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A reassessment of the leafy shoots of Pennsylvanian-age arborescent lycopods

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ABSTRACT

The known fossil-species of upper Carboniferous (Pennsylvanian) arborescent lycopod leafy shoots are re-examined. The leaf characters used in species characterisation include size (length and breadth), angle of departure from the stems and the overall shape (straight, curved or S-shaped). Sometimes leafy shoots can be directly related to known species of stems that are defined on their surface features of leaf cushions as in *Lepidodendron*, *Lepidophloios* and *Ulodendron*, or directly on the stem surface as in *Bothrodendron*. They are also assessed in terms of the determinate growth pattern of the plants. A key is given to identify the fossil-species of leafy shoots described here.

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Lepidodendron;
Lepidophloios;
Bothrodendron; *Ulodendron*;
Pennsylvanian

Introduction

Arborescent lycopods were among the most abundant plants of the Palaeozoic coal swamps (Figure 1) having spread over large areas of tropical land during the late Mississippian (Serpukhovian) to Cisuralian (early Permian), and were ecological keystone taxa of this important biome (DiMichele and Phillips 1995). A combination of this abundance and a favourable taphonomic setting has meant that adpressions of these plants are widespread in rocks of this age. However, because they shed organs during life and were disarticulated during the fossilisation process, different parts of the plant are assigned to different fossil-taxa (Cleal and Thomas 2010, 2021). This has sometimes caused confusion, especially when the fossil record of these plants is being used for diversity, palaeoecological or floristic studies (as discussed by Cleal et al. 2021).



Particularly difficult has been the taxonomy of their leafy shoots. The stems are normally classified using features of the leaf cushions, but in the shoots, these cushions tend to be obscured by the leaf laminae (Figure 2). There have been a number of earlier taxonomic accounts of these leafy shoots (Fischer 1904; Němejc 1947; Crookall 1964; Chaloner 1967) but there has been little consensus as to how many taxa can be recognised and how to determine the variability within them. It is, therefore, time to reappraise the taxonomy of these fossils, and present here a revised classification and an identification key based on characters that should allow them to be reliably and consistently recorded.

Growth and taphonomy

Palaeozoic arborescent lycopods had a main vertical trunk borne on a stigmarian rhizomorph base that provided a platform to facilitate growth in unstable, swampy substrates (Thomas and Seyfullah 2015a; DiMichele et al. 2022). The trunk, which was at least partly covered by elongate linear leaves (named *Cyperites* Lindley and Hutton 1831-1831b), could be at least 35 m tall (Thomas and Watson 1976; Thomas 1978).

Some of these lycopods retained the elongate leaves on their stem throughout their life (Thomas 1967b) and occasionally the lower part of the trunk has been found with leaves still attached (e.g. Thomas 1970; Leary and Thomas 1989). In most fossils of such stems, however, the leaves are no longer present because they have dried and withered (Thomas 1978; Thomas and Meyen 1984a, 1984b) leaving a mark on the cushion where the leaf blade entered the matrix of the counterpart called a false leaf scar (Chaloner 1967).

In most Pennsylvanian species, however, the leaves were actively abscised as the trunk grew (Thomas and Cleal 1999) leaving the swollen clasping bases of the leaves (leaf cushions), each with a scar where the leaf lamina had been detached. A real leaf scar resulting from leaf abscission can be distinguished from a false scar by the presence of three foliar prints marking where the vascular trace and two parichnos entered the leaf, and a different surface-cellular arrangement to that on the surrounding leaf cushion (Thomas 1978; Thomas and Cleal 1999). The leaf cushions remained photosynthetic and so were presumably green (Thomas 1966, 1974; Thomas and Cleal 2018). With further growth of the plant, however, the outer tissue

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Figure 1. Reconstruction of arborescent lycopsids of the Pennsylvanian-age palaeotropical coal swamps of Euramerica. Artist Annette Townsend.

of the trunk with the leaf cushions was also sloughed off exposing the underlying non-photosynthetic periderm (remains of the stems where the outer tissue has been shed are referred to the fossil-genus *Knorria* Sternberg 1825). Sloughed-off portions of the outer tissue with the characteristic leaf cushions are the most abundant remains of these stems.

The anatomy of the trunk (Walton 1935; Andrews and Murdy 1958; Eggert 1961) and the exponential relationship between stem diameter and leaf length (Chaloner and Meyer-Berthaud, 1983) indicates these plants had determinate growth. On reaching maturity the plants produced sporangia, which could either be attached singly to the trunk (e.g. *Omphalophloios* White 1898 – Bek et al. 2015; Wagner and Álvarez-Vázquez 2015) or borne in strobili. The strobili of *Sigillaria*-plants were attached laterally to the trunk but in most other genera they were borne terminally on slender leafy shoots that formed a crown at the top of the plant (e.g. Opluštil 2010). These shoots are the subject of this paper.

Taxonomic and nomenclatural background

Stem adpressions of the plants that produced the leafy shoots are assigned to the fossil-genera *Lepidodendron* Sternberg 1820, *Lepidophloios* Sternberg 1825, *Sublepidophloios* Sterzel 1907, *Ulodendron* Lindley and Hutton 1831 and *Bothrodendron* Lindley and Hutton 1833a mainly on leaf cushion features (Figure 3). However, Kidston (1886) showed that the species taxonomy of these stem adpressions can be extremely difficult because of the variation in cushion size and shape. Kidston believed that the smaller and larger cushions were from the young and older stems, but we now know that this variation in size was an expression of the position of the cushions on the plant (Eggert 1961).

There are about 20 named species of leafy lycopod shoots, which is far fewer than the several hundred stem species, so there must be other species of leafy shoots waiting to be identified. There is also the problem of how to relate the leafy shoots to the larger leaf cushion-bearing stems because there are only a few examples known where continuity has been

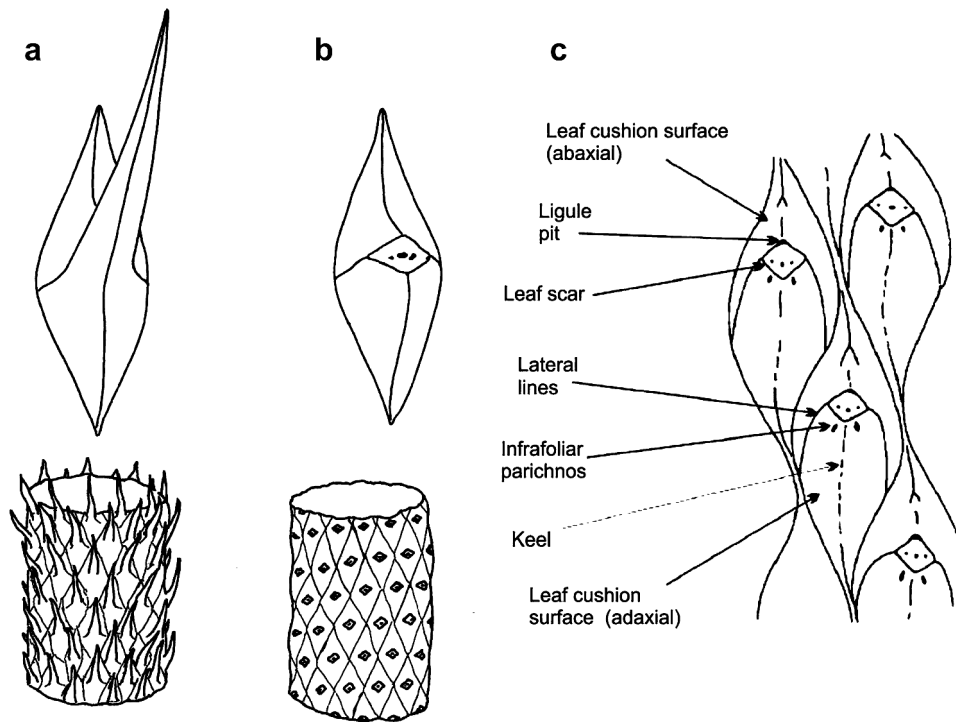


Figure 2. *Lepidodendron* stems. (a) Stems with leaves still attached; (b) Stems showing scars after leaves have been abscised; (c) Main characters of leaf cushions and scars used to identify stems. Adapted from Cleal and Thomas (1994, 2019), based on drawings by D. Spillards.

