specimens of *L. coulterii* Felix by Balbach (1966) and *L. minor* Leisman & Rivers by Leisman & Rivers (1974) are also of similar morphology, however, the cones themselves are difficult to compare because of different modes of preservation.

Based on cone morphology, the specimens described here have the greatest similarity to *Lepidostrobus spinosus* Kidston, *L. jacksoni* Arber, *L. obovatus* (Rénier) Bek & Opluštil, *L. haslingdenensis* Thomas & Dytko and *L.* sp. D Bek & Opluštil. Kidston's specimens of *Lepidostrobus spinosus* comprise small, nearly cylindrical cones from the Somerset (Asturian) and Ayrshire (Duckmantian) coalfields. The morphology of Kidston's syntypes (Kidston's collection Nos 712, 1548) is very similar to that of the specimens described here, with the exception that the axis is about twice as wide in the Kidston specimens. *In situ* microspores of the Kidston syntypes are known only from specimen No. 1548, which provided a morphologically similar type of *in situ* lycospore (*i.e.* with relatively narrow cingulum and narrow zona (Fig. 2F, G). Nevertheless, differences in axis width point to the conclusion that the specimen described here and *Lepidostrobus spinosus* are different species.

Another morphologically similar form is *L. jacksonii,* which has a closer resemblance to *L. boltonensis* than the previous species. It is a small cylindrical cone of the same size as *L. boltonensis*. It can be clearly distinguished by its 6–7 mm thick wide stalk, which is a common feature of all known specimens. Spores of permineralized specimen interpreted as *L. jacksonii* were macerated by Felix (1954)

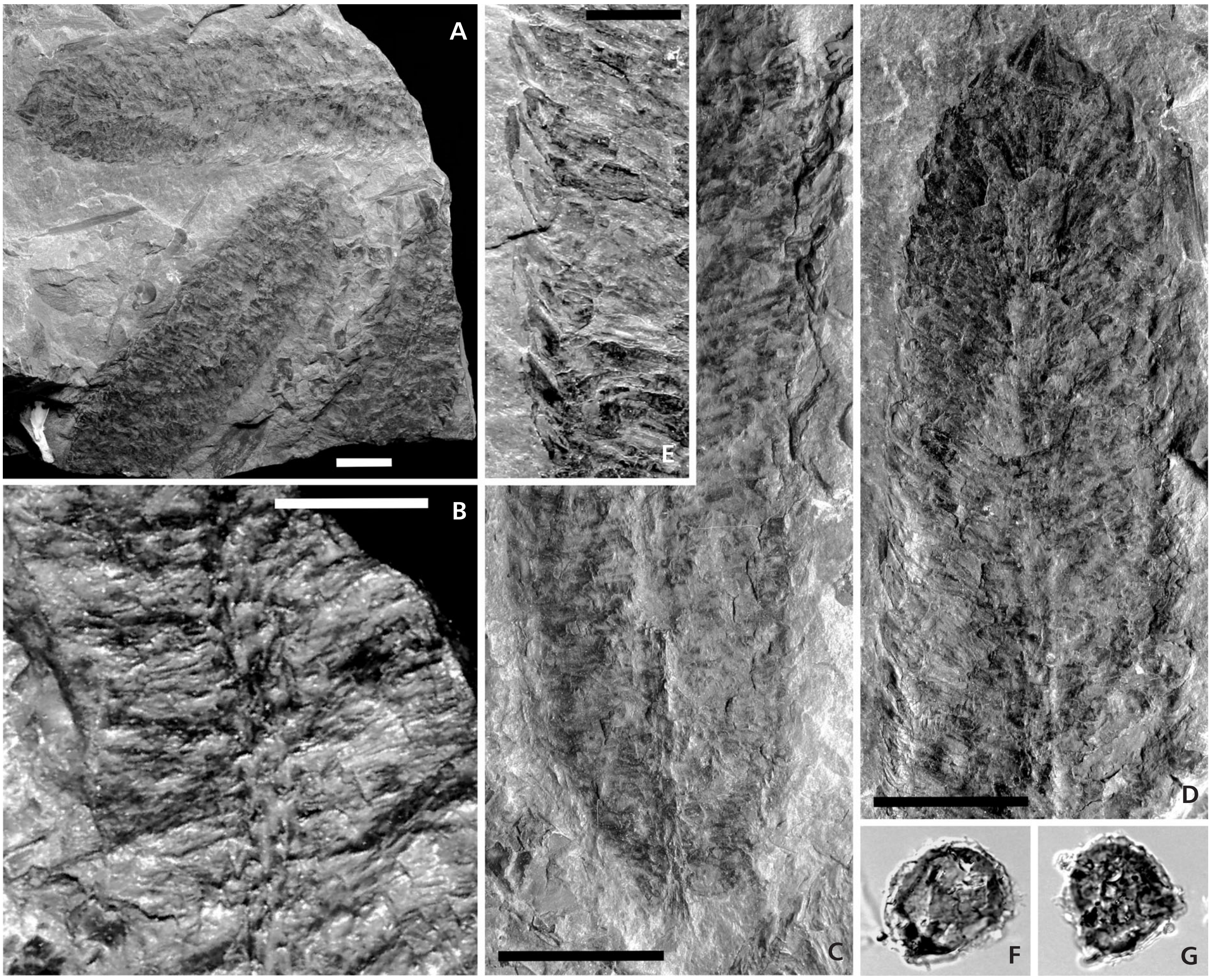

Figure 2. *Lepidostrobus boltonensis* n. sp. • A – specimen BMNH V.12045A (the holotype), from Chequerbent Pit, Bolton, South Lancashire Coalfield. Lower Coal Measures (Langsettian), Roof of the Royal Arley Coal, scale bar 10 mm. • B – detail view of the smallest cone fragment from the same specimen, scale bar 10 mm. • C – detail of the cone with preserved base, scale bar 10 mm. • D – cone fragment with preserved apex. This specimen provided spores, scale bar 10 mm. • E – detail of sporophylls of the specimen that provided spores, scale bar 5 mm. • F, G – *in situ* trilete cingulizonate lycospores with relatively narrow cingulum and narrow zona, all × 500.

who obtained different types of cingulate and not cingulizonate lycospores similar to those of *L. boltonensis*. This difference in spore types supports the idea about its questionable classification. On the other hand, Thomas (1965) described cingulizonate lycospores with wide cingulum and wide zona from an adpression specimen also assigned to *L. jacksonii*. These *in situ* lycospores described from *Lepidostrobus jacksonii* by Thomas (1965) are different from those isolated by us from *L. boltonensis* and from specimen assigned to *L. jacksonii* by Felix (1954).

L. obovatus is another similar species which comprises cones of comparable size and morphology. They can be distinguished from *L. boltonensis* by their oval shape, which tapers gently from the mid point of the cone towards both ends. Moreover, *L. obovatus* is commonly attached to the leafy shoots of *Lepidodendron mannabachense* Sternberg (= *L. obovatum* Sternberg), which is not the case for the specimen described here. *Lepidostrobus obovatus* also differs in having longer laminae. More importantly, the *in situ* spores of *L. obovatus* are also different from those of *L. boltonensis*. Those of the *L. obovatus* were described by Bek & Opluštil (2004) and compared with the dispersed species *Lycospora loganii*, which is characterised by narrow cingulum and wide zona.

L. haslingdenensis described from the Late Namurian of the Lancashire Millstone Grit is similar to *L. boltonensis* in being a rather small cylindrical cone of the same width. However, it can be distinguished by its wider axis that is about 3–5 mm thick compared to the 2 mm thickness of *L. boltonensis*. Laminae of both species are generally short, but those of *L. haslingdenensis* are even shorter. However, as stated by Thomas & Dytko (1980), length of laminae can be related to rather poor preservation. *In situ* lycospores isolated from *L. haslingdenensis* are of a different type (relatively wide cingulum and wide zona) than those of *L. boltonensis* (relatively narrow cingulum and narrow zona).

Willard (1989b), who obtained spores from 61 lycopsid cones from the North American and British coalfields, described a similar type of cingulizonate lycospores with relatively narrow cingulum and narrow zona from two adpression cone species *Lepidostrobus variabilis* Lindley & Hutton (Langsettian-Bolsovian of the Illinois and Appalachian basins) and *L. praelongus* Lesquereux (Asturian of Pennsylvania). Willard (1989b) compared lycospores isolated from both cone species to the dispersed spore species *Lycospora torquifer* (Loose) Potonié & Kremp. Another similar type of *in situ* lycospore of the *Lycospora punctata*-type was described by Willard (1989b) from adpression specimens of *Lepidostrobus* cf. *squarrosus* from the Asturian or Cantabrian of the Forest of Dean, England. *L. variabilis* of Willard (1989b) is generally a larger cone which is up to 180 mm long, 17–31 mm wide, and with an axis 3–7 mm thick. Cones gradually taper from the middle part to the apex. Only laminas are generally similar in shape. Nevertheless, above mentioned differences clearly indicate that Willard's (1989b) *L. variabilis* and the specimen described here represent different species. Even more apparent morphological differences exist between *L. boltonensis* and Willard's *L. praelongus*. The latter is a type of large lycopsid cone which is about 210 mm long and 40–60 mm wide. The axis is 8 to 10 mm thick, and also the laminae are generally larger, up to 20 mm long. The greatest similarity exists between the specimens described here and Willard's (1989b) *L.* cf. *squarrosus* from Forest of dean, U.K. She depicted an oval cone, about 80 mm long and 18–22 mm wide, similar in size to *L. boltonensis*. However, it can be distinguished from *L. boltonensis* by its oval outline, and most probably represent a different species.

Stratigraphic range and geographic distribution. – This species is known only from the holotype, which comes from the Lower Coal Measures (Langsettian) of the South Lancashire Coalfield.

***Lepidostrobus huttonii* sp. nov.**
Figure 3

Material. – Specimen BMNH 36465.

Locality. – Jarrow, Durham, North Cumberland-Durham Coalfield.

Stratigraphy. – Coal Measures, Westphalian.

Etymology. – In honour of W. Hutton, an early British palaeobotanist.

