



Two new species of megasporangiate *Sigillariostrobus* Schimper (Sigillariostroboaceae) fructifications from the British Coal Measures

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Abstract. The arborescent lycophyte group known as the sigillarians bore pedunculate fructifications, including *Sigillariostrobus* Schimper, which has a known propensity to disaggregate, making comparisons of cones and in situ spores often difficult if not impossible. *Sigillariostrobus* is monosporangiate, containing either megaspores or microspores. Two new species of *Sigillariostrobus* with megaspores are described from the British Coal Measures. Two cones of *Sigillariostrobus saltwellensis* sp. nov. are described from Langsettian–Duckmantian strata of Great Britain, containing in situ *Laevigatisporites glabratus* (Zerndt) Potonié and Kremp spores, making this the first British *Sigillariostrobus* species described containing such spores. *Sigillariostrobus barkeri* sp. nov. is given here to the previously described cone with in situ *Tuberculatisporites brevispiculus* (Schopf) Potonié and Kremp spores. This is the first *Sigillariostrobus* cone with this megaspore species in situ, and thus shows that *T. brevispiculus* and *T. mamillarius* (Bartlett) Potonié and Kremp are not conspecific as others have previously suggested.

1 Introduction

Sigillarian trees are one of the distinctive groups of Carboniferous arborescent lycophytes that are not as tall, or as branched, as *Lepidodendron* Sternberg. Arnold (1947) mentions *Sigillaria reniformis* to be 18 ft (ca. 6 m) tall and 6 ft (ca. 2 m) in diameter at the base, tapering to 1 foot (30.5 cm) at the top. This description suggests that the stem was incomplete. Balfour (1872) states that they can be 40–50 ft (12–15 m) tall and 5 ft (ca. 1.5 m) in diameter. Balfour also gives measurements of 20 stems as 10–20 ft (3–6 m) high and 1–

3 ft (30.5 cm–1 m) in diameter, standing erect in alternating strata of shales and sandstones, near Morpeth in Northumberland (UK). They bear cones (fructifications) on peduncles off the main stem or branches. The first figures of a fructification belonging to *Sigillaria* Brongniart were given by Goldenberg (1855, pl. 4, Fig. 3; 1857, pl. 10, Figs. 1, 2), but he gave no name to them. Schimper (1870, pl. 47, Figs. 12–14) refigured some of Goldenberg's illustrations and gave them the name *Sigillariostrobus* but did not propose a holotype. Andrews (1970) included *Sigillariostrobus* (Schimper) Geinitz 1873 in the index that he published because the first specific name *S. bifidus* was given by Geinitz. However, Seward (1910) and Chaloner (1967) believed *S. bifidus* to be a conifer cone belonging to the genus *Gomphostrobus* Marion, 1890. For this reason Chaloner (1967) took *S. goldenbergi* of Feistmantel (1876) as the type species and gave the generic authorship as *Sigillariostrobus* (Schimper 1870) Feistmantel, 1876, *non* Geinitz. Feistmantel (1876) had merely given the specific name to specimens figured by Goldenberg (1855) and Schimper (1870), leaving it to Zeiller (1884) to give the first clear description and figure of *S. goldenbergi*. For this reason Chaloner (1967) proposed the type species authorship as *Sigillariostrobus goldenbergi* (Feistmantel) Zeiller, 1884. Feistmantel's other species, *S. feistmanteli*, was first regarded to be not a cone but a fertile zone and, therefore, is the type of *Sporangiostrobus* Bode – a genus which has since been synonymised with *Omphalophloios* White (Opluštil et al., 2010; Bek et al., 2015).

In situ spores have become an integral part of describing fructifications, e.g. Chaloner (1953), Thomas (1970), Brack-Hanes and Thomas (1983), Bek and Opluštil (1998, 2004), Thomas and Bek (2014). This leads onto a comparison of the in situ spores with named genera and species of dispersed

spores and then to using this information for palaeoecological interpretations.

Although the spores of the type specimens of *Sigillariostrobus* (*S. goldenbergi*) are unknown, Sen (1958) described the spores of a specimen he identified to be *S. goldenbergi* as *Laevigatisporites mamillarius*. Examination of the spore contents of other species has shown the genus to be made up of monosporangiate cones that contain either megaspores or microspores. Of the megasporangiate cones, the megaspores spore walls are generally about 20–30 µm with triradiate marks that are approximately half the radius of the spore. If the entire surface of the spore is smooth and usually with prominent curvaturae, it is of the type referred to the dispersed spore genus *Laevigatisporites* (Ibrahim) Potonié and Kremp. If the spore wall is ornamented with tubercles on the dorsal surface it would be referred to the dispersed spore genus *Tuberculatisporites* (Ibrahim) Potonié and Kremp. The number of dispersed megaspores species belonging to these two genera far exceeds the number of known cones, which must be partially due to the fact that most, if not all, *Sigillariostrobus* cones fall to pieces by losing their sporophylls and can even be reduced to a bare axis (Fig. 1).