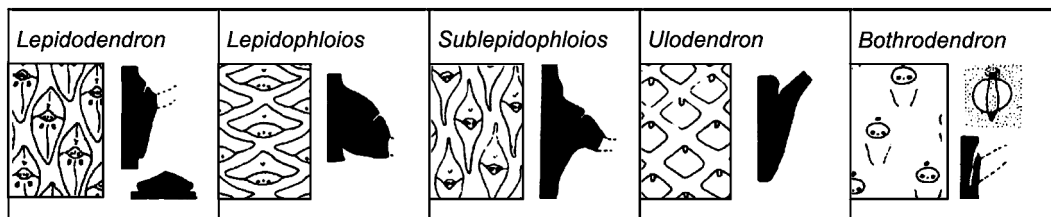


Figure 3. Main fossil-genera of stems recognised in the Pennsylvanian arborescent lycopods. Adapted from Cleal and Thomas (1994, 2019).

demonstrated between the two (e.g. Němejč 1947; Chaloner and Meyer-Berthaud 1983; Thomas et al. 2010; Opluštil 2010).

We have not attempted a detailed analysis of the distribution of the fossil-species of lycopod leafy shoots. Rather, we have tried to develop the basis of a taxonomy that will allow these fossils to be accurately documented. Where we have included stratigraphic details of species, it has been where we are confident about the records (including of the relevant nomenclatural types), but this should in no way be regarded as a comprehensive documentation of their distribution.

Descriptions of species

These descriptions deal mainly with the morphological features. Epidermal features preserved on cuticles are discussed by Thomas (1966, 1967a, 1967b, 1968,

1970, 1974, 1977). Where possible, we have illustrated photographs of the relevant type specimens and, in some cases also the original published figure.

Genus: *Lepidodendron* Sternberg 1820

Remarks

This generic name was originally given to remains of stems covered with leaf cushions, each with an abscission scar, but it has also been used for the leafy shoots that formed the crown of the plants. Brongniart (1822, p. 209) referred any fossil shoots bearing simple, linear leaves arranged helically or in two rows to the genus *Lycopodites*. This was based on the earlier but invalidly published *Lycopodiolithes* Schlotheim 1820, but which Brongniart re-spelled to avoid the implication that the genus only included lycopod shoots; using a similar

logic Sternberg (1825) subsequently further changed the spelling to *Lycopodiolites*. Brongniart divided *Lycopodites* into four informal sections, the first of which included shoots produced by plants with *Sagenaria* Brongniart 1822 (\equiv *Lepidodendron* Sternberg) stems. However, he also specifically stated that the most typical species of *Lycopodites* were those in the second of the sections (*Lycopodites taxiformis* Brongniart 1822, *Lycopodites piniformis* Schlotheim ex Brongniart 1822) which are now regarded as coniferous shoots (Florin 1938–1945). Because of this confusion, the generic name has now been formally conserved as *Lycopodites* Lindley and Hutton 1833b and is restricted to the remains of herbaceous lycopods (Pal and Gosh 1990).

Álvarez-Vázquez and Wagner (2014) and Álvarez-Vásquez et al. (2018) also suggested that the leafy shoots and shoots lacking true leaf scars should be assigned to a different fossil-genus, which they called *Bergeria* Sternberg 1838. As pointed out by Thomas and Cleal (2020), however, the lectotype species of *Bergeria* (*B. acuta* Presl in Sternberg 1838 – designated by Andrews 1955) has leaf cushions very similar in shape to *Lepidodendron* except that they lack true leaf scars. It is known that *Lepidodendron* stems with rhomboidal cushions retained their leaves for much of their life (e.g. Thomas 1978; Leary and Thomas 1989), only shedding them when the terminal crown was produced. Most adpressions of *Lepidodendron* represent portions of the periderm that had been sloughed-off from the trunk and after the leaves had

been abscised producing true leaf scars. It seems likely, therefore, that the leafy shoots that have been assigned to *Bergeria* are merely the more distal parts of a *Lepidodendron* branching system where the leaves have not been abscised. Whilst different biological species may have had different proportions of the stem that abscised their leaves, possibly related to the stature of the species (species that grew larger may have sloughed-off more periderm and so produced more adpressions of leaf cushions with true leaf scars), there seems to be no sharp delineation between those leaf cushions that would be assigned to *Bergeria* and those that would be assigned to *Lepidodendron*. The distinction is, therefore, of doubtful taxonomic merit at least at the rank of genus (Thomas et al. 2019; Thomas and Cleal 2020; DiMichele and Bateman 2020).

Lepidodendron dawsonii Bell 1838

Fig. 4A

1938 *Lepidodendron dawsonii* Bell, p. 94, pl. 98, fig. 12; pl. 99, figs 1–4.

1980 *Lepidodendron dawsonii* Bell; Zodrow and McCandlish, p. 80, pl. 119.

Holotype

Geological Survey of Canada, Ottawa, Specimen No. 3250 (Bell 1938, pl. 99, fig. 3); Provenance, Dominion No. 16 Colliery, Sydney Coalfield (Cape Breton, Canada); roof of the Phalen Seam, Morien Group (Asturian).