Diagnosis. – Cone oval, about 68 mm long and about 20 mm wide at its mid point. Length/width ratio 3.4. Cone axis 1.5 mm wide. Laminae triangular, 8–9 mm long, with entire margins slightly concave. Cone microsporangiate. Parent plant with rhomboidal to roughly hexagonal, slightly imbricated and keeled leaf cushions, slightly longer than wide or as long as wide, between 2.2 and 3.1 mm wide and/or long. Lower angle acute, remaining angles rounded. Leaf scar rhomboidal, in upper part of leaf cushion, between 1.8 and 2.1 mm wide and 1.3 and 1.6 mm long. Microspores subtriangular to subcircular trilete cingulizonate. Proximal and distal surfaces are irregularly scabrate, finely or densely microgranulate to microspinate.

Description. – Cone and sterile shoot: The specimen represents a complete cone attached to a sterile shoot without leaves and preserved as adpression with remains of coally matter (Fig. 3A, B). The cone is split completely along the surface which precludes direct observation of cone architecture beneath the imbricated laminae.

The cone is small, only 68 mm long and about 20 mm wide at its mid point. The length/width ratio is 3.4. The cone is oval to nearly cylindrical, gently tapering from the middle part downward to an obtuse base and upward to a gently pointed apex (Fig. 3A–C). At the cone base, there is a thin, roughly 1.5 mm wide and 8 mm long stalk that connects cone and sterile shoot (Fig. 3A, B). This stalk most probably represents the basal part of the cone axis but may also be a decorticated part of a sterile shoot. Single-veined laminae are 8–9 mm long, of narrow triangular shape with entire and slightly concave margins. They are adpressed to the cone. The shoot to which the cone is attached is 9 mm wide and lacks leaves (which were evidently absent during fossilisation). Leaf cushions are rhomboidal, a little longer than wide or as long as wide, keeled, and directed upward to the cone (Fig. 3A, D). Their surface is smooth, and they are only slightly imbricated. The exposed part is rhomboidal to roughly hexagonal, between 2.2 and 3.1 mm wide and/or long. The lower angle is acute, remaining ones more or less rounded. The rhomboidal leaf scar is located in the upper part of the leaf cushion. It is about 1.8–2.1 mm wide and 1.3–1.6 mm long and covers about one third of the leaf cushion. The leaf scar has acute lateral angles and rather rounded upper and lower angles. It bears three foliar prints; a central (vascular) one and smaller parichnos located laterally.

Spores: These are subtriangular to subcircular trilete microspores 28 (32.3) 35 μm in diameter (Fig. 3F–I). The laesurae is simple, extending to the outer margin of central body. Cingulum 2.5 (3.1) 3.8 μm wide developed as a dark thickened ring on the outer margin of the central body. Zona may occasionally be perforated and usually is laevigate to

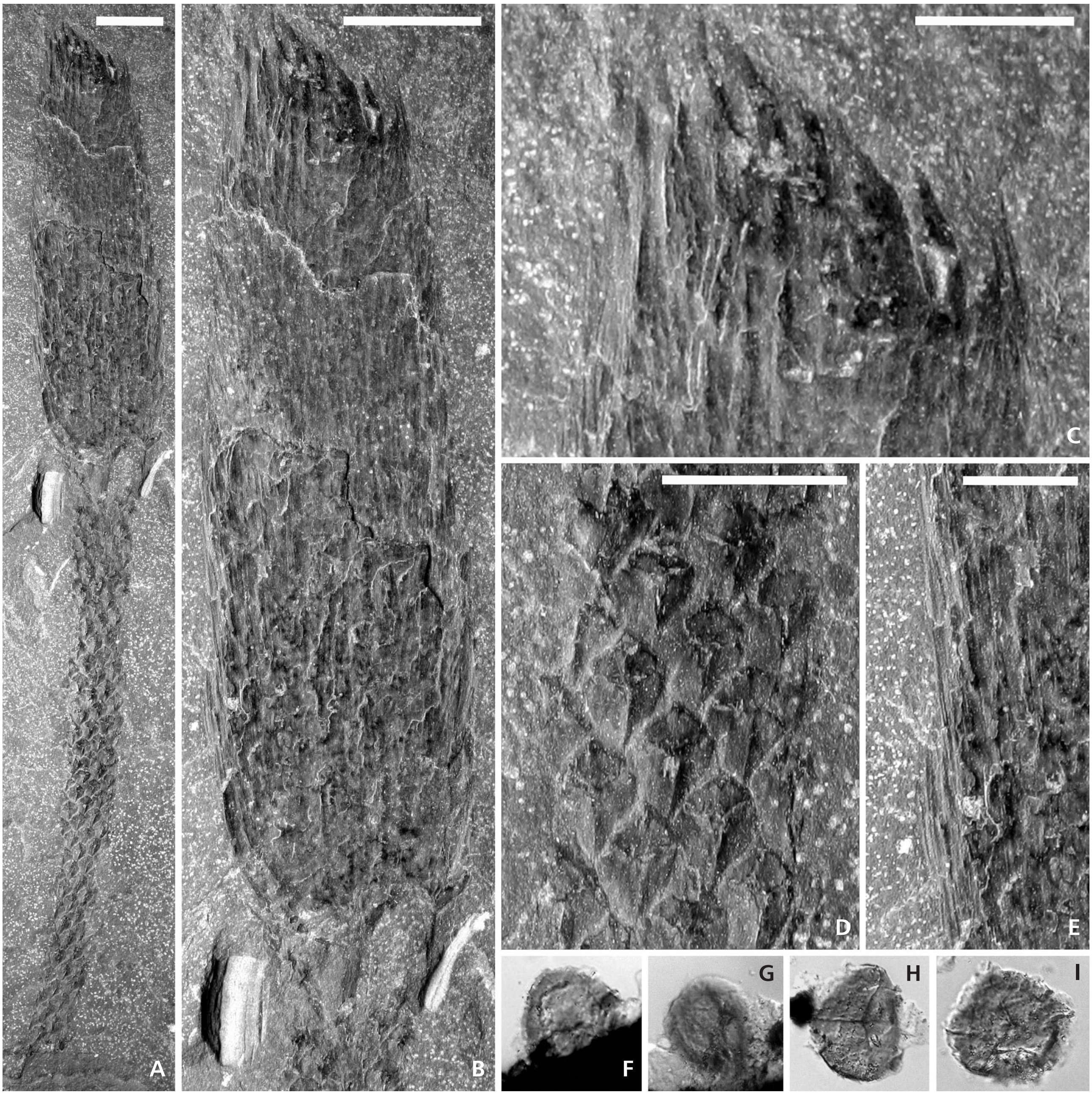

Figure 3. *Lepidostrobus huttonii* n. sp. • A – cone of *Lepidostrobus huttonii* n. sp. attached to a leafy shoot of *Lepidophloios acerosus* Lindley & Hutton, 1831. Specimen BMNH 36465 (the holotype). Jarrow, Durham, North Cumberland-Durham Coalfield. Coal Measures (Westphalian), scale bar 10 mm. • B – detail of cone, scale bar 10 mm. • C – detail of apical part of the cone, scale bar 5 mm. • D – detail of shoot with leaf cushions, scale bar 5 mm. • E – detail of sporophylls, scale bar 5 mm; F–I – *in situ* trilete cingulizonate lycospores with relatively narrow cingulum and narrow zona, all × 500.

finely scabrate and 1.2 (1.5) 2.1 μm wide. Proximal and distal surfaces are irregularly scabrate, finely or densely microgranulate, microverrucate or microspinate. The number of sculpture elements is higher on the distal than on the proximal surface. Isolated *in situ* microspores belong to the subgroup of cingulizonate lycospores with relatively narrow cingulum and narrow zona (Bek & Opluštil 2006) and can be correlated to the dispersed miospore species *Lycospora subjuga*, *L. brevijuga*, *L. triangulata*, *L. microgranulata* or *L. contacta*.

Parent plant. – The cone is attached to a shoot of *Lepidophloios acerosus* Lindley & Hutton. On the specimen label it is identified as *Lepidophloios carinatus* Weiss, which, as stated by Kidston (1893/4) and Němejc (1947), is a synonym of *Lepidophloios acerosus* (see also Crookall 1964, p. 315). This species differs from similar *Lepidophloios laricinus* Sternberg in having apparently keeled leaf cushions that are roughly as wide as long.

Comparisons and discussion. – If this cone is found isolated without any connection to its parent plant and without any knowledge of its spores, it can easily be mistaken for *Lepidostrobus spinosus*, *L. obovatus* or even juvenile stages of *L. ornatus*. The most apparent similarity is to *L. spinosus* instituted by Kidston (1888) based on a single specimen from Radstock (Asturian/Cantabrian boundary, see Cleal *et al.* 2003), Somerset Coalfield as *nomen nudum*. Later, in 1893, he provided full description of the species based on additional material from the Duckmantian (specimens Nos 712 and 1548) of the Kilmarnock Coalfield. These specimens contain several cones of the same size and shape as *L. huttonii*. *L. spinosus* cones of specimen No. 712 are widest about a quarter of the way up from the base, compared to *L. huttonii* where maximum width is achieved at approximately the mid point. The cone of *Lepidostrobus huttonii* is also more cylindrical compared with that of *L. spinosus* (No. 1548). However, this is not the case for the remaining Kidston specimen (No 371) from Radstock, which apparears to be a different species (see below), most probably *L. obovatus*. Spores of *L. spinosus* were obtained only from the Kidston specimen (No. 1548), and probably belong to the same group of cingulizonate lycospores with relatively narrow cingulum and narrow zona (Fig. 3F–I).

Another similar cone species, *Lepidostrobus obovatus* represents oval to nearly cylindrical cones of comparable size, 65–100 mm long and 18–28 mm wide (Bek & Opluštil 2004). Some specimens of *L. obovatus* are indistinguishable from *L. huttonii* when the parent plants and *in situ* spores are not preserved. Spores of *L. obovatus* (*Lycospora loganii*-type) possess a narrow cingulum and wide zona, whereas spores of *L. huttonii* possess a narrow cingulum and narrow zona. The parent plant of *L. obovatus* is *Lepidodendron mannabachense* (= *L. obovatum*), whereas the parent plant of *L. huttonii* is *Lepidophloios acerosus*. In addition, most specimens of *L. obovatus* are oval in shape compared to the nearly cylindrical form of *L. huttonii*.