The rarity of finding two more or less intact cones allows us here to describe a new *Sigillariostrobus* species from the British Coal Measures, with spores referable to the smooth-surfaced dispersed spore genus *Laevigatisporites*. We also give a name to another *Sigillariostrobus* cone from the British Coal Measures (Bolsovian) that has previously been described (Thomas, 1980) with spores referable to the tuberculate-surfaced dispersed spore genus *Tuberculatisporites*.

Megaspores that are trilete and circular in outline, with an originally concavo-convex shape, and having a complex exine ornamentation of tubercles, would clearly, if found isolated, be included within the genus *Tuberculatisporites* (Ibrahim) Potonié and Kremp (1954).

There are two species of *Tuberculatisporites* that concern us in this study: *T. mamillarius* (Bartlet) Potonié and Kremp (1955) and *T. brevispiculus* (Schopf) Potonié and Kremp (1955). Some authors, including Zerndt (1932), Dijkstra (1946, 1955a, 1955b), Arnold (1950) and Winslow (1959), believed the two species to be conspecific, while Potonié and Kremp (1955), Bhardwaj (1957a, b), Arnold (1961) and Selosse (1953) kept them separate. Spinner (1964) re-examined and redefined the genus *Tuberculatisporites* and included a list of species in which he distinguished *T. mamillarius* from *T. brevispiculus*. Following Spinner (1968) the two differ in their ornamentation. The tubercles are larger in *T. mamillarius*, being up to 130 µm tall and 94 µm in basal diameter on the distal surface, with them up to 28 µm tall and 25 µm in basal diameter on the proximal contact faces. In *T. brevispiculus* they are only 10 µm tall and vary from 25 to 30 and 40 to 45 µm in basal diameter on the distal surface, while the proximal contact faces are covered in apiculi that are 15 µm in diameter and less than 5 µm tall.

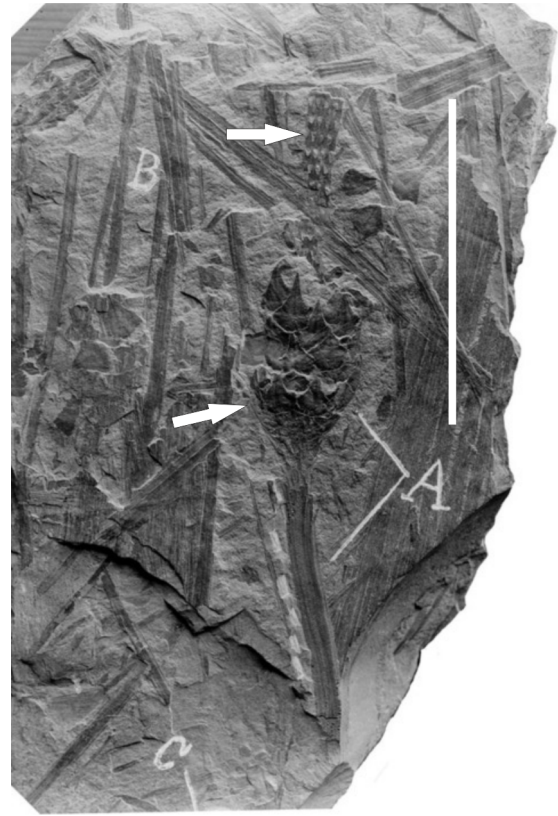


Figure 1. *Sigillariostrobus* fructification with only a few basal sporophylls (lower arrow), having shed most of its sporophylls exposing the upper part of the axis (upper arrow) as illustrated by Kidston (1897) (scale bar 50 mm). From the Kidston Collection at the British Geological Survey. Catalogue number: P686530. Reproduced with permission of the British Geological Survey ©NERC. All rights reserved.

2 Materials and methods

The cones were investigated using a Carl Zeiss Stemi 2000 microscope with incident light equipped with a Canon 450D digital camera. Spore preparations were made by maceration with Schulze solution and cleared using dilute (4%) ammonia solution. The resulting spores were slide-mounted in glycerine jelly as with dispersed spores. These spore preparations were observed with a transmitted light microscope (Carl Zeiss Axioscope A1) also equipped with a Canon 450D digital camera, and will be deposited with the specimens.