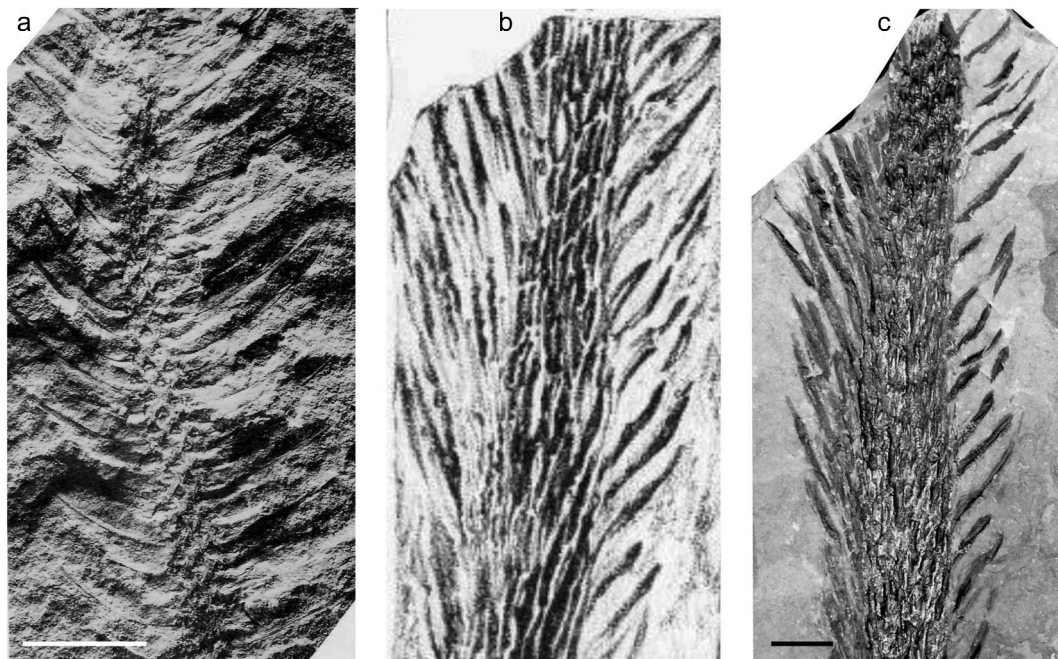


Figure 4. (a) *Lepidodendron dawsonii* Bell, Geological Survey of Canada, Specimen 3250 (holotype), Dominion No. 16 Colliery, Sydney Coalfield (Cape Breton, Canada); roof of the Phalen Seam, Morien Group (Asturian); original illustration by Bell (1938, pl. 99, fig. 4). (b, c), *Lepidodendron pictoense* Dawson, Redpath Museum, McGill University, Specimen 3478 (lectotype); Sydney Coalfield, Nova Scotia (Canada); Morien Group (Asturian). (b), Original illustration by Dawson (1866, fig. 37a). (c), Photograph of specimen (reproduced with permission of the Redpath Museum, McGill University).

Description

Leaf cushions of low relief, 4–5 times longer than wide, with leaf scars just above the middle of the cushion and up to $\frac{3}{4}$ its width. Leafy shoots, 3–30 mm wide with acutely pointed leaves up to 17 mm long and 0.75 mm wide, departing from the leaf cushions at right angles before obliquely arching upwards.

Remarks

This species is mainly known from leafy shoots and slender stems up to ca. 10 mm wide with leaf cushions. The most detailed discussion of this species since the publication of the protologue has been by Zoderow et al. (2012), who included details of the cuticles. The only other species with leaves attached at right angles to the cushion is *L. ophiurus* Brongniart, but the latter has more curved leaves that become approximately parallel to the shoot in their distal parts.

Occurrence

This species has so far only been recorded from the Morien Group (between Emery and Point Aconi seams – Asturian) of the Sydney Coalfield, Nova Scotia, Canada.

Lepidodendron dilatatum Lindley and Hutton

1831

Fig. 5

- 1831 *Lepidodendron dilatatum* Lindley and Hutton, pl. 7 fig. 2.
 1838 *Bergeria acuta* Presl in Sternberg, pl. 48, figs 1a, b.
 1848 *Lycopodites dilatatus* (Lindley and Hutton) Göppert ex Bronn, p. 681.
 1854 *Lepidodendron haidingeri* Ettingshausen, p. 55, pls, 22, 23.
 1854 *Lepidodendron vestitum* Lesquereux, p. 428.
 1858 *Lepidodendron vestitum* Lesquereux, p. 874, pl. 16, fig. 3.
 1880 *Lepidodendron scutatatum* Lesquereux, p. 369 (1879, pl. 63, figs 6–6c).
 1880 *Lepidodendron lanceolatum* Lesquereux, p. 369 (1879, pl. 63, figs 3–5).
 1911 *Lepidodendron acutum* (Presl in Sternberg) Kidston, p. 146.
 1947 *Lepidodendron simile* Kidston; Němejc (non Kidston), p. 68, pl. 1, figs 1–3, 9, 10.
 2014 *Bergeria dilatata* (Lindley and Hutton) Álvarez-Vázquez and Wagner, p. 201, figs. 13, 14a–h, 16g–h.
 2018 *Bergeria dilatatum* (Lindley and Hutton) Álvarez-Vázquez et al., p. 10, figs. 2–10b.

Holotype

Great North Museum, Newcastle-upon-Tyne, Hutton Collection, Specimen No. NEWHM G02.16; Provenance, Felling Colliery, Gateshead, Tyne and

Wear (UK); roof of the Low Main Seam (Duckmantian). Figured photographically here in Figure 5b (see also Álvarez-Vázquez et al. 2018, fig. 2).

Description

Leafy stems with elongated cushions with acute upper angles, blunt pointed bases and gently rounded sides. The laminae depart at less than 45° to the stem axis and are broader than 3 mm at the base; the leaves are S-shaped at their base and then curve upwards, up to 20–70 mm long.

Remarks

Álvarez-Vázquez and Wagner (2014) and Álvarez-Vázquez et al. (2018) have provided a detailed taxonomic treatment of this species (under the name *Bergeria dilatatum*). They in particular documented a range of well-preserved leafy shoots from Canada and Spain, which provide an excellent overview of the variation within the species. However, in our view, their synonymy has tended to lump together too wide a range of shoots, which using the classification suggested here would be assigned to various other fossil-species, notably *Lepidodendron lycopodioides*, *Lepidodendron ophiurus*, *Ulodendron majus* and *Ulodendron landsburgii*. Reasons for this are given under the remarks on those species.

Němejc (1947) described and figured examples of this species as *Lepidodendron simile* Kidston (see also Opluštil et al. 2009b, pl. 1) but the status of that name is doubtful. It was first used as a *nomen nudum* in Jongmans (1909). Kidston (1911) subsequently provided an ambiguous diagnosis, merely stating that it differed from *L. lycopodioides*. Although no type was illustrated or described, Kidston made specific reference to the specimens figured by Brongniart (1837, pl. 14) as *Lepidodendron elegans* Sternberg. The Brongniart (1837, p. 47) text for *L. elegans* provided what might be regarded as a validating diagnosis (“... un autre rameau qui porte des feuilles implantées presque perpendiculairement sur l’axe, coudées et renflées toutes à la même distance de cet axe”) but both this description and the specimens illustrated by Brongniart differ from *L. simile* as interpreted and illustrated by Němejc (1947); the latter consists of shoots with S-shaped leaves and compares closely with the type of *L. dilatatum*. In view of this ambiguity as to its type, diagnosis and circumscription, we regard *L. simile* as a taxonomically unusable name.