Comparison of *L. huttonii* to *L. ornatus* is complicated because a number of authors have described various cones (species?) from different coalfields as *L. ornatus* (*e.g.*, Brongniart 1828; Lindley & Hutton 1831, 1835; Geinitz 1855; Němejc 1954; see also the synonymy in Crookall (1966). Therefore our comparisons are restricted to the holotype, which is a 3-dimensionally preserved specimen in an ironstone nodule lacking distal laminae. It is a 140 mm long fragment of a nearly cylindrical cone without base or apex, which are broken off. The cone is therefore twice as long as *L. huttonii*. Spores of the holotype belong to the lycospores with narrow cingulum and wide zona (Brack-Hanes & Thomas 1983) and thus, they are not of the same type as those of *L. huttonii*.

Lycospores morphologically similar to *L. huttonii* were isolated from Czech adpression cone species *Lepidostrobus* sp. C and *L.* sp. D (Bek & Opluštil, 2006) and *L. nemejcii* by Bek & Opluštil (2004). All of these Czech specimens, however, differ in their cone morphology and cannot be assigned to any of the British species examined. Hagemann's (1966) specimen of *L.* sp. D from the Campine Basin, Belgium, also provided comparable *in situ* spores. However, this cone is larger and the sporophylls shorter compared to those of *L. huttonii*, and therefore most probably represent a different species.

Willard (1989b) described a roughly comparable type of *in situ* lycospores with relatively narrow cingulum and narrow zona from two adpression specimens of *Lepidostrobus variabilis* (Langsettian-Bolsovian of the Illinois and Appalachian basins) and *L. praelongus* (Asturian of Pennsylvania). Willard (1989b) compared *in situ* microspores from both cone species to the dispersed spore species *Lycospora torquifer*. Willard (1989b) mentioned another similar type of *in situ* lycospore, the *Lycospora punctata*-type, isolated from adpression specimens of *Lepidostrobus* cf. *squarrosus* from the Asturian of Forest of Dean, England. Of the above mentioned cone species, only *L.* cf. *squarrosus* is morphologically comparable to *L. huttonii*. Remaining species represent evidently much larger cones, which cannot be compared with the specimen of *L. huttonii* described here. *L.* cf. *squarrosus* is similar in size and shape to the cones described here, but unfortunately, only a very brief description was provided. Thus, a precise comparison between *L. huttonii* and *L. squarrosus* is not possible (Willard 1989b).

***Lepidostrobus spinosus* Kidston, 1888**
Figure 4

Material. – Specimen BMNH 40587.

Locality. – Sunderland, Durham, North Cumberland-Durham Coalfield.

Stratigraphy. – Coal Measures, late Langsettian–early Duckmantian, Westphalian.

Description. – Cone: The specimen is preserved in a grey mudstone slab and represents one complete cone split along the surface showing only limited details of inner morphology overprinted on the cone surface. The cone is oval, 78 mm long and 26 mm wide; maximum width is achieved between one quarter and one half of the cone length. The cone tapers gently from its mid point to an obtuse apex, length/width ratio is 3.0. The cone axis is exposed only in the lower half where it is 4 mm thick (Fig. 4A–C). Pedicels are not clearly visible and therefore cannot be described in detail. However, pedicel overprint on the cone surface indicates that they are attached to the cone axis at an angle of about 60°. The pedicels are between 7 and 8 mm long. Laminae are

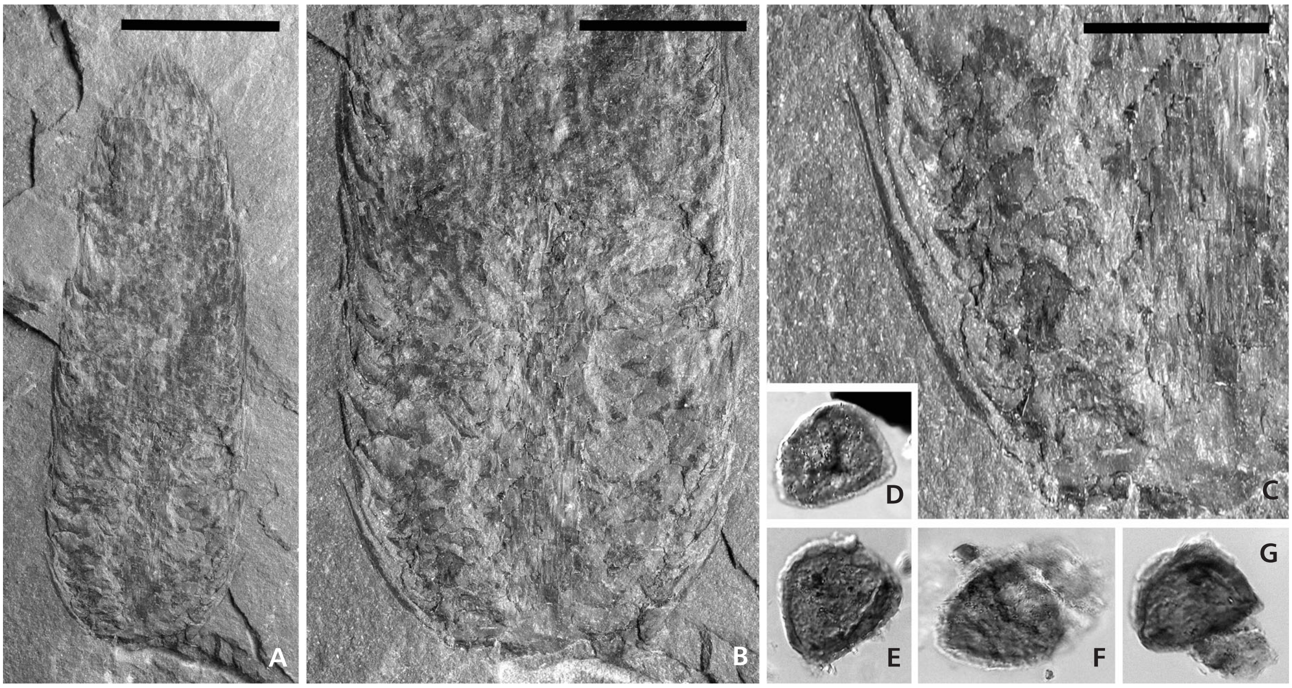

Figure 4. *Lepidostrobus spinosus* Kidston, 1888. • A – cone of *Lepidostrobus spinosus*. Specimen BMNH 40587. Sunderland, Durham, North Cumberland-Durham Coalfield. Coal Measures, Westphalian, scale bar 20 mm. • B – detail of lower part of the cone, scale bar 10 mm. • C – detail of sporophylls, scale bar 5 mm. • D–G – *in situ* trilete cingulizonate lycospores with relatively narrow cingulum and narrow zona, all × 500.

triangular with gently concave entire margins, about 10 mm long with very fine longitudinal striations.

Spores: These are subtriangular to subcircular trilete microspores 29 (33.8) 35 μm in diameter. The laesurae is simple, extending to the outer margin of the central body. Cingulum is 2.0 (2.7) 3.9 μm wide and developes as a dark thickened ring on the outer margin of the central body. Zona may be sometimes perforated and usually is laevigate to finely scabrate and 1.3 (2.2) 3.3 μm wide. Proximal and distal surfaces are irregularly scabrate, finely or densely microgranulate, microverrucate or microspinate. The number of sculpture elements is higher on the distal than on the proximal surface. Isolated microspores belong to the subgroup of cingulizonate lycospores with relatively narrow cingulum and narrow zona (Bek & Opluštil 2006) and can be correlated to the dispersed miospore species *Lycospora subjuga*, *L. brevijuga*, *L. triangulata*, *L. microgranulata* or *L. contacta*.

Parent plant of *L. spinosus* is not known. One of the cones from the Kidston type specimen (No. 1548) has a 4.5 mm wide decorticated stalk, which may represent a leafy shoot of the parent plant.

Comparisons and discussion. – *Lepidostrobus spinosus* is a rarely occurring lepidodendrid cone species. In the Kidston collection, there are only three specimens identified as *L. spinosus*: No. 371 (Asturian/Cantabrian, Somerset Coalfield) and Nos 712 and 1548 (Langsettian to Duckmantian, Kilmarnock Coalfield). Examination of these specimens, however, indicates that Kidston most probably conflated two different species. Specimen No. 371 is very similar to *Lepidostrobus obovatus* borne on *Lepidodendron mannabachense*, which is a common plant species of the middle Namurian to the late Westphalian. This re-interpretation is further corroborated by the presence of several centimetres long grass-like leaves typical of leafy shoots of the parent plant with which *L. obovatus* is often found in organic connection. The remaining Kidston specimens of *L. spinosus* from Kilmarnock (Nos 712 and 1548) are most probably the same species, and therefore can be compared with the specimens described here. Specimen No. 712 contains three complete or nearly complete cones of the same shape as the cone in BMNH 40587. These cones are 70–87 mm long and between 21 and 28 mm wide with a 4 mm broad cone axis. Specimen No. 1548 is a large slab containing three complete cones and four cone fragments. The cones are about 90 mm long, and their width varies between 23 and 30 mm. The axis is also of comparable width to BMNH 40587. The sample taken from cones of this Kidston specimen (No. 1548) yielded *in situ* spores with relatively narrow cingulum and narrow zona (Fig. 4D–G), similar to the spores obtained from the cone of *L. spinosus* described here. This is further corroborating evidence that both belong to the same species.

Comparison with similar cones from coalfields outside the British Isles proved that the specimen of *L. spinosus* described here yielded spores similar to Hagemann's (1966) specimen of *Lepidostrobus* sp. D from the Campine Basin in Belgium. However, Hagemann's specimen differs in the shape of the laminae, which are longer and possess less concave margins. *L. spinosus* cones also appear to be oval, whereas the preserved part of the Belgian specimen is clearly a cylindrical cone. Thomas (1965) reported *in situ* lycospores isolated from an adpression specimen of *L. spinosus*. These microspores belong to the group of cingulizonate lycospores with relatively narrow cingulum and narrow zona (*i.e.* similar to those isolated from specimens described here and also classified as *L. spinosus*).