There are three cones that form the basis of this paper. One cone (Pb. 53-C.203, Hunterian Museum, Glasgow) comes from the southern part of the South Staffordshire coalfield from Saltwells Pit (now part of the Saltwells National Nature Reserve). The exact horizon of the specimen is unknown, although Besley (1988) refers to the general horizon as alluvial coal-bearing facies of the upper Langsettian–Duckmantian, which represent continuously emergent conditions allowing the extensive development of swamp soils. A second cone

(Pb. 707, Hunterian Museum, Glasgow) has no record of where it was collected. The third specimen, no. 1971.I28 from the Barker collection, Sheffield City Museum, was collected from above the Shafton Coal, Brierley Colliery, Yorkshire – top of the Similis-Pulchra Zone (Bolsovian).

3 Systematic descriptions

(B. A. Thomas, L. J. Seyfullah)

Family Sigillariostroboaceae Thomas and Brack-Hanes, 1984

Genus *Sigillariostrobus* (Schimper 1870) Feistmantel, 1876, *non* Geinitz E.

Type species: *Sigillariostrobus goldenbergi* (Feistmantel) Zeiller, 1884

Sigillariostrobus saltwellensis sp. nov.

(Figures 2–3)

Holotype: Specimen Pb. 53-C.203, stored in the Hunterian Museum, Glasgow.

Type locality: Saltwells Pit, near Cradley Heath, Staffordshire, Great Britain.

Type stratum: Alluvial coal-bearing facies – upper Langsettian–Duckmantian.

Etymology: Named after the locality of the specimen that we designate as the type.

Diagnosis: Cone at least 86 mm long, ca. 17–20 mm in diameter, axis 1.2 mm, pedicel ca. 8 mm long, sporangia 7 mm long, sporophyll laminae 12 broad at base, 6.3 mm long spreading outwards from the cone. Sporangia 7 mm long, 2.5 mm high. Megaspores trilete, probably originally plano-convex, average diameter 2000 µm in their equatorial planes, smooth walls with a thickened area between the arms of the trilete mark. Lesurae approximately half the spore radius, ca. 15 µm broad at the centre of the spore.

Description: Both cones are preserved as dark compression (Figs. 2a–b, 3a–b), although they are broken somewhere above their bases (Figs. 2a, c, 3a, c), so their complete length is unknown. The megasporophylls have free tips approximately 6.3 mm long (Fig. 3d), only slightly diverging from the sides of the cone. The megasporophylls are not well preserved (Figs. 2b–c, 3d) and the compression material is very brittle, so the cuticle could not be prepared. Numerous obvious large red-brown megaspores are visible to the naked eye (Figs. 2d, 3e). They all measure approximately 2000 µm in diameter in their equatorial plane, with lesurae 50 µm long. The entire surfaces of the spores are smooth (Figs. 2e, 3f).

Comments: A second specimen, Pb. 707, also stored in the Hunterian Museum, Glasgow, is referred to this species, but

the locality and horizon information for this specimen is not known.

Discussion: The megaspores clearly fit within the parameters of the dispersed spore genus *Laevigatisporites* and are closest to the species *L. glabratus* (Zerndt) Potonié and Kremp, 1956. We agree with Karczewska (1967) that the spores described by Zerndt (1930) as Types 9 and 10 should be referred to *Laevigatisporites glabratus* as a result of Bochenski's (1936) description of the spores from his *Sigillariostrobus czarnockii*. Bochenski (1936) described the spores as 440 to 2700 µm in diameter, and underdeveloped spores which were triangular, thicker than the normal ones and with strongly marked lesurae. Zerndt (1932) agreed that Bochenski's finding of his megaspores of Types 9 and 10 (Zerndt, 1930) in the same cone was considerably important to the understanding of *Triletes glabratus* (now *Laevigatisporites glabratus*).

We also agree that there are no reliable grounds to distinguish such species as *Laevigatisporites primus* Wicher and *Laevigatisporites reinschi* Ibrahim, as has been done by Potonié and Kremp (1955). Erecting the species *Sporites primus*, Wicher (1934) assigned only the specific name to the spores, described by Bennie and Kidston (1886) and Zerndt (1930) as *Triletes* Type I Kidston. Wicher (1934) interpreted the species *Sporonites reinschi* Ibrahim to be identical to *Sporites primus*; he erected himself and – contrary to the law of priority – included *Sporonites reinschi* Ibrahim in the synonymy of *S. primus* Wicher. After the publication of Bochenski's work, it became clear that the spores of *Triletes* Type I Kidston (= *Sporonites reinschi* = *Sporites primus*) and *Triletes glabratus* Zerndt belong to the same species. *Triletes glabratus* Zerndt, 1930, is the oldest specific name and, therefore, has specific priority.