Němejc (1947) compared his “*L. simile*” with the types of *L. acutum* (\equiv *Bergeria acuta*), the only difference being that the leaf cushions of the latter were larger and lacked attached leaves. Němejc (1947) also pointed out that *Lepidodendron haidingeri*

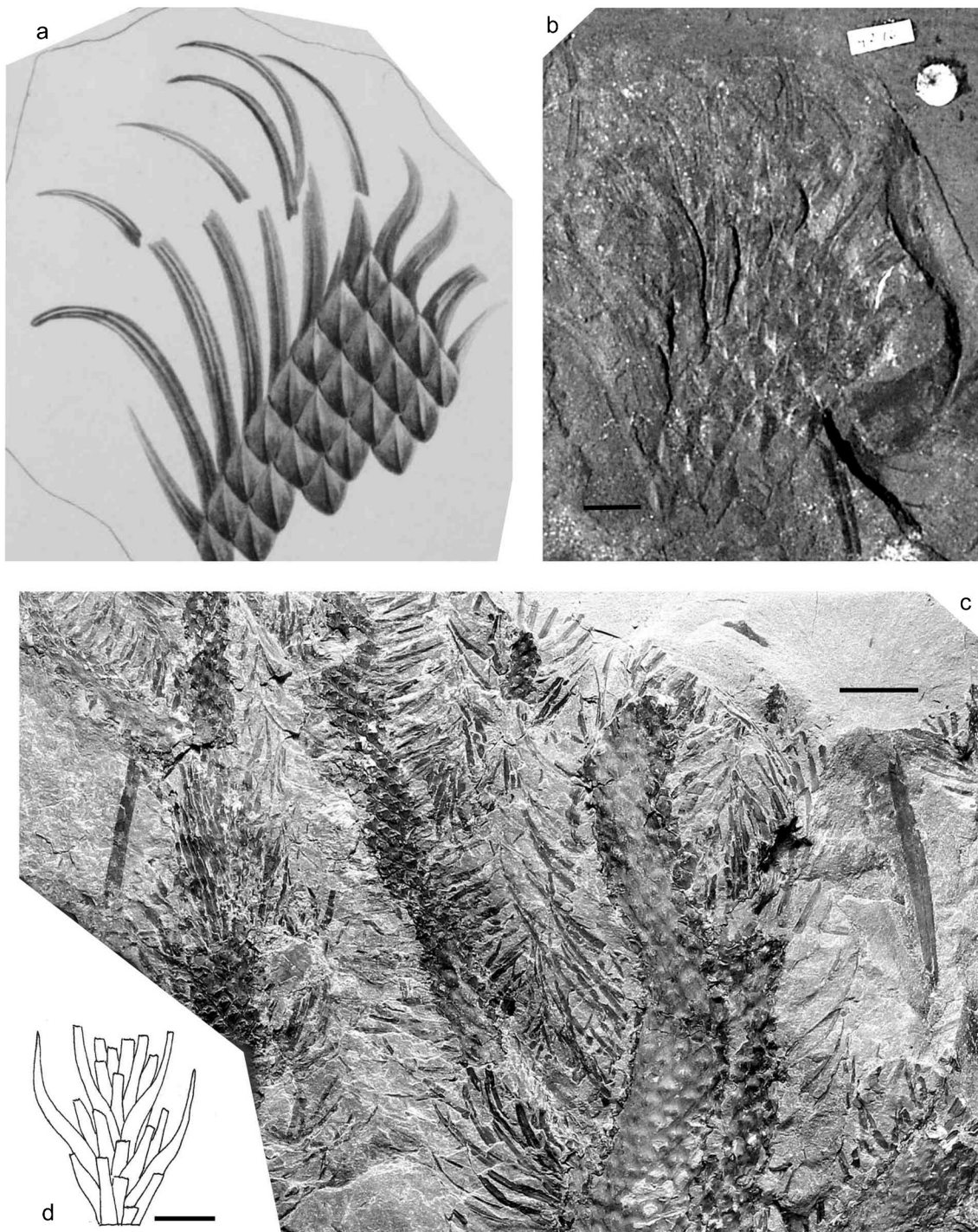


Figure 5. *Lepidodendron dilatatum* Lindley and Hutton. (a, b), Great North Museum, Specimen No. NEWHM G02.16 (holotype); Felling Colliery, Gateshead, Tyne and Wear (UK); roof of the L Main Seam (Duckmantian); (a), original illustration given with protologue (Lindley and Hutton 1831); (b), photograph, by Sylvia Humphrey. (c), National Museum Wales, Specimen NMW Appleton BB0076A; Brymbo Opencast near Wrexham, Denbigh Coalfield, north Wales, UK; Middle Coal Measures (Duckmantian) (photo by P. Appleton). (d), Drawing of leafy shoot by Deborah Spillards (from Cleal and Thomas, 1994). All scale bars = 10 mm.

Ettingshausen, 1854 seems to be intermediate between the two species: it has smaller but very similar-shaped leaf cushions to *L. acutum*, and leaves that are very similar in shape but a little smaller to those of *L. dilatatum*. Although Nĕmejc (1947) did not combine these species, we suggest that *L. acutum*,

L. haidingeri and *L. dilatatum* (i.e. Nĕmejc's *L. simile*) represent progressively more distal branches from the same biological species.

Nĕmejc (1947) regarded his "*L. simile*" as conspecific with upper Mississippian leafy shoots from northern France figured by Bureau (1913, pl. 30

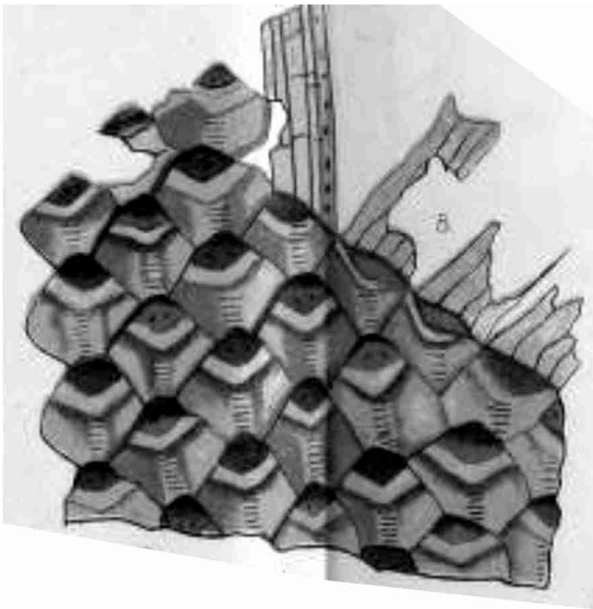


Figure 6. *Lepidodendron latifolium* Lesquereux; Botanical Museum, Harvard University, Specimen No. HU8200; Oliphant coal mines, Pennsylvania (USA); stratigraphical horizon not recorded; original illustration given with protologue (Lesquereux, 1880).

bis, fig. 11; pls 32–34) as *Lepidodendron lycopodioides* Sternberg. However, these shoots have more linear leaves attached at a more acute angle especially in the slightly wider stems (Strullu-Derrien et al. 2021). We have yet to see any shoots older than Pennsylvanian that could be assigned to *L. dilatatum*.

Thomas et al. (2019) synonymised *L. dilatatum* with *Lepidodendron vestitum* Lesquereux, *Lepidodendron scutatum* Lesquereux, and *Lepidodendron lanceolatum* Lesquereux. Kidston (1891) referred *L. dilatatum* to *Lepidodendron ophiurus* (Brongniart) Brongniart, 1828 but Crookall (1964) argued that the leaf cushions of the former are much larger. The *L. ophiurus* leaves are also attached at a more acute angle to the cushions than in *L. dilatatum*.