L. spinosus can also be compared with similar lepidodendrid cone species, especially with *L. obovatus* and with the specimens described here as *L. boltonensis* and *L. huttonii*. *L. obovatus* is a cone of comparable size and similar oval outline with maximum width at its mid point. Its pedicels are, however, attached perpendicularly to the cone axis compared with those of *L. spinosus* that attach at an angle of around 60°. Moreover, both species can be clearly distinguished by their *in situ* spores. Those of *L. obovatus* are compared with *Lycospora loganii* (*i.e.* lycospores with narrow cingulum and wide zona). The similar species *L. boltonensis* differs from *L. spinosus* only in cone morphology, especially its slender axis, apparently cylindrical shape, and characteristic slightly pointed apex. It is more difficult to distinguish *L. spinosus* from *L. huttonii*. Both species produced very similar spores, and the cone morphology also appears to be very similar. The only difference appears to be the position of the maximum width; in *L. huttonii* maximum width is achieved at the mid-point of the cone length, whereas in *L. spinosus* it is below this point and toward the base.

In situ spores isolated from the specimen of *Lepidostrobus spinosus* described here are comparable to spores obtained from several Czech cone species (*Lepidostrobus nemejcii*, *L.* sp. C and *L.* sp. D) already discussed in the sections related to *L. boltonensis* and *L. huttonii*. Unfortunately, none of these Czech cone species are comparable with the British *L. spinosus*. *L. nemejcii* is an obviously much larger cone; the largest (and still incomplete) specimen is 320 mm long and 45 mm wide, with a cone axis about 9 mm wide. *L.* sp. D is cylindrical in shape with a rounded apex, and is also evidently a different cone. The only specimen is 125 mm long and only 20 mm wide, and is incomplete. The most similar Czech cone species is *L.* sp. C. However, the only known specimen is a 70 mm long fragment of a medium-sized cone, the shape of which is impossible to determine. This specimen is about 45 mm wide and has an 8.5 mm wide axis.

Willard (1989b) described a roughly similar type of cingulizonate lycospores with relatively narrow cingulum and narrow zona from two adpression cone species, *Lepidostrobus variabilis* (Langsettian-Bolsovian of the Illinois and Appalachian basins) and *L. praelongus* Lesquereux (Asturian of Pennsylvania). Willard (1989b) compared lycospores isolated from both cone species to the dispersed spore species *Lycospora torquifer*. Another similar type of *in situ* spores of the *Lycospora punctata*-type were described by Willard (1989b) from adpression specimens of *Lepidostrobus* cf. *squarrosus* from the Asturian or Cantabrian of Forest of Dean, England. Except for *L.* cf. *squarrosus*, all of Willard's (1989b) above-mentioned species represent morphologically different cones. Her *L.* cf. *squarrosus* is an oval shaped cone up to 87 mm long, with maximum width at its mid point. All of the specimens of *L. spinosus*, in contrast, achieve their maximum width in the first quarter of the length above the base.

***Lepidostrobus* cf. *obovatus* (Němejc, 1947) Bek & Opluštil, 2004**
Figure 5

Material. – Specimen BMNH V.65201b.

Locality. – Dudley, Worcestershire.

Stratigraphy. – Coal Measures, ?Duckmantian, Westphalian.

Note on the locality. – The specimen most probably comes from the Coseley nodule flora locality; Coseley in suburb of Dudley. The locality is of Duckmantian age (Cleal, written comm.).

Description. – Cone: This specimen is a rusty-brown ironstone nodule containing two fragments of lepidodendrid cones. The larger fragment is about 100 mm long and is the middle part of a cone with broken base and apex. The smaller fragment is a 40 mm long apical part of a cone most probably detached from the larger cone fragment. The cone is split longitudinally, partly along the cone surface and partly along the cone axis. The combined length of the two fragments is about 150 mm, thus it can be assumed that this is the length of the complete cone. The cone is about 20 mm wide without distal laminae (axis and sporangia-bearing part of sporophylls) and 25 mm wide including distal laminae. The cone is widest near its mid-point, from where it very slowly tapers to the base and apex. Cone axis is 2.5 mm thick. Pedicels are inserted perpendicular to the cone axis, but near the base they are slightly downward pointing. The pedicels are up to 8 mm long in the middle part of the cone.

The height of pedicels increases from about 0.5 mm near the cone axis to about 1 mm at a distal end. The keel is not prominent; the heel is about 1 mm long. Neighbouring pedicels are about 2.2 mm apart. Sporangia are

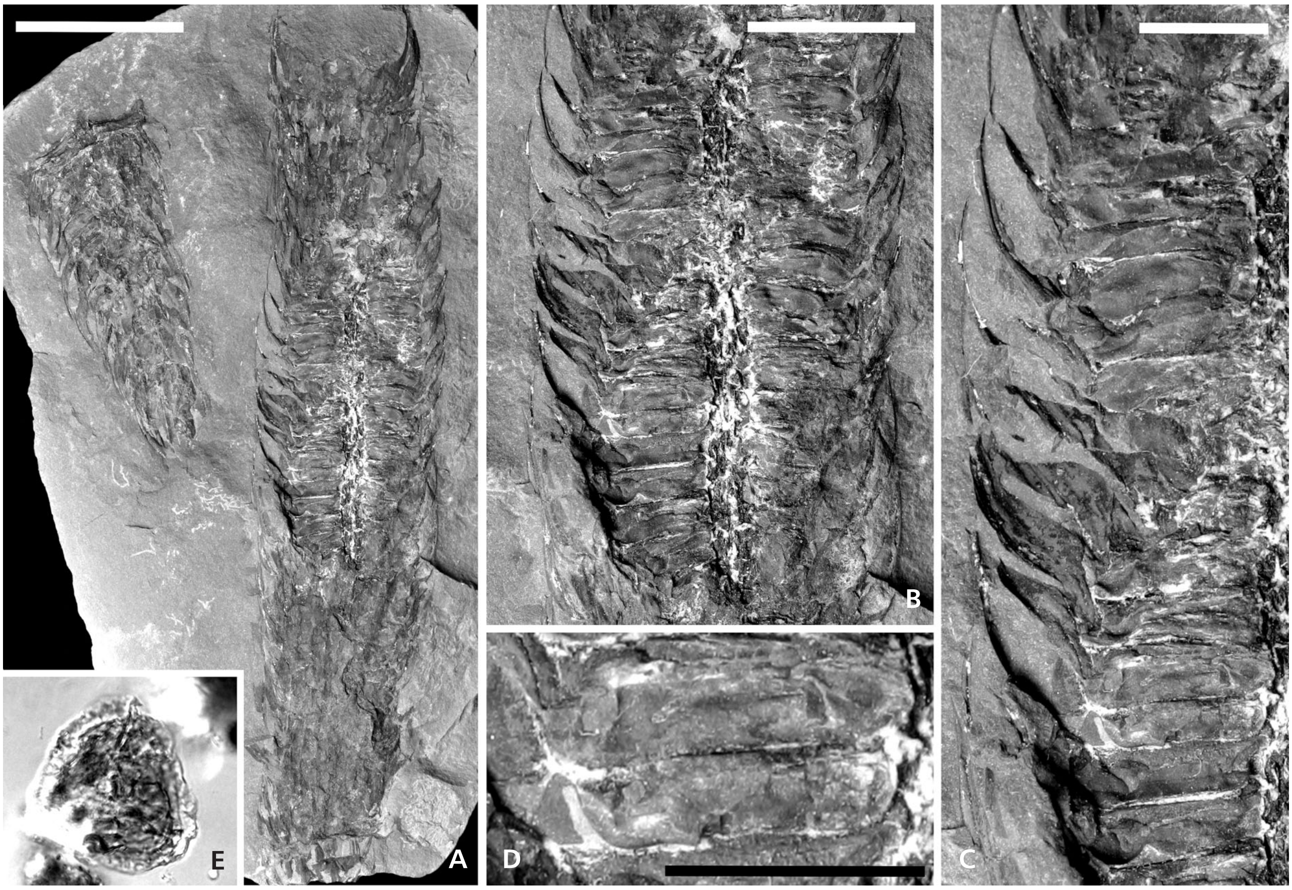

Figure 5. *Lepidostrobus* cf. *obovatus* (Němejc, 1947) Bek & Opluštil, 2004. • A – *Lepidostrobus* cf. *obovatus*. Specimen BMNH V.65201b. Dudley, Worcestershire. Coal Measures, Westphalian, scale bar 20 mm. • B – detail of middle part of the cone, scale bar 10 mm. • C – detail of sporophylls with laminae, scale bar 5 mm. • D – detail of pedicels with sporangia, scale bar 5 mm. • E – *in situ* trilete cingulizonate lycospore with relatively narrow cingulum and wide zona, × 500.

oval; in the middle part of cone they are about 7.5 mm long and 1.8 mm high (Fig. 5C, D). Distal laminae are triangular with entire margins and midrib. Distal laminae are 9–10 mm long and 3.5 to 4 mm wide at the base, bent arch-like to the apex, and adpressed to the cone (Fig. 5C). They are concave in the lower one third of the length.

Spores: These are trilete microspores with circular to subtriangular amb, outline is smooth or slightly undulate; the size ranges from 38 (41.2) 43.0 μm. The laesurae is simple, extending to the outer margin of central body, sometimes with labrum 1–3 μm large. The cingulum is 1.6 (1.8) 2.0 μm wide. Zona 3.0 (4.2) 5.6 μm wide, is laevigate, punctate or sometimes can be perforated. The sculpture of the proximal and distal parts of zona is laevigate, irregularly scabrate or pitted. The sculpture of the proximal surface is laevigate to finely scabrate; the distal surface is finely micrograpulate (Fig. 5E).

Isolated microspores belong to the subgroup of cingulizonate lycospores with relatively narrow cingulum and wide zona (Bek & Opluštil 2006). The width of the zona is more than 4 μm. For example, dispersed species *Lycospora loganii*, *L. pellucida*, *L. micropapillata*, *L. micrograna*, *L. intermedia*, *L. pseudoannulata* and *L. perforata* belong to this subgroup. Some specimens can possess more or less prominent perforations of the zona (like *L. perforata*, *L. pseudoannulata*).