In situ spores identified as being identical to *Laevigatisporites glabratus* (Zerndt) Potonié and Kremp have been also described from four species of *Sigillariostrobus*. They are *S. tieghemi* Zeiller, 1884 (Schenk 1885, Zeiller 1888), *S. quadrangularis* (Lesquereux) White, 1903 (Wood, 1957), *S. czarnockii* Bochenski, 1936, and *S. leiosporous* Abbott, 1963. The features of these cones together with those of the British cones are summarised in Table 1.

Both *S. czarnockii* and *S. leiosporous* have sporophyll laminae with ciliate edges, which is a feature not observed in the cones from localities in Britain. *S. quadrangularis* has its sporophylls in whorls, which is a most unusual character for *Sigillariostrobus*. This again is different from the helical arrangement in the cones from localities in Britain. *S. tieghemi* is described as having downward-projecting heels at the distal end of the pedicel, a feature which is again not shown by the cones from localities in Britain. Although all these cones contain megaspores that would be included in the same dispersed spore species, *Laevigatisporites glabratus*, there are characters of the cones which lead us to the conclusion that they are all different in some respects. For that reason we ac-

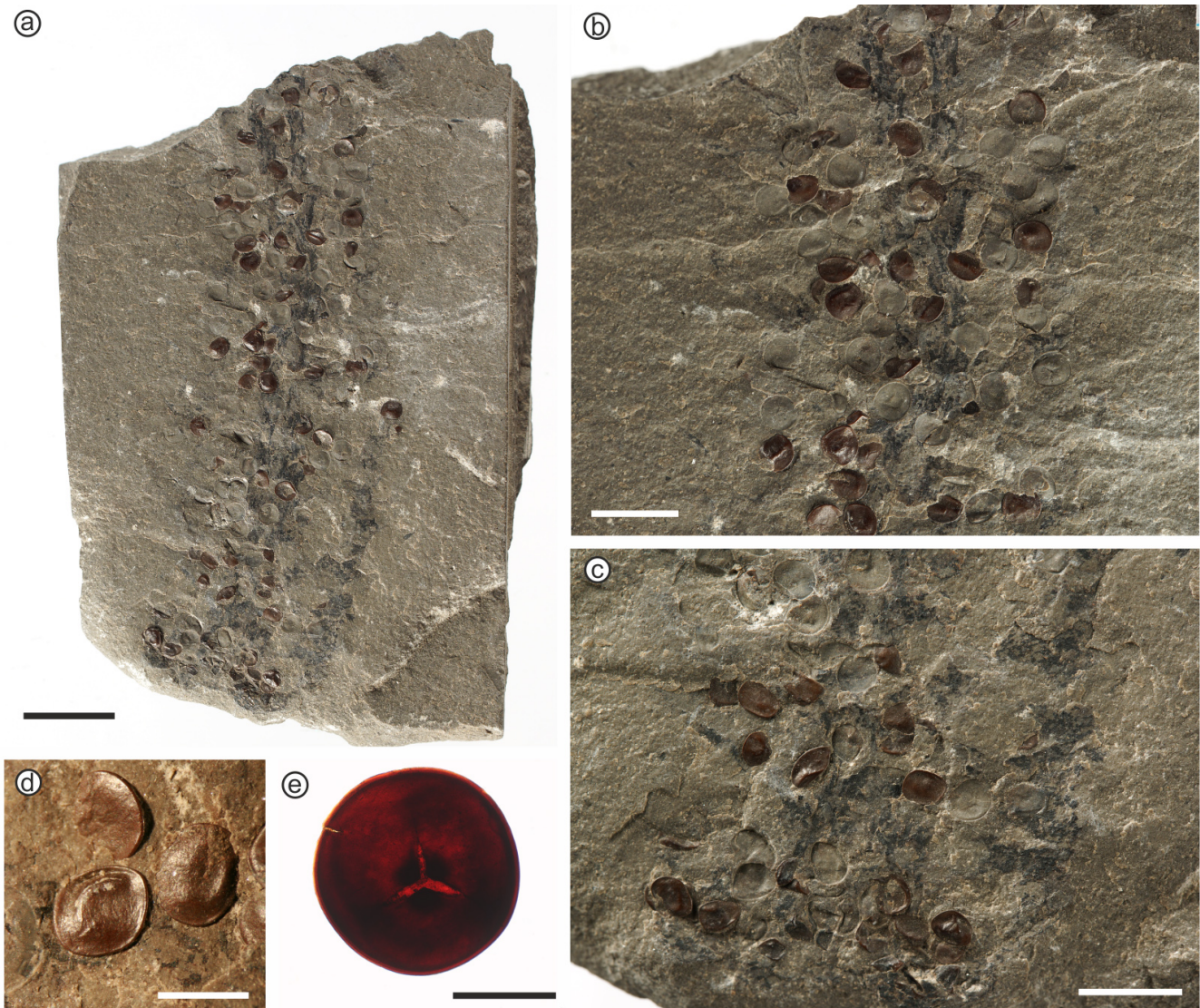


Figure 2. Type specimen of *Sigillariostrobus saltwellensis* sp. nov. Specimen Pb. 53-C.203, Hunterian Museum, Glasgow. Alluvial coal-bearing facies – upper Langsettian–Duckmantian. (a) Cone (scale bar 10 mm). (b) Detail of apical portion of the cone (scale bar 5 mm). (c) Detail of basal portion of the cone (scale bar 5 mm). (d) In situ glabrous megaspores (scale bar 2 mm). (e) Spore referable to *Laevigatisporites glabratus* macerated from the cone (scale bar 1000 µm).

cept them all as distinct species and therefore refer the British specimens to a new species.

The anatomically preserved monosporangiate *Mazocarpon* Benson, 1918 includes two species that contain spores referable to *Laevigatisporites glabratus*. They are *M. oedipterum* Schopf, from the McLeansboro Group, in Illinois (Schopf, 1941, late Pennsylvanian (Stephanian A)), and *M. bensonii* Pigg, from the Duquesne Coal, Conemaugh Group, Ohio (late Pennsylvanian (Stephanian B)). Pigg (1983) showed the two species to have sufficiently different anatomical features to be separated. Although it is almost certain that *Sigillariostrobus* and *Mazocarpon* represent the same type of sigillarian cone but are merely preserved