Occurrence

L. dilatatum is one of the commonest species of leafy lycopod shoots having been recorded (often as *L. acutum*) from all the major Euramerican coalfields and from the Langsettian to the Asturian (Crookall 1964; Thomas 2007; Thomas and Tenchov 2004; Álvarez-Vásquez and Wagner 2014). The type of *L. acutum* was from Nýřany Member (Asturian) of Bohemia, Czech Republic, and the type of *L. haidingeri* was from the Radnice Member (upper Duckmantian) of the same coal-basin. In Pennsylvania it is reported from Brown's Colliery, Pittston; Archibald Mine B & C vein, Wilkes-Barre (Asturian); and

Wanamie, near Wilkes-Barre (Thomas et al. 2019); also from the Northern Anthracite Basin (Asturian) as *L. lanceolatum* (Olesksyshyn 1982).

Lepidodendron latifolium Lesquereux 1880 Fig. 6

1880 *Lepidodendron latifolium* Lesquereux, p. 370 (1879, pl. 63, figs 7, 8).

Holotype

Botanical Museum, Harvard University, Cambridge MA (USA), Specimen No. HU8200 (Figure 6; Lendemer 2002); Provenance, coal mines at Oliphant, Pennsylvania (USA); stratigraphical horizon not recorded. We have been unable to obtain a photographic image of the specimen and so we have reproduced the original illustration given with the protologue.

Description

Stems with clearly marked, vaulted, isodiametric-rhomboidal leaf cushions, with a prominent leaf scar in the upper part and transverse wrinkles in the lower part. When attached, long leaves are at least 7 mm broad.

Remarks

There are few records of this extremely rare but distinctive species; other than the protologue, it has only been documented by Noé (1925, pl. 7, fig. 4; pl. 8, fig. 3) and Gastaldo (1977, fig. 5) (there were also equivocal records from Indiana by Canright, 1959 and Wood, 1968). Although based on only limited characters, we know of no other species that it could be synonymised with. In terms of leaf length, a close comparison can be made with *L. longifolium*, but the leaves are much broader on *L. latifolium*.

A single specimen from the Ruhr Coalfield figured by von Röhl (1868, pl. 11, fig. 2) as *Lepidodendron dichotomum* Sternberg has similar large leaves and isodiametric-rhomboidal leaf cushions.

Occurrence

This species is mainly known from Oliphant, Pennsylvania (USA) and from Mazon Creek and the Herrin (No. 6) Coal at Carterville, Illinois (USA). There is also a possible record from the Ruhr Coalfield (Germany),

Lepidodendron longifolium Brongniart ex Lindley and Hutton 1835 Fig. 7

1820 *Lepidodendron dichotomum*, var., Sternberg, pl.3.
1828 *Lepidodendron longifolium* Brongniart, p. 85 (nom. illegit.).

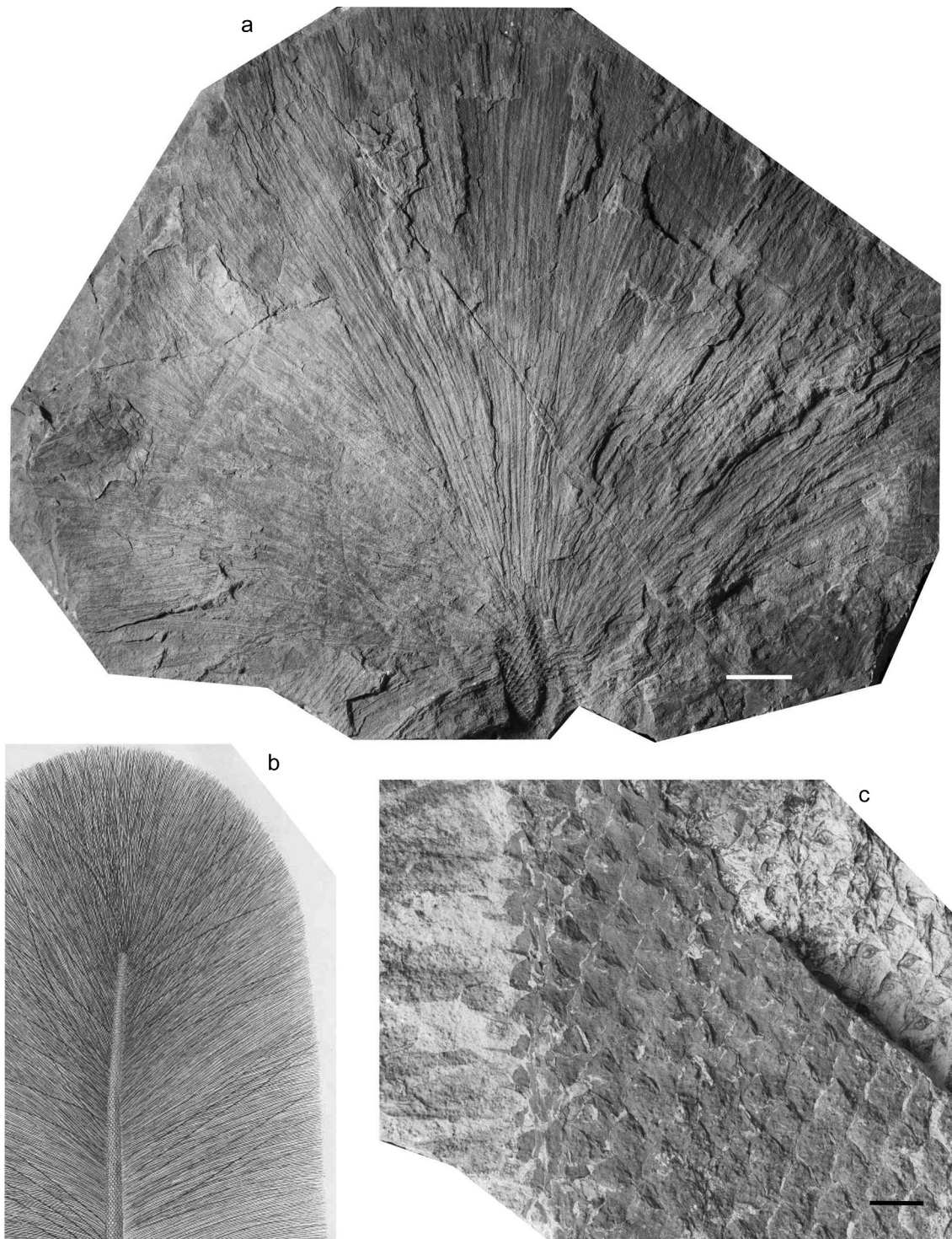


Figure 7. *Lepidodendron longifolium* Brongniart ex Lindley and Hutton, Národní muzeum (Prague); all specimens from Whetstone Horizon (Duckmantian). (a), Specimen E 7647 (holotype); Svinná, Czech Republic (photo by Lenka Váňová); scale bar = 30 mm. (b), Illustration of the holotype from Sternberg (1820). (c) 1820, close-up of wider stem showing leaf cushions and attached leaves; Chomle, Czech Republic (photo by S. Opluštil; figured by Němejč, 1934, pl. 2, fig. 3); scale bar = 10 mm.

1835 *Lepidodendron longifolium* Brongniart ex Lindley and Hutton, p. 37, pl. 161.

1848 *Lycopodites longifolius* (Brongniart) Göppert in Bronn, p. 682.

1870 *Lepidodendron morrisianum* Lesquereux, p. 430, pl. 22, figs 1, 2.

1880 *Lepidodendron morrisianum* Lesquereux; Lesquereux, p. 370.

1880 *Lepidodendron longifolium* Brongniart; Lesquereux, p. 373.