Comparisons and discussion. – This cone strongly resembles *Lepidostrobus obovatus* and is also similar to *L. huttonii*. In its type area (the basins of central and western Bohemia, Czech Republic), *L. obovatus* belongs to common lepidodendrid fructifications and is well-known, including both *in situ* spores and parent plant, *Lepidodendron mannabachense* (= *L. obovatum*). Both Bohemian cones and the British specimen described here are of the same cone morphology, including the sporophylls and their characteristic perpendicular insertion to the cone axis. They possess a similar type of lycospores and the parent plant, *Lepidodendron mannebachense*, is a common species of the British coalfields. The only difference is the larger size of the British specimen, especially its length. The largest Czech specimens are about 100 mm long, whereas the length of the British specimen is estimated to be about 150 mm. This difference might be explained by ecological conditions, but could also indicate a different species. The larger size of the British specimen compared with the Czech cones could, in part, be explained by preservation in a siderite nodule. This style of preservation can prevent plant remains from shrinkage, which can reduce size by up to 13% during fossilisation (Cleal & Shute 2007).

However, because all other features are comparable and fit within the range of variability of *Lepidostrobus obovatus* from the central and western Bohemia, and because the parent plant is also known from the British coalfields, specimen No. BMNH V.65201b is assigned to this species. Comparable *in situ* lycospores were also isolated from other Czech adpression species *L.* sp. A and *L.* sp. B (Bek & Opluštil 2006). *Lepidostrobus* sp. A is a fragment of cone of similar width which differs significantly in having an 8 mm thick axis compared to the 2.5 mm axis of the described specimen of *Lepidostrobus obovatus*. Both species also differ in their stratigraphic distribution: *Lepidostrobus* sp. A is of middle Stephanian age compared to the lower Westphalian age of the British specimen. *Lepidostrobus* sp. B is of similar age (Bolsovian), however, it is too poorly preserved for reliable comparison with the British specimen. Both specimens correspond in size but the sporophylls of *L.* sp. B are shorter. Also the cone axis is wider in the Czech specimen.

Very similar types of *in situ* lycospores were mentioned by Hagemann (1966) from German adpression species of *Lepidostrobus* sp. C from the Duckmantian strata of the Ruhr Basin. Unfortunately this specimen is a cone fragment that is only about 2 cm long. It is split along the surface thus excluding reliable comparison with the specimen described here. Willard (1989b) obtained roughly comparable lycospores from American adpressed specimens of *L. praelongus* and *L. variabilis*. The former is a large lycopsid cone about 200 mm long with a thick axis, whereas the latter is about 185 mm long, oval and with short laminae about 10–11 mm long. Except for the length, the morphology of *L. variabilis* of Willard (1989b) is similar to the specimen described in this paper, and it is possible that both are the same species. Nevertheless, her specimen is not a type specimen and therefore we do not refer our specimen to this species.

This type of *in situ* lycospore is known also from American permineralized species *L. fayettevillense* Taylor & Eggert described by Taylor & Eggert (1968) and *L. oldhamius* Williamson (associated with *Lepidofloyos harcourtii*-type of parent plant) published by Willard (1989a). Thomas (1988) described roughly similar lycospores from permineralized specimens of *Lepidostrobus binneyanus* Arber.

Genus *Flemingites* (Carruthers, 1865) Brack-Hanes & Thomas, 1983

Type species. – *Flemingites gracilis* (Carruthers, 1865) Brack-Hanes & Thomas, 1983.

***Flemingites* cf. *russelianus* (Binney, 1871) Brack-Hanes & Thomas, 1983**
Figure 6

Material. – Specimen No. BMNH V.5888.

Locality. – Devonside, Tillicoultry, Clackmannan.

Stratigraphy. – Coal Measures, Westphalian.

Description. – Cone and parent plant: The specimen contains an incomplete cone associated with lepidodendrid leafy shoots and branches preserved in a mudstone slab. The cone apex and right margin of the cone are missing. The cone is preserved as an adpression split longitudinally along the surface and covered by imbricated distal laminae. No details of the cone axis and pedicel arrangement can be observed.

The cone is cylindrical tapering rapidly only above the obtuse base. The cone fragment is 110 mm long, but the original length is difficult to estimate because there is no indication of any tapering at the preserved upper part of the cone (Fig. 6A, B). The maximum preserved width is 18.5 mm, which must be very close to original width of the cone. Sporophyll laminae are lanceolate with entire margins. They are 10–11 mm long and about 2.5 mm wide at or near the base. Sterile fragments associated with the cone represent some thin leafy shoots, but mostly leafy branches with well-preserved leaf cushions. The 20 mm thick branch has elongated rhomboidal leaf cushions, which are between 7 and 8 mm long and about 3 mm wide. The widest part is situated between the middle and upper two thirds of the cushion. Leaf cushions are longitudinally asymmetrical, but some of them can be nearly symmetrical (Fig. 6C). They have acute lower and upper angles and rounded lateral angles. They are smooth and quite flat, or raised only slightly in the apical part. In longitudinal section, the keel is straight, very slightly raised, and runs through the whole length of the cushion. Infrafoliar parichnos is absent. True leaf scars are also absent because the leaves are still attached to the leaf cushions. Instead, very small punctiform false leaf scars appear near the cushion apex. The leaves are lanceolate and about 25 mm long and about 2 mm wide. They are bent in a slightly S-like shape in the lower part and curved in an arch in the upper part. The younger leafy shoots have leaves that are only about 12 mm long and 1 mm wide near the base. The characteristics of leaf cushions bearing S-bend leaves resemble those of *Lepidodendron acutum* and possibly also

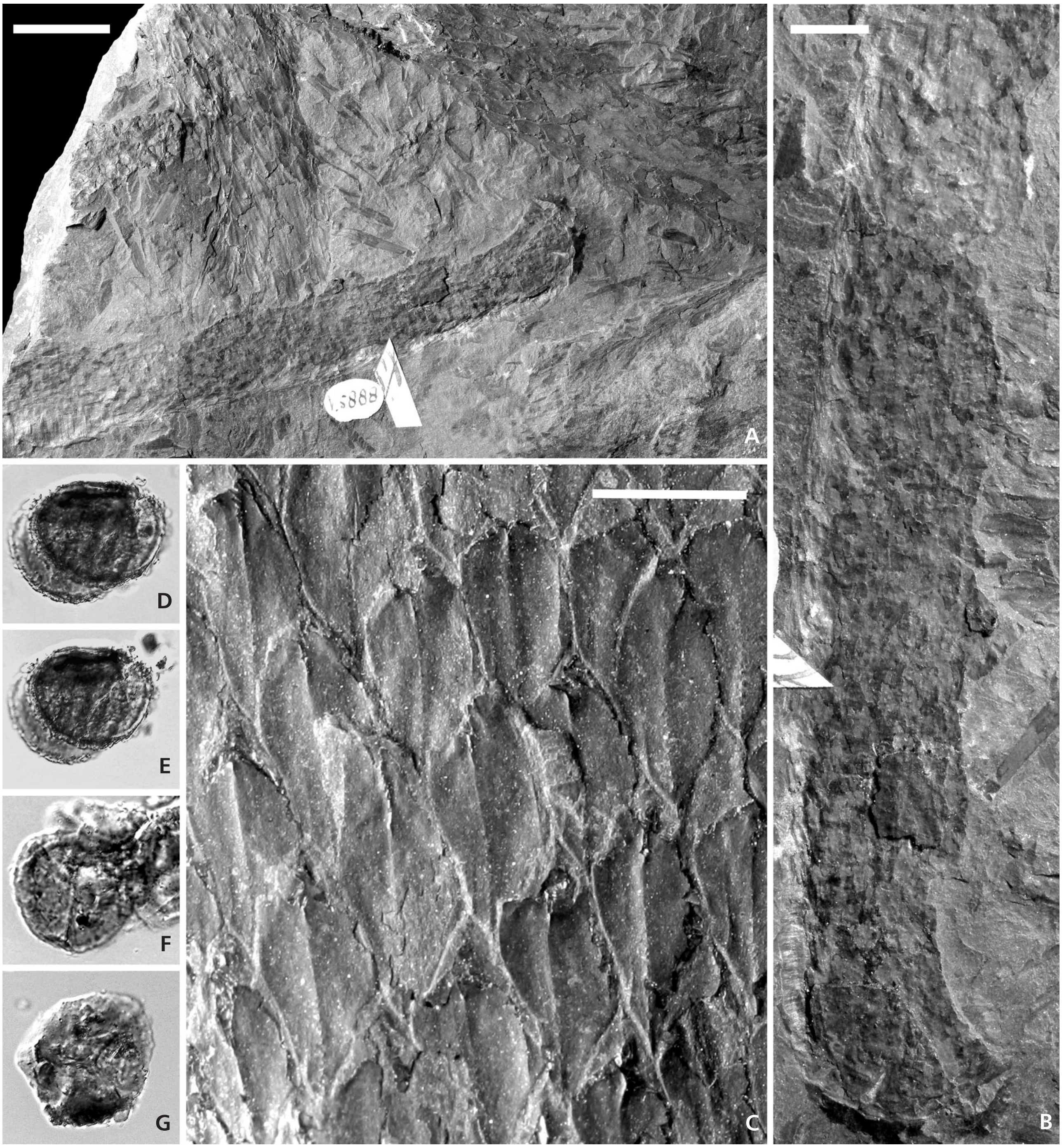

Figure 6. *Flemingites* cf. *russelianus* (Binney, 1871) Brack-Hanes & Thomas, 1983. • A – cone of *Flemingites* cf. *russelianus* with leafy shoots and branches of *Lepidodendron acutum* – *L. simile*-type. Specimen BMNH V.5888. Devonside, Tillicoultry, Clackmannan, Scotland. Coal Measures, Westphalian, scale bar 15 mm. • B – detail of cone, scale bar 5 mm. • C – detail of leaf cushions of associated branches with false leaf scar, scale bar 5 mm. • D–G – *in situ* trilete cingulate lycospores with relatively narrow cingulum and prominent microspinate sculpture of the proximal surface, all × 500.

those of *Lepidodendron simile sensu* Němejc (1947), which is a very similar species. Both species are very difficult to distinguish based on small fragments only. *L. acutum* differs in having generally larger and broader leaves and small leafy shoots compared to *L. simile*. Unfortunately, the branch remains of this specimen are not sufficiently complete for more reliable identification. There is also a fragment of a poorly preserved branch of *Lepidophloios* sp. This, however, has nothing in common with the cone since *Flemingites* cones were not borne on *Lepidophloios*.