differently, we hesitate to include our *S. saltwellensis* within either of these two species because of the lack of anatomical evidence and their rather different ages.

***Sigillariostrobus barkeri* sp. nov**
(Figure 4)

Holotype: Specimen number 1971.I28 held in the Barker collection, Sheffield City Museum.

Type locality: Brierly Colliery, Yorkshire, Great Britain.

Type horizon: Shale above the Shafton Coal, top of the Similis-Pulchra Zone, Bolsovian.

Etymology: Named after the collection where the speci-

Table 1. Morphological comparison of *Sigillariostrobus* cones with in situ spores referable to *Laevigatisporites glabratus*.

	<i>S. tieghemi</i> Zeiller, 1884	<i>S. quadrangularis</i> (Lesquereux) White, 1903	<i>S. czarnockii</i> Bochen-ski, 1936	<i>S. leiosporous</i> Abbott, 1963	<i>Sigillariostrobus saltwellensis</i> sp. nov.
Cone size	160 mm long 25–50 mm broad	Up to 160 mm long, av- erage width 11.6 mm	ca. 180 mm long, 17– 25 mm broad	Up to 180 mm long, 20 mm broad	At least 86 mm long, 17–20 mm broad
Cone axis		1 mm	7–8 mm	4–7 mm	1.2 mm
Sporophyll arrangement	Alternating whorls with 8–10 per whorl	In whorls	Helical with sporo- phylls lying above one another	Alternating verticils of 4–5 sporophylls; 3–4 mm between verticils	Helical
Sporophyll shape	With prominent heel	Sporophyll laminae 9 mm long	Sporophylls 20–25 mm long; upper part sharply pointed with a hollowed-out deltoid shape, margin ciliate.	Pedicels: 5–7 mm long, 1 mm broad at attach- ment point, widening to 4 mm Laminae: broadly triangular, acuminate, 5–8 mm long, 4–6 mm broad, margin ciliate	Laminae ca. 6.5 mm long, spreading out- wards from cone
Sporangia	None observed	4 mm long, 5 mm high, 4 mm broad	4–7 mm long, breadth 2–4.5 mm; contain three tetrads of megaspores	4–5 mm long, 2 mm high, 4–4.5 mm wide; contains one tetrad of megaspores	7 mm long, 2.5 mm high
Peduncle	Acicular leaves or bracts attached to the upper portion	None observed	At least 40 mm long and 7–8 mm broad, uppermost 30 mm with long, triangular and pointed sterile leaves 25 mm long and 25 mm wide at the base	At least 65 mm long and 2–5 mm broad, covered with minute stiff spines up to 1 mm long	None observed
Age and locality	Age unknown, Valenciennes, France	Brazil Formation, Upper Pottsville, Duckmantian/ Bolsovian Indiana, USA	Duckmantian, Upper Silesian Basin, Poland	Upper Freeport (no. 7) Coal Allegheny, mid-Pennsylvanian, Bolsovian/Asturian, southeastern Ohio, USA	Upper Langsettian– Duckmantian

men had been deposited, the Barker collection held at the Sheffield Museum, Great Britain.