1894 *Lepidodendron longifolium* Brongniart; Kidston, p. 599, pl. 1, fig. 1.

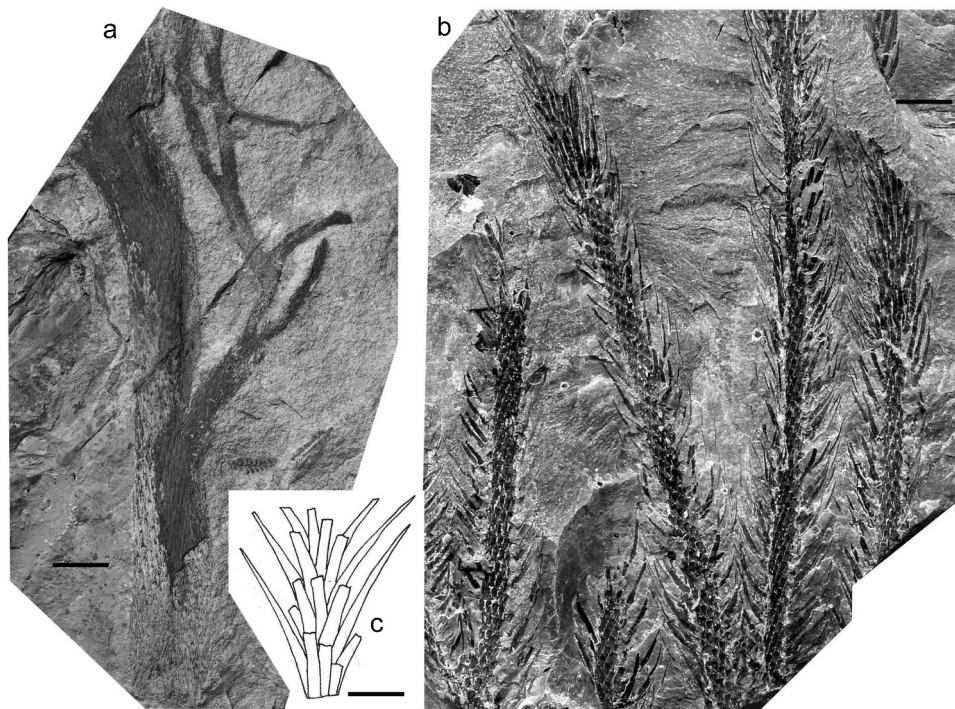


Figure 8. *Lepidodendron lycopodioides* Sternberg. (a), Národní muzeum (Prague), Specimen E 4743 (lectotype); Svinná, Czech Republic; Whetstone Horizon (Duckmantian) (photo by Lenka Váchová). (b), National Museum Wales, Specimen NMW 2013.43 G.108; Brymbo Opencast near Wrexham, Denbigh Coalfield, north Wales, UK (photo by P. Appleton); Middle Coal Measures (Duckmantian). (c), Drawing of leafy shoot by Deborah Spillards (from Cleal and Thomas, 1994). All scale bars = 10 mm.

1947 *Lepidodendron longifolium* Brongniart; Němejc, p. 55.

Holotype

Brongniart (1828) renamed one of the syntypes of *L. dichotomum* Sternberg as a new species, *L. longifolium* (Figure 7). The specimen was recorded as originating from Svinná (West and Central Bohemia Coalfield, Czech Republic), presumably from the upper Duckmantian Whetstone Horizon ash band in the Radnice Coal Seam, lower Kladno Formation.

Description

The leaves in *L. longifolium* are extremely narrow and very long, reaching c. 500 mm in length. Leaf cushions fusiform with a distinct median keel.

Remarks

Although Brongniart (1828, p. 85) first used this species epithet he failed to provide a diagnosis. The earliest legitimate use was by Lindley and Hutton (1835) who made a direct reference to Brongniart (1828 – and so also to the Sternberg type) and provided a diagnosis, albeit rather brief. Unger (1850) doubted the validity of *L. longifolium* and included it in his “Species dubius nudum descriptae”, but Kidston (1894) and Jongmans (1929) accepted it as a distinct species; Kidston also figured two specimens of his own from South Wales. The main distinguishing character

is that the leaves are extremely narrow and very long, reaching 380 mm in Lindley and Hutton’s specimen and 500 mm in Sternberg’s specimen.

The most extensive recent treatment of the species has been by Opluštil et al. (2007, 2009a, 2014, 2016) and Libertín et al. (2009) based on newly collected material from the Whetstone Horizon ash band in the West and Central Bohemia Coalfield, including some stems with the distinctive, long leaves still attached. They found that the leaf cushions lacked infrafoliar parichnos and bore strobili with *Cappasporites* microspores, and may have been produced by relatively small arborescent lycopods only some 4 m tall.

Lesquereux (1866) based *Lepidodendron morrisianum* on a single specimen with indistinct leaf cushions, and leaves at least 300 mm long and 5½ mm broad with a central vein. On the length of the leaves and the lack of other distinguishing features, it is included here as a synonym of *L. longifolium*.

Occurrence

Svinná, Štílec and Ovčín, West and Central Bohemia Coalfield (Czech Republic), upper Duckmantian Radnice Coal Seam, lower Kladno Formation; Brown colliery, E Vein, Pittston, Pennsylvania (USA) (Lesquereux 1880); Ebbw Vale, Rhondda Cynon Taff, Wales (UK), South Wales Coal Measures Group (Langsettian to lower Bolsovian).

Lepidodendron lycopodioides Sternberg 1821**Fig. 8**

- 1821 *Lepidodendron lycopodioides* Sternberg, p. 26, pl. 16, fig. 2.
 1825 *Lycopodiolithes elegans* Sternberg, p. viii (homotypic synonym).
 1828 *Lepidodendron elegans* (Sternberg) Brongniart, p. 85.
 1831 *Lepidodendron sternbergi* Brongniart; Lindley and Hutton (non Brongniart), p. 15, pl. 4.
 1834 *Lepidodendron elegans* Brongniart; Lindley and Hutton, p. 99, pl. 118.
 1837 *Lepidodendron elegans* (Sternberg) Brongniart; Brongniart, pl. 14.
 1848 *Lycopodites elegans* (Sternberg) Göppert in Bronn, p. 681.
 1880 *Lepidodendron lycopodioides* Sternberg; Zeiller, p. 111 (Zeiller 1878, pl. 171; refigured Zeiller 1886, pl. 70).
 1947 “*Lepidodendron*” *selaginoides* Sternberg; Němejč (non Sternberg), pl. 2, fig. 6; pl. 3, fig. 2.
 1959 *Sublepidodendron lycopodioides* (Sternberg) Remy and Remy, p. 100; fig. 79.
 2007 *Lepidodendron lycopodioides* Sternberg; Opluštil et al., pl. 5, fig. 9.
 2009 *Lepidodendron lycopodioides* Sternberg; Opluštil et al., fig. 7A, B.
 2021 *Lepidodendron lycopodioides* Sternberg; Kvaček et al., p. 98, pl. 32.

Lectotype (designated here):

Národní muzeum (Prague), Specimen No. E 4743 (Figure 8a; photographically refigured by Němejč 1947, pl. 2, fig. 6, pl. 3, fig. 2; Kvaček et al. 2021, pl. 32); Provenance, Svinná, Bohemia (Czech Republic); Whetstone Horizon ash bed (upper Duckmantian). This is the only one of Sternberg’s syntypes of this species that can now be located (Kvaček et al. 2021).