Spores: These are circular to subtriangular trilete microspores 26 (32.6) 37 µm in diameter. Their outline is denticulate. The laesurae is simple, reaching to the equator. The cingulum is 0.8 (1.3) 2.0 µm wide. The proximal surface is laevigate; the distal surface is densely microspinate, and the exine thin, sometimes with narrow secondary folds. An inner body is sometimes visible.

Isolated microspores (Fig. 6D–G) belong to the subgroup of cingulate lycospores, which have a narrow cingulum with a densely microspinate distal surface (Bek & Opluštil 2006). These are comparable to the dispersed spore species *Lycospora orbicula* Potonié & Kremp.

Remarks. – Chaloner (1953a) described the same type of *in situ* microspores and isolated megaspores compared to the dispersed spore species *Lagenicula horrida* Zerndt from several specimens of *Lepidostrobus dubius* Binney (two specimens from the Sedgwick Museum, Cambridge; three specimens from the Kidston's collection, British Geological Survey, Keyworth; one from the Natural History Museum, London and one from the Royal Holloway College, University of London). The authors were unable to isolate megaspores from specimen BMNH V.5888 due to the tiny amount of sample allowed for the maceration. For description, measurement of *in situ* megaspores of *Flemingites russelianus* and discussion, see *Lepidostrobus russelianus* of Chaloner (1953a, pp. 277–283).

Parent plant. – The cone is associated with two types of branches, which can be assigned to *Lepidophloios* cf. *acerosus* and to *Lepidodendron acutum* Sternberg – *L. simile sensu* Němejc (1947). The former is represented only by a small and poorly preserved fragment that is unlikely to be connected with the cone because *Lepidophloios* bears monosporangiate cones assigned to *Lepidostrobus* if microsporangiate, or to *Lepidocarpon* if megasporangiate (Bateman *et al*. 1992). The latter species, *Lepidodendron acutum* or *L. simile* (cannot be distinguished from the preserved remains) are often associated with this type of small to medium size cylindrical cone that bears both microspores and megaspores (*e.g*., Chaloner 1953a). We consider these to be part of the parent plant of the cone.

Comparisons and discussion. – According to Chaloner (1953a) cones associated with *Lepidodendron acutum* belong to *Lepidostrobus russelianus* (Binney) Chaloner (now *Flemingites russelianus* – for explanation see Crookall 1966 and Brack-Hanes & Thomas 1983) and those associated with *Lepidodendron simile* Kidston belong to *Lepidostrobus dubius*, now assigned to *Flemingites gracilis*. Therefore, this cone was first compared with these species and later with some other similar *Flemingites* fructifications (*F. olryi* Zeiller).

Morphologically, this cone best resembles *F. russellianus* and *F. gracilis* (formerly *Lepidostrobus dubius*) in being narrow and more or less cylindrical. According to Crookall's (1966) description, except for the generally smaller habit of *F. russellianus* (up to 150 mm long and 20 mm wide) in comparison to *F. dubius* (up to 250 mm long and 18 mm wide), there is no significant morphological difference between these species. Not surprisingly, as late as 1953, Chaloner, who macerated both of Binney's (1871) original specimens of *F. russellianus*, recorded different *in situ* megaspores in each, which were referred to *Triletes horridus* Nowak & Zerndt and *T. rugosus* Loose, *i.e. Lagenicula horrida* Zerndt and *Lagenoisporites rugosus* (Loose) Potonié & Kremp. The specimen that provided *Lagenicula horrida* megaspores (Pl IX, Fig. 2) was selected by Chaloner as the lectotype for his emended description of *Lepidostrobus dubius*, now *Flemingites gracilis*. Chaloner (1953a) also stated that both cone species could be distinguished in having different parent plants: *F. russellianus* was borne on *Lepidodendron acutum*, whereas *F. gracilis* was borne on *Lepidodendron simile*. Megaspores and parent plants thus remain the main criterion for separating *Flemingites gracilis* and *F. russelianus*. Specimen BMNH V.5888 described here provided only microspores of *Lycospora orbicula*-type, which indicate a position within the genus *Flemingites*. However, megaspores important for determination at specific level have not been obtained. Therefore, only the association with the parent plant can be used to support the determination. Unfortunately, as explained above, the remains of parent plant are not sufficiently well preserved for reliable determination (*i.e. L. acutum* or *L. simile*). The authors lean towards an affinity with *L. acutum*, which means that fructification should correspond to *Flemingites russelianus*.

Another species, *F. olryi*, is evidently a different species characterised by smaller and gently tapering cones, about 100 mm long and about 10 mm wide. The spores of the holotype, which comes from Northern France, are unknown. However, Chaloner (1953a) isolated megaspores of the *Lagenoisporites rugosus*-type and microspores of the *Lycospora orbicula*-type from some British specimens identified by Kidston as *Lepidostrobus* (= *Flemingites*) *olryi* Zeiller.

In the coalfields of central and western Bohemia, Czech Republic, cones similar to the specimen described here occur in the middle Westphalian strata and are also associated with *Lepidodendron acutum* and *L. simile*. However, there is no published systematic study of *Flemingites* from the Czech Carboniferous.

Genus *Sigillariostrobus* Schimper, 1870 ex Feistmantel, 1871

Type species. – *Sigillariostrobus bifidus* Geinitz, E. 1873.

Table 4. Review of selected *Flemingites* cones and their *in situ* micro- and megaspores

cone species	microspores	megaspores	references
Flemingites allatonensis	–	*Lagenicula crassiaculeata*	Chaloner 1953b
Flemingites diversus	*Lycospora orbicula*	*Lagenoisporites rugosus*	Felix 1954, Courvoisier & Philips 1975
Flemingites gracilis	*Lycospora orbicula*	*Lagenicula horrida*	Chaloner 1953b, Brack-Hanes & Thomas 1983
Flemingites noei	?	*Lagenicula*	Felix 1954, Mathews 1940
Flemingites olryi	*Lycospora orbicula*	*Lagenoisporites rugosus*	Chaloner 1953b
Flemingites russelianus	*Lycospora orbicula*	*Lagenoisporites rugosus*	Chaloner 1953b
Flemingites schopfii	*Lycospora*	*Lagenicula horrida*	Brack 1970
Flemingites scottii	*Lycospora*	*Lagenicula subpilosa* f. *major*	Chaloner 1953b
Lepidostrobus sp. C	*Lycospora orbicula*	*Lagenoisporites rugosus*	Hagemann 1966
Lepidostrobus sp. U	*Lycospora orbicula*	–	Balbach 1966
Flemingites lycopoditis	*Lycospora orbicula*	*Lagenoisporites rugosus*	Drábek 1967, Bek 1998, Bek & Opluštil 1998

***Sigillariostrobus acicularis* sp. nov.**
Figure 7

Material. – Specimen No. BMNH V.65200.

Locality. – Ashton-under-Lyme, Lancashire Coalfield.

Stratigraphy. – Middle Coal Measures, Duckmantian.

Etymology. – Name derived according to the acicular shape of sporophylls.

Diagnosis. – Cone cylindrical, about 130 mm long and 22–24 mm wide including laminae. Peduncle 3 to 5 mm wide and more than 25 mm long. Cone axis 4.5 mm wide. Sporophylls in alternate whorls, internode longitudinally ribbed. Sporophylls 20 to 25 mm long and 4 to 5 mm wide near the base, acicular-lanceolate in shape with rhomboidal base and prolonged acute apex, locally with cilia. Trilete microspores with circular to oval amb. Equatorial thickening. Distal surface microgranulate to microspinate, proximal surface scabrate to smooth.

Description. – Cone: The specimen preserved in a mudstone is a small cylindrical strobilus with a blunt apex. It is about 130 mm long and 22–24 mm wide and borne on a 25 mm long (not complete) and 3 to 5 mm wide peduncle (Fig. 7A, B). The cone axis is 4.5 mm wide. Sporophylls are arranged into alternate whorls. Internodes are longitudinally ribbed. Sporophylls possess a single central vein about 20 to 25 mm long and about 4 to 5 mm wide near the base. They are acicular-lanceolate with rhomboidal base and prolonged acute apex (Fig. 7C). Margins in the upper two thirds are almost entirely slightly concave, and in the apical part they bear a few cilia (Fig. 7C1–3). However, due to vagaries in preservation this can only be seen on some sporophylls.

Spores: These are circular to oval trilete microspores 62 (72.9) 86 μm in diameter. In equatorial view their shape is more or less lenticular with prominent thickening 4.8 (6.3) 7.4 μm in diameter at the equator (Figs 7D–G). The laesurae is simple, extending nearly to amb, and not always visible. The distal surface is microgranulate to microspinate, and the proximal surface is typically almost smooth or very finely scabrate. Exine in the region of crassitudinous thickening is darker in colour than in polar region. The equatorial thickening extends towards the poles for a distance 5–10 μm.

Isolated microspores can be compared to the dispersed spore species *Crassispora kosankei* (Potonié & Kremp) Bharadwaj.

Comparisons and discussion. – The specimen described above (BMNH V.65200) was compared first with the British *Sigillariostrobus* species, as well as with species from other European coalfields. Crookall (1964) reported only *Sigillariostrobus nobilis* Zeiller, *S. rhombibracteatus* Kidston and *S. ciliatus* Kidston from the British Coal Measures, whereas Chaloner (1953b) synonymised *S. ciliatus* with *S. rhombibracteatus* based on identical spores and described only two species from the British coalfields. There are, however, several other species from similar stratigraphic levels known from other European coalfields to which this specimen could be compared (for overview see Amerom & Gaipl 1995).