Diagnosis: Cone at least 13 mm in diameter without sporophyll laminae; axis 3 mm in diameter. Sporangia ca. 5.5 mm long and 2 mm high, megasporangiate. Megaspores trilete, probably originally plano-convex with greatest diameters of 1400–1800 µm in their equatorial planes. Lesurae one-third to one-half the spore radius, ca. 15 µm broad. Spore walls are about 20 µm thick, covered with numerous conical apiculi. Apiculi on distal walls ca. 10 µm high, varying in basal diameter and in numbers from 300 apiculi, 40–45 µm broad at the base, to 550 apiculi, 25–30 µm broad at the base. Apiculi on the contact faces are about 15 µm broad at the base and less than 5 µm high.

Description: The specimen is a fragment of a cone with lit-

tle remaining except the megaspores arranged in the positions they must have occupied in the sporangia (Fig. 4a–b). This is a single *Sigillariostrobus* cone 13 mm in diameter that lacks sporophyll laminae (Fig. 4a), with an axis 3 mm in diameter. The sporangial remains are ca. 5.5 mm long and 2 mm high, containing in situ spores, referable to the dispersed spore genus *Tuberculatisporites* (Ibrahim) Potonié and Kremp. Megaspores recovered from the specimen have a maximum diameter of 1400–1800 µm in their equatorial planes, with lesurae one-third to one-half of the spore radius, and are clearly trilete (Fig. 4c) and tuberculate (Fig. 4d). The spore walls are about 20 µm thick and are covered with numerous conical apiculi (Fig. 4d–e). The size and distribution of the apiculi vary over the surface of the megaspores, with the apiculi on the contact faces being smaller than those elsewhere on the surface. On the distal walls of the megaspores,