Description

Long, slender leafy shoots with narrow leaves that are closely arranged on the stem. Individual leaves are 5–7 mm long, and 1 mm broad, narrowly lanceolate and gradually acuminate. The leaves open out, then incurve from about their middle.

Remarks

There is some similarity with *L. dilatatum* (e.g. Álvarez-Vásquez et al. 2018) but the leaves of *L. lycopodioides* tend to be straighter or slightly curving away from the axis, rather than S-shaped with the distal part of the leaf tending to be more parallel to the axis. There is also some similarity with *L. selaginoides* but the leaves of the latter tend to be more closely adpressed to the stem.

The name *Lepidodendron lycopodioides* was first used by Sternberg (1820) for lycopsid branches and leafy shoots from the Whetstone Horizon of Svinná.

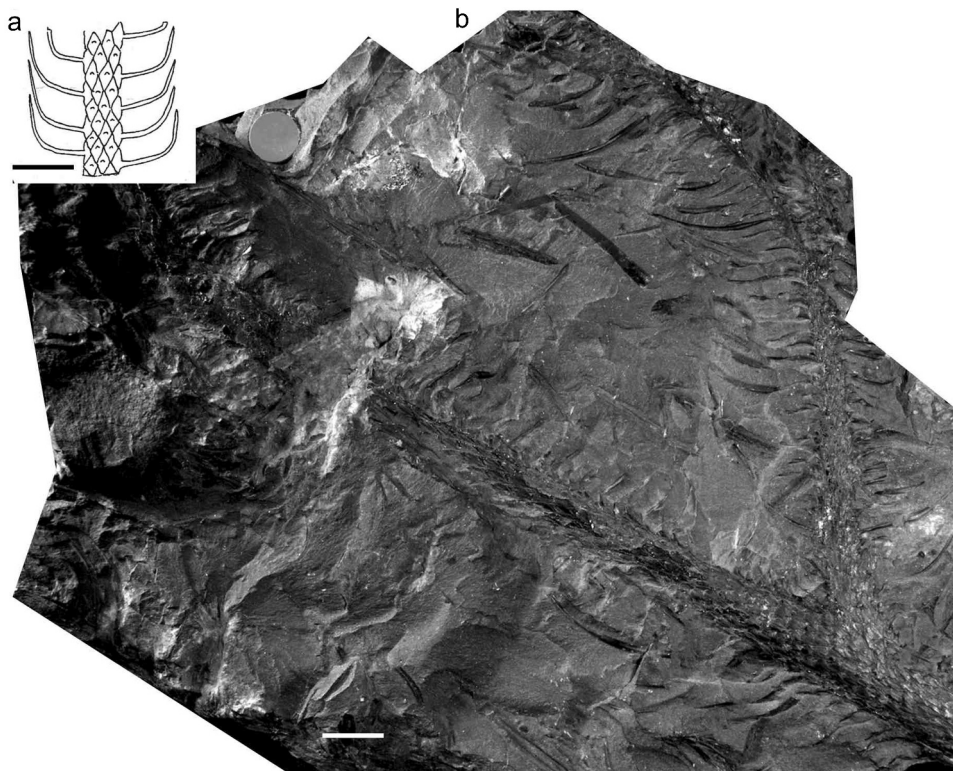


Figure 9. *Lepidodendron ophiurus* (Brongniart) Brongniart. (a), Drawing of leafy shoot by Deborah Spillards (from Cleal and Thomas 1994). (b), Muséum national d’Histoire naturelle (Paris), Specimen F.1327 (holotype); Newcastle upon Tyne, Tyneside, UK; Pennines Coal Measures. All scale bars = 10 mm.

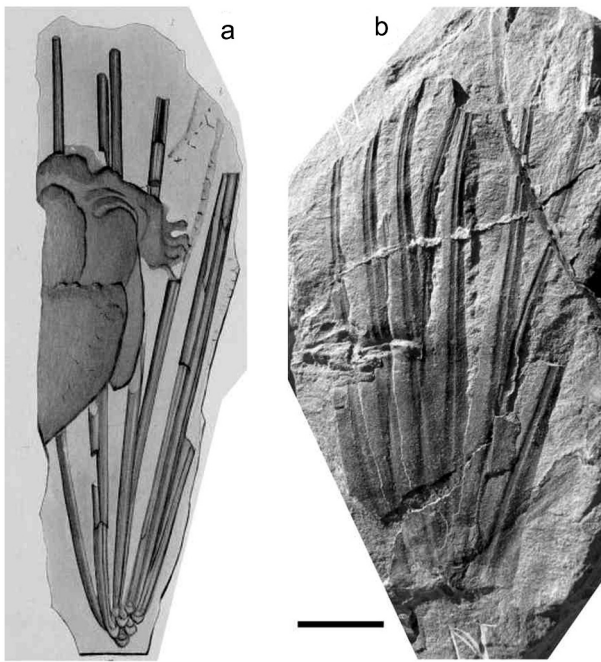


Figure 10. *Lepidodendrom rigens* Lesquereux (lectotype), Smithsonian Museum of Natural History, Specimen No. 15516, Mazon Creek, Illinois (USA). (a), Original illustration given with protologue in Lesquereux (1870). (b), Photograph of lectotype. Scale bar = 10 mm.

Sternberg (1826) later transferred these specimens to the genus *Lycopodiolithes* but in doing so he also illegitimately changed the species epithet to *elegans*. Brongniart (1828) disagreed with this generic distinction but accepted Sternberg's illegitimate species epithet, and so created the combination *Lepidodendron elegans*. The latter name continued to be used until Zeiller (1880) recognised the error and re-established the name *Lepidodendron lycopodioides*.

Lindley and Hutton (1831) later figured a very similar specimen to the *L. lycopodioides* type as *Lepidodendron sternbergii* Brongniart 1828. As pointed out by Fischer (1904), however, this was illegitimate as *L. sternbergii* is a later homotypic synonym of *Lepidodendron dichotomum* Sternberg 1820 (see also Thomas 1970). Álvarez-Vásquez et al. (2018) assigned this Lindley and Hutton specimen (also that figured in 1834 as *L. elegans*) to *L. dilatatum* but their leaves are far straighter than are normally seen in that species.

Lesquereux (1880) followed Lindley and Hutton (1831) in the misuse of the name *L. sternbergii* for this species, despite the fact that he recognised that its type was conspecific with the type of the earlier published *L. lycopodioides*; no reason was given for not using the earlier legitimate name. In addition, Lesquereux included the type of *Lepidodendron gracile*

Lindley and Hutton 1830 in this species, but which we believe belongs to *Lepidodendron ophiurus* (see later), and a specimen figured by Lindley and Hutton (1831-1833b) as *L. selaginoides* Sternberg, which we have retained in that species (also see later). A study by BAT of Lesquereux's specimens in the Smithsonian Institution has shown that most of those identified as *L. sternbergii* are leafy shoots very similar to *L. lycopodioides*, although some have distinctive leaf cushions that enable them to be transferred to *Lepidodendron andrewsii* Lesquereux 1880 and *Lepidodendron cuspidatum* Lesquereux 1880 (Thomas et al. 2019).