When comparing the London specimen BMNH V.65200, we took into account not only cone morphology but also stratigraphic range of species and their spores. We consider the character of spores as an important part of the species diagnosis, and therefore even morphologically similar cones with different spores are considered different species. This view is at odds with that of Amerom & Gaipl (1995) who would place *Sigillariostrobus* cones with different spores in the same species. For example, cones of *S. rhombibracteatus*, one of the most common species, yield both *Crassispora*-type microspores and *Tuberculati-*

Table 5. The diameter and classification of sigillarian permineralized (P) and adpression (A) *in situ* micro- and megaspores and their parent cones

cone species	diameter of spores (µm)	classification of *in situ* spores	references
Mazocarpon bensonii (P)	1200–1500 48–54	*Laevigatisporites reinschii Crassispora*	Feng & Rothwell 1989, Pigg 1983
Mazocarpon oedipternum f. *megalophorum* (P)	1600	*Laevigatisporites reinschii*, *L. glabratus*	Chaloner 1967, Schopf 1941
Megalocarpon oedipternum f. *microphorum* (P)	45–60	*Crassispora kosankei*	Courvoisier & Phillips 1975, Schopf 1941, Chaloner 1967
Mazocarpon shorense (P)	1200–1900	*Tuberculatisporites*	Chaloner 1967
Sigillariostrobus souchii (A)	2500	*Tuberculatisporites mamillarius*	Chaloner 1967
Sigillariostrobus czarnockii (A)	1200–1700 50–70	*Laevigatisporites Crassispora*	Bocheński 1939, Chaloner 1967
Sigillariosporus leiosporous (A)	2000	*Laevigatisporites glabratus*	Abbott 1963
Sigillariostrobus quandangularis (A)	? 55	*Tuberculatisporites mamillarius* *Crassispora?*	Wood 1957, Chaloner 1967
Sigillariostrobus rhombibracteatus (A)	920–1200 55	*Tuberculatisporites mamillarius* *Crassispora*	Bocheński 1939, Remy & Rettschlag 1954, Chaloner 1953a
Sigillariostrobus tieghemii (A)	1500	*Laevigatisporites*	Carpentier 1933
Sigillariostrobus souchii (A)	2500	*Tuberculatisporites mamillarius*	Zeiller 1886, Carpentier 1933
Sigillariostrobus goldenbergii (A)	1452–1718	*Tuberculatisporites mamillarius*	Sen 1958
Sigillariostrobus angustus (A)	–	*Crassispora kosankei*	Amerom & Gaipl 1995
Sigillariostrobus ciliatus		*Crassispora kosankei*	herein

sporites mammilarius (Bartlett) Potonié & Kremp megaspores. This is, however, not in agreement with the ICBN (McNeill *et al*. 2006).

In addition, sigillarian cones are almost always found without any connection to parent plants. Thus, it is not possible to state with certainty whether morphologically similar cones with megaspores or microspores were borne on the same parent plant. For this reason, we prefer separation of cones based not only on cone morphology, but also on whether they are microsporangiate or megasporangiate.

The species described here is characterised by very long and narrow bracts. Morphologically similar species with long and narrow bracts include *S. gothanii* Bode, *S. strictus* Zeiller, *S. czarnockii* Bocheński and *S. prolifer* Stockmans & Willière. The only two known British species, *Sigillariostrobus nobilis* Zeiller and *S. rhombibracteatus* Kidston are clearly different. The cones of *S. nobilis* are more than 300 mm long and up to 65 mm wide, and thus differ significantly in size. The bracts are also short compared to their width and they are less cuspidate. *Sigillariostrobus rhombibracteatus* represents cones of comparable size to the specimen described here (BMNH V.65200), but appear to differ in having a shorter and less acicular part of the bract above the rhomboidal sporangium-bearing base. Excluding Moore's description, which is incorrect, spores of *Sigillariostrobus rhombibracteatus* were obtained and described by Bocheński (1939), Moore (1946), Chaloner (1953b) and Remy & Rettschlag (1954). Bocheński (1939) obtained both megaspores of *Tuberculatisporites* and microspores of *Crassispora*-types from specimens in the Upper Sileasian Coal Basin. However, only Chaloner studied spores from some of Kidston's syntypes (both of *S. ciliatus* and *S. rhombibracteatus*), which provided only megaspores of *Tuberculatisporites mamillarius*. This indicates an apparent heterogeneity of the concept of *Sigillariostrobus rhombibracteatus* that will be discussed elsewhere. Here we focus on the Kidston syntypes of *S. rhombibracteatus* (incl. *S. cilliatus*) that we regard as a different species because they bear only megaspores. This conclusion is further supported by the morphological differences of the bracts as mentioned above.

The sigillarian cone described here (BMNH V.65200) displays a certain degree of similarity to the following species: *S. gothanii* Bode, *S. strictus* Zeiller, *S. czarnockii* Bocheński and *S. prolifer* Stockmans & Willière from the western or central European coalfields. The holotype of *S. strictus* is associated with *Sigillaria brardii* Brongniart, which comes from the northern part of the Massif Central Basin (Decize) and is of Late Stephanian age. It is a cone fragment measuring about 120 mm in length, the body of which is about 15 mm wide (25 mm wide including laminae). Sporophylls are narrow, about 230 mm long and 4 mm wide near the base. The laminar part of the sporophyll is acicular, about 15 mm long and gradually passes into a basal sporangium-bearing part. Sporophylls of *S. strictus* resemble those of *S. acicularis*, with the exception that the acicular part of the sporophyll of the new species is thinner (about 1 mm wide). Amerom & Gaipl

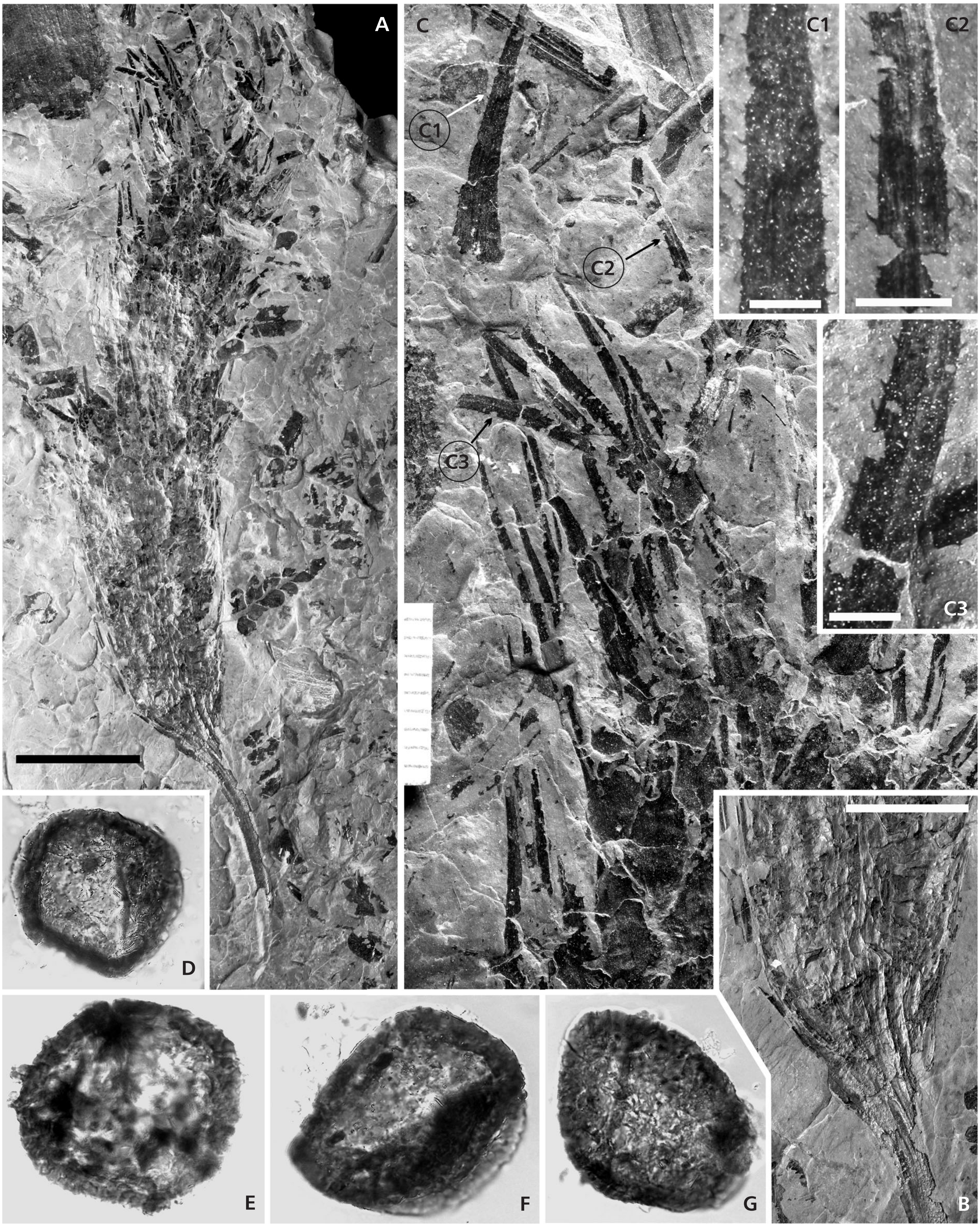

Figure 7. *Sigillariostrobus acicularis* n. sp. • A – cone of *Sigillariostrobus acicularis* n. sp. with peduncle. Specimen BMNH V.65200. Ashton-under-Lyme, Lancashire Coalfield. Middle Coal Measures, Duckmantian, scale bar 20 mm. • B – detail of cone base with the transition to peduncle, scale bar 10 mm. • C – acicular sporophylls; C1–C3 – details of acicular sporophylls, all scale bars 1 mm. • D–G – *in situ* trilete spores with crassitudous thickening of the *Crassispora kosankei*-type, all × 500.