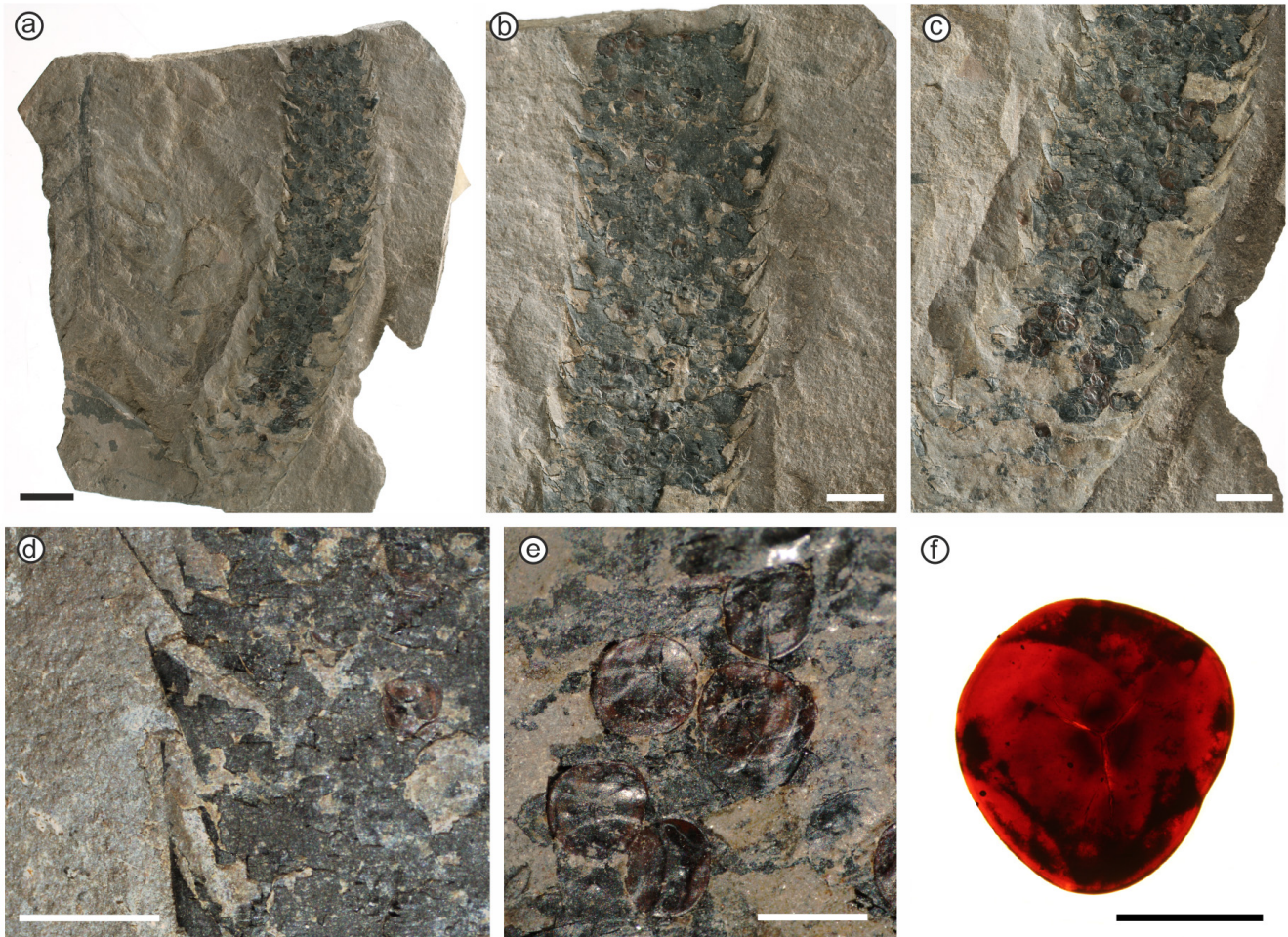


Figure 3. Second cone of *Sigillariostrobus saltwellensis* sp. nov. Specimen Pb. 707, Hunterian Museum, Glasgow. (a) The cone (scale bar 20 mm). (b) Detail of the upper part of the cone (scale bar 5 mm). (c) Detail of the mid-region of the cone, showing the megasporophyll impressions at the edge of the cone, often without the cuticle preserved (scale bar 5 mm). (d) Detail of (c), showing the megasporophylls with fissile compression and scattered megaspores (scale bar 5 mm). (e) Detail of (d), showing details of megaspores within the cone (scale bar 2 mm). (f) Megaspore referable to *Laevigatisporites glabratus* macerated from the spore mass shown in (e) (scale bar 2000 μm).

the apiculi are ca. 10 μm high, varying in basal diameter and in numbers from 300 apiculi, 40–45 μm broad at the base to 550 apiculi, 25–30 μm broad at the base. On the contact faces of the megaspores, the apiculi are about 15 μm broad at the base and less than 5 μm high.

Discussion: This *Sigillariostrobus* cone was originally described by Thomas (1980: Figs. 3–6). Although the megaspores were closely compared with *Tuberculatisporites brevispiculus* (Schopf) Potonié and Kremp, which was the first record of this spore, the cone was not given a specific name. Spores belonging to the genus *Tuberculatisporites*, like those referred to the smooth-walled *Laevigatisporites* (Zerndt) Potonié and Kremp (1954), have been recovered several times from sigillarian cones but from no others. Spores referable to *Tuberculatisporites mamillarius* have been previously described from *Sigillariostrobus rhombibracteatus* by Bochen-ski (1936), Chaloner (1953) and Wood (1957), but this is the

only record of in situ spores referable to *T. brevispiculus*. As explained above, *Tuberculatisporites brevispiculus* has been discussed many times in relation to its possible affinity with *T. mamillarius* (Bartlett) Potonié and Kremp (1955). We are following Spinner (1968), who kept them separate. As Thomas (1980) regarded the present cone as sigillarian and referred it to *Sigillariostrobus*, we now consider that it would be preferable to make it the basis of a new species.

The age of the new cone is also of some importance since Spinner (1968) gives the stratigraphical range of *T. brevispiculus* as generally Asturian and early Stephanian. In contrast, *T. mamillarius* and *Sigillariostrobus rhombibracteatus* have been only described from the Langsetian and Duckmantian. The present cone, in coming from the early Bolsovian, seems to fall between the two zones mentioned by Spinner (1968). Nevertheless, no real problem is posed by this new record as this extended stratigraphical