We do not accept Unger's (1850) inclusion of *L. lycopodioides* as a synonym of *Lepidodendron obovatum* Sternberg 1820, the latter being a synonym of the rather different *Lepidodendron aculeatum* Sternberg 1820 (see Němejc 1947; Thomas 1970).

Remy and Remy (1959) transferred this species to *Sublepidodendron* Nathorst in Hirmer 1927 as they regarded the stems as being elingulate. However, this was because the upper part of the leaf cushions tends to be obscured by the persistent leaves.

Occurrence

Many of the records are unreliable because of various synonyms. The type came from Whetstone Horizon ash bed at Svinná, Bohemia (Bolsvian); Thomas et al. (2020) recorded it from the Duckmantian of North Wales (UK).

Lepidodendron ophiurus (Brongniart) Brongniart, 1828

Fig. 9

- 1822 *Sagenaria ophiurus* Brongniart, p. 27, pl. 4, figs 1, 1a.
- 1825 *Lycopodiolithes ophiurus* (Brongniart) Sternberg, p. ix.
- 1825 *Lycopodiolithes affinis* Sternberg, p. ix, pl. 56, fig. 2.
- 1828 *Lepidodendron ophiurus* (Brongniart) Brongniart, p. 85.
- 1830 *Lepidodendron gracile* Lindley and Hutton, p. 29, pl. 9.
- 1947 *Lepidodendron ophiurus* (Brongniart) Brongniart; Němejc, pl. 1, figs 4–6; pl. 2, figs 1, 2.
- 1964 *Lepidodendron ophiurus* (Brongniart) Brongniart; Crookall, p. 287, text-fig. 93; pl. 61, fig. 4; pl. 62, fig. 5; pl. 63, fig. 4.
- 2015b *Lepidodendron ophiurus* (Brongniart) Brongniart; Thomas and Seyfullah, figs 1–3.

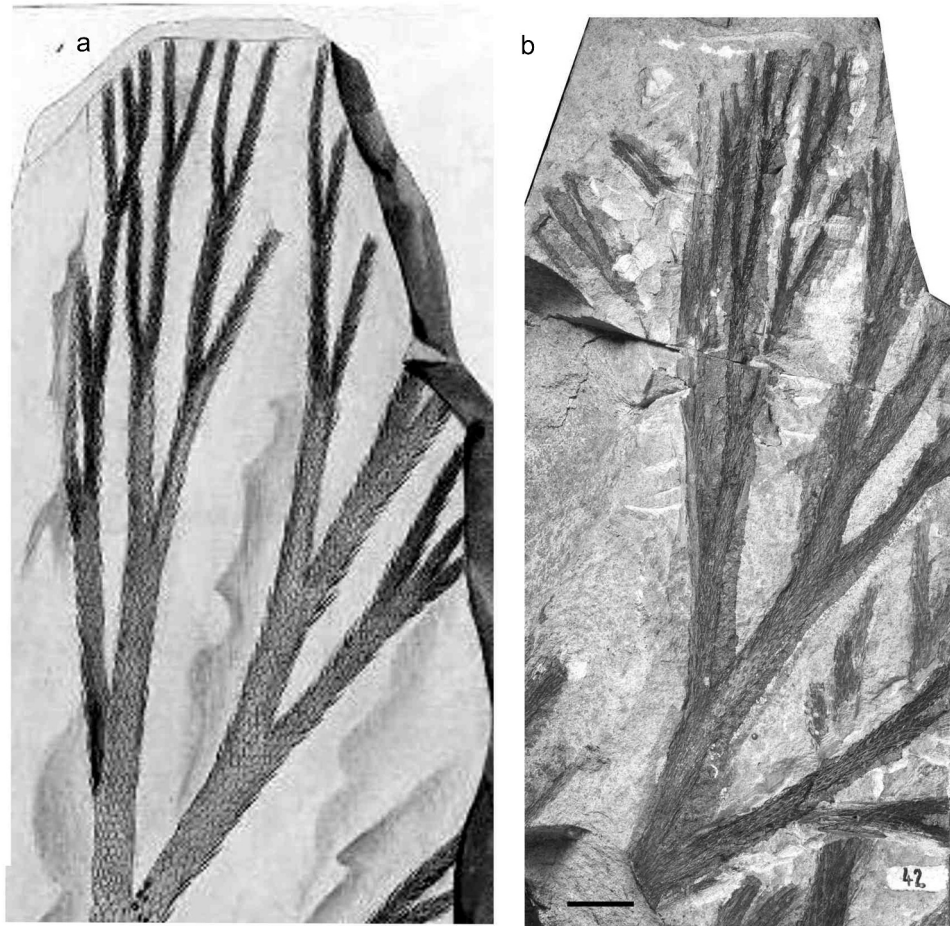


Figure 11. *Lepidodendron selaginoides* Sternberg, Národní muzeum (Prague), Specimen E 4744 (lectotype); Svinná, Czech Republic; Whetstone Horizon (Duckmantian). (a) Original illustration from Sternberg (1821). (b), photo by Lenka Váchová; scale bar = 10 mm.

Holotype

Muséum national d'Histoire naturelle (Paris), Specimen No. 1327 (Figure 9b). Provenance, Newcastle upon Tyne, Northumberland (now Tyneside) UK; Pennines Coal Measures.

Description

Stems with longitudinally elongated, rhomboidal to fusiform leaf cushions with acute upper and lower angles and rounded lateral sides. The leaf laminae are attached about one-third down the leaf cushions. Keels are above and below the attachment area of the leaf laminae and lateral lines run from the attachment area to the cushion edges. The leaves are linear, single veined, gradually tapering to an acute point, attached to cushions at nearly right angles, but then directed upwards with only slight divergence from the stem axis (based on Thomas and Seyfullah 2015b).

Remarks

The taxonomy of this species has been resolved by Thomas and Seyfullah (2015b). The latter authors included *L. dilatatum* Lindley and Hutton as a synonym of *L. ophiurus*, but we now reject this as the former has leaves more S-shaped leaves that are acutely attached to the stem.

Álvarez-Vásquez et al. (2018) assigned the type of *L. gracile* Lindley and Hutton 1831 to *L. dilatatum*. However, the leaves are clearly attached at a very obtuse angle to the leaf cushion and are far more similar to *L. ophiurus*.

Bureau (1913, pl. 30, figs 1–4; pl. 36, fig. 2; pl. 37, fig. 1) figured several leafy shoots as *L. ophiurus* from the upper Mississippian of northern France. As pointed out by Strullu-Derrien et al. (2021), however, the leaves are rather longer and thicker, and are not as consistently curved at the end. We know of no examples of *L. ophiurus* from earlier than the Pennsylvanian.

Occurrence

In the UK (e.g. Thomas et al. 2020): Coal Measures of Durham; from above the Barnsley Coal, East Gawber Colliery, near Barnsley, West Yorkshire (Duckmantian); from the Percy colliery, Newcastle-on-Tyne above the Sourmilk Coal, New Caledonian Railway, Airdrie, West Lothian (Bolsovian); Crookall (1964; 1966) stated it to be a very common and widespread, but the records are unreliable because of his broad interpretation of the species; Thomas (2007) recorded the species from the Asturian of Southern