(1995) also mentioned the megaspores assigned to *Laevigatisporites glabratus* (Zerndt) Potonié & Kremp and compared these with *Crassispora kosankei* microspores of *S. acicularis*. Slight differences in cone morphology and completely different types of spores, as well as diffreneces in stratigraphic appearance led us to the conclusion that they represent different species. Two other similar species, *S. czarnockii* and *S. gothanii*, are a little larger (over 125 mm and over 150 mm in length, respectively), but their sporophylls are long and quite narrow, resembling those of *S. acicularis*. Nevertheless, these sporophylls differ in being still wider and having prominently ciliate margins. Both *S. czarnockii* and *S. gothanii* bear *Laevigatosporites* megaspores, but one cone of *S. czarnockii* also provided microspores of the *Crassispora*-type (Bocheński 1936, 1939). The remaining comparable species is *S. prolifer* from the Westphalian of Belgium. It is characterised by very narrow and 30 mm long sporophylls, which are very similar to those of *S. acicularis*. The cone of *S. prolifer* is also of comparable dimensions to *S. acicularis*, being only slightly longer (over 130 mm) but of the same width. The only major difference seems to be the spores, which, in the Belgian species are only megaspores *Laevigatisporites reinschii* Ibrahim. This difference in spores is the only reason that we have assigned the cone described here to the new species *S. acicularis*. There are probably no similar forms in the Czech coalfields to which this new species could be compared.

Discussion and comparison of described cones with the Czech species

We have restricted our comparison of Czech and British tree lycopsid cones to species that are based not only on cone morphology, but also spores and, where possible, fragments of leafy branch. Only such broadly characterised species can provide a reliable basis for comparing fructifications among different Euramerican coalfields.

Based on *in situ* lycospores, the lepidodendrid cones described here can be subdivided into three groups. The first group consists of cingulizonate lycospores with relatively narrow cingulum and narrow zona (Bek & Opluštil 2006). These lycospores were isolated from specimens BMNH V.12045A (*Lepidostrobus boltonensis*), BMNH 36465 (*L. huttonii*) and BMNH 40587 (*L. spinosus*). These specimens represent broadly similar cones that differ only in small morphological details. The parent plant is known only for specimen BMNH 36465, which is compared with *Lepidophloios acerosus*. Morphologically similar microspores were also isolated from the Czech adpression cone species *Lepidostrobus* sp. C and *L.* sp. D (Bek & Opluštil 2006) and *L. nemejcii* (Bek & Opluštil 2004). However, these Czech species differ in their cone morphology and cannot be assigned to any of the other species. The most similar is *Lepidostrobus* sp. C, which can be compared in part with *Lepidostrobus spinosus*. Unfortunately, *L.* sp. C is only a cone fragment and therefore a full comparison cannot be provided. The remaining Czech species are medium to large-sized cones, which appear to represent different species. A similar type of *in situ* lycospore was described by Hagemann (1966) in a cone adpression of *L.* sp. D from the Ruhr Basin, Germany. *In situ* lycospores isolated from permineralized (coal-balls) specimens of *L. coulterii* by Balbach (1966) and *L. minor* by Leisman & Rivers (1974) are also of similar morphology.

The second group of *in situ* lycospores, characterised by relatively narrow cingulum and wide zona (Bek & Opluštil 2006) is represented by specimen BMNH V.65201b only. Roughly similar *in situ* lycospores were isolated from Czech adpression species *L.* sp. A and *L.* sp. B (Bek & Opluštil 2006) and also *L. obovatus*. *L.* sp. A is a middle Stephanian species (comparing to lower Westphalian age of the English species) which is a slightly larger cone with an apparently wider axis than the English specimen. However, the greatest similarity is between the specimen described here and *L. obovatus*, which represents both cones of comparable shape and sporophyll arrangement. The only difference is that the English specimen is a little larger and it has a more cylindrical shape.

The third subgroup comprises *in situ* cingulate lycospores with narrow cingulum and a densely microspinate distal surface (Bek & Opluštil 2006). Spores of the *Lycospora orbicula*-type were isolated from a cone of specimen BMNH V.5888. These microspores were produced by cones of the genus *Flemingites*. In Britain similar microspores were obtained by Chaloner (1953a, 1967) from adpression specimens of *Flemingites olryi* and by Thomas (1965) from *F. diversus* and *F. russelianus*. In the Czech Republic spores of *Lycospora orbicula*-type were reported by Drábek (1967) from cones of *Lepidostrobus brongniartii* Goeppert (Bek 1998) and by Bek & Opluštil (1998) from *Lepidostrobus lycopoditis* Feistmantel. The latter specimen is associated (not in organic connection) with *Lepidodendron simile sensu* Němejc (1947). A revision of the Czech *Flemingites* is in preparation, so the full comparison cannot yet be made. We can only confirm that different species of parent plants occur, including *Lepidodendron simile* and *L. acutum*. Also, various species of *in situ* megaspores (*Lagenicula* and *Lagenoisporites*) have been obtained, indicating the existence of several *Flemingites* species in the Czech coalfields.

Comparison of Czech and British sigillarian fructifications is practically impossible because no sigillarian cones have been described from the Czech coalfields. The cones of sigillarias are quite rare in the Czech coalfields, and in the collections of the National Museum in Prague there are only few undescribed specimens (Bek

1998). Cones of the genus *Sigillariostrobus* are also relatively infrequent in the British coalfields (Crookall 1966). This is because mature cones disintegrated on dispersal into isolated sporophylls, whereas lepidodendrid cones remained intact. Moreover, sigillarian cones, when preserved, possess only very low variability, so comparatively few morphotaxa have been described. Known cone diversity does not reflect the species diversity in this group. There is a well-documented disparity between the numbers of *Sigillaria* species and their cone species recognised in the British coalfields. Crookall (1964, 1966) listed 54 species of sigillarias but only 3 species of *Sigillariostrobus* cones. It is possible that some *Sigillariostrobus* species represent several natural taxa. This state is impossible to improve even through the use of spores. Microspores isolated from these cones are all assigned to the dispersed microspore genus *Crassispora* Bharadwaj, the variability of which is also generally low. This suggests that cone and spore morphology in this group was much more conservative than in the case of lepidodendrid lycopsids.

Summary and conclusions

The tree lycopsid fructifications from the British Coal Measures (Pennsylvanian) described here are based on material selected from the collection of the Natural History Museum, London. They provided a new set of complex data on cone morphology, *in situ* spores and, in some instances, also on leaf-bearing branches of the parent plants.

Six of the fifteen selected and sampled specimens yielded *in situ* microspores. These were described in detail and compared with similar forms from the Czech Republic and some other Euramerican coalfields. Cones of the genus *Lepidostrobus* were represented by four specimens that can be subdivided into two groups based on their spores. The first group includes cones assigned to *Lepidostrobus boltonensis*, *L. huttoni* and *L. spinosus*. These contain cingulizonate lycospores with relatively narrow cingulum and narrow zona that are comporable to the dispersed species *Lycospora subjuga*, *L. brevijuga*, *L. triangulata*, *L. microgranulata* or *L. contacta*.

The second group includes a single specimen identified as *L.* cf. *obovatus*, and has lycospores characterised by relatively narrow cingulum and wide zona. These are comparable to the dispersed species *Lycospora loganii*, *L. pellucida*, *L. micropapillata*, *L. micrograna*, *L. intermedia*, *L. pseudoannulata* and *L. perforata*.

Cones of the genus *Flemingites* are represented by the specimen identified as *F.* cf. *russelianus*. This cone yielded microspores identified as *Lycospora orbicula*.

Cones described here were compared with species from outside Britain and especially with those from Czech coalfields in central and western Bohemia. The comparison shows that *Lepidostrobus* cf. *obovatus* is common to both areas. It is likely that *Flemingites* cf. *russelianus* also occurs in the Czech coalfields, but this requires confirmation through revision of the Bohemian specimens. The remaining species either do not occur in the Czech coalfields, or their occurrence remains unproven. *Lepidophloios acerosus* described by Němejc (1947) from central and western Bohemia most likely represents a different species because its cones are very different from those described here (*Lepidostrobus huttonii*), and are found in organic connection with shoots of *Lepidophloios acerosus*. We have found several cylindrical cones up to 800 mm long attached to *Lepidophloios acerosus sensu* Němejc (1947) in the Radnice Basin in western Bohemia. The cone of *L. acerosus* from the British Coal Measures is much smaller, less than 100 mm long.

The only sigillarian cone was a specimen that is assigned to the new species *Sigillariostrobus acicularis* which yielded *Crassispora kosankei* microspores.

The study of tree lycopsid fructifications of the British Coal Measures combining palynological and macrophytopalaeontological methods should continue to provide further results necessary for the general comparison of lycopsid floras with other European coalfields.

This is the first attempt to compare and correlate Pennsylvanian lepidodendrid fructifications and their *in situ* spores from Great Britain and the Czech Republic. The results are preliminary because they are based on a small initial sample (only fifteen from about two hundreds stored in the Natural History Museum in London). Approximately 50% of the sampled specimens yielded valuable new data on *in situ* spores. Given the large numbers of cone specimens housed in museum collections in Europe and North America, we anticipate that these will provide an invaluable source of materials for refining the taxonomic framework of tree lycopods and for developing a better understanding of their stratigraphic and geographic ranges.

Acknowledgement

This research received support from the SYNTHESYS Project which is financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme. This support UK (GB-TAF – 1759) allowed the authors to visit and study the Carboniferous plant collection in the Natural History Museum, London. Maceration and some other work related to sample preparation were undertaken in the Department of Palaeobiology and Palaeoecology, Institute of Geology v.v.i. in Prague. We are also grateful for financial support from the Research programme (AVOZ30130516) of the Institute of Geology, v.v.i., Academy of Sciences of the Czech Republic, and project MSM 0021620855 of the Faculty of Science, Charles University. Special thanks to Peta Hayes and Paul Kenrick from the Natural History Museum, London, UK for help with accessing specimens of Carboniferous plants in the Natural History Museum, London, UK. Paul Kenrick is also thanked for language correction of this article. The authors are also very grateful to Chris Cleal from the National Museums and Galleries of Wales, Cardiff and Jason Hilton from the University of Birmingham for their constructive comments for revision of the manuscript.

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