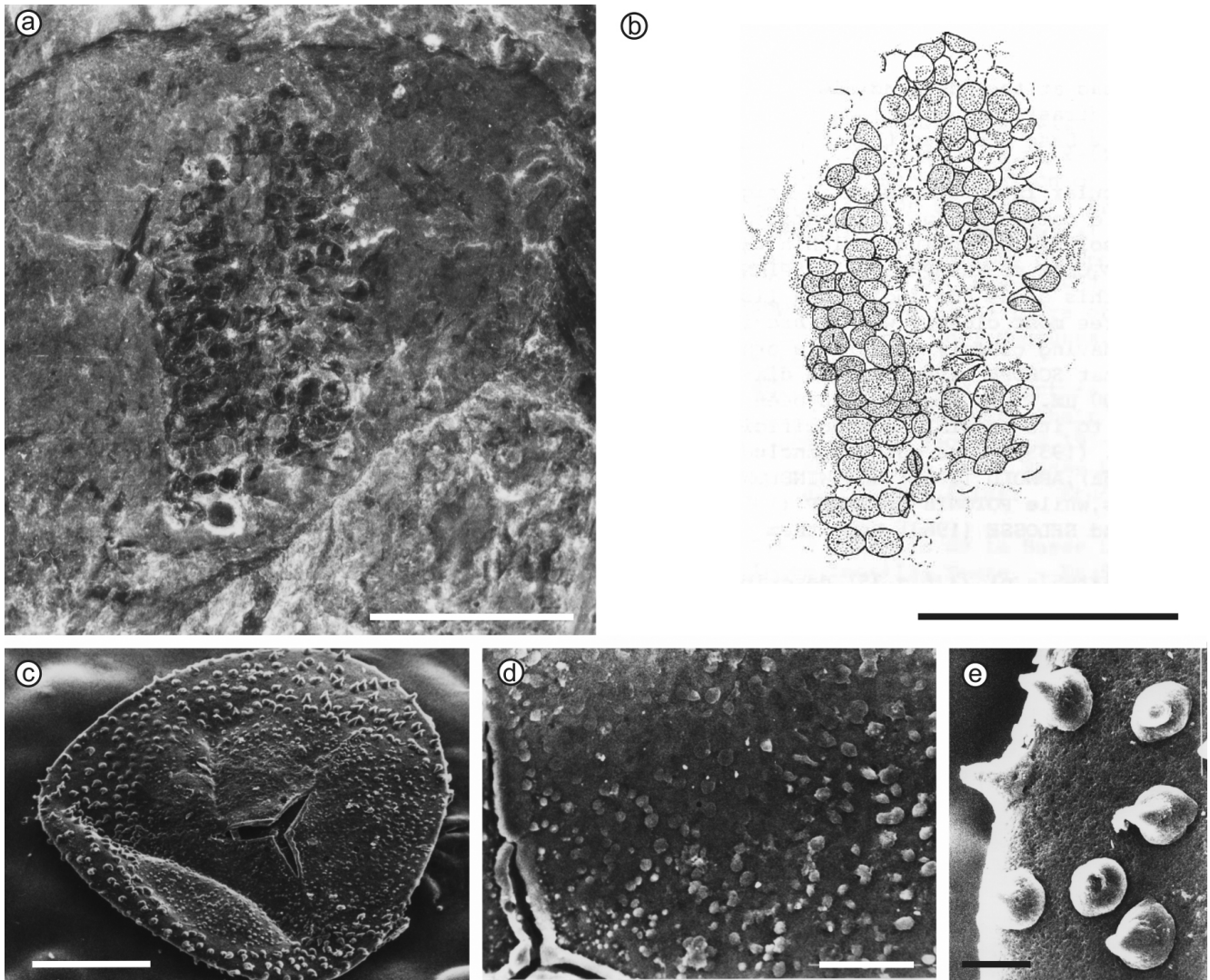


Figure 4. *Sigillariostrobus barkeri* sp. nov. No. 1971.I28, Barker collection, Sheffield City Museum, from the shales above the Shafton Coal, Brierly Colliery, Yorkshire (top of the Similis-Pulchra Zone, Bolsovian, Moscovian). (a) The remains of the cone showing the arrangement of the megaspores (scale bar 10 mm). (b) Camera lucida drawing of the cone in (a) (scale bar 10 mm). (c) Macerated in situ megaspore assigned to *Tuberculatisporites mamillarius* (Bartlett) Potonié and Kremp (scale bar 500 μ m). (d) Contact face of the in situ megaspore (scale bar 150 μ m). (e) Apiculi on the distal surface of the in situ megaspore (scale bar 10 μ m). Figure previously published by Thomas (1980).

range of *T. brevispiculus* still does not overlap with the range of *T. mamillarius*.

4 Conclusions

Despite the tendency of the sigillarian fructification *Sigillariostrobus* to fall apart, two cones of *Sigillariostrobus saltwellensis* sp. nov. are described from the British upper Langsetian–Duckmantian strata, containing spores referable to the dispersed spore species *Laevigatisporites glabratus*, and these have been compared to the four other *Sigillariostrobus* cones that contain *L. glabratus* spores. This is also

the first *Sigillariostrobus* cone species described containing *L. glabratus* spores from localities in Great Britain.

Sigillariostrobus barkeri sp. nov. of Bolsovian age is given to the previously described but unnamed cone with in situ spores referable to *T. brevispiculus*. This is the first cone with this megaspore species in situ, and thus shows that *T. brevispiculus* and *T. mamillarius* are not conspecific.

Author contributions. B. A. Thomas and L. J. Seyfullah prepared the specimens, made the descriptions and comparisons, and prepared the manuscript together.

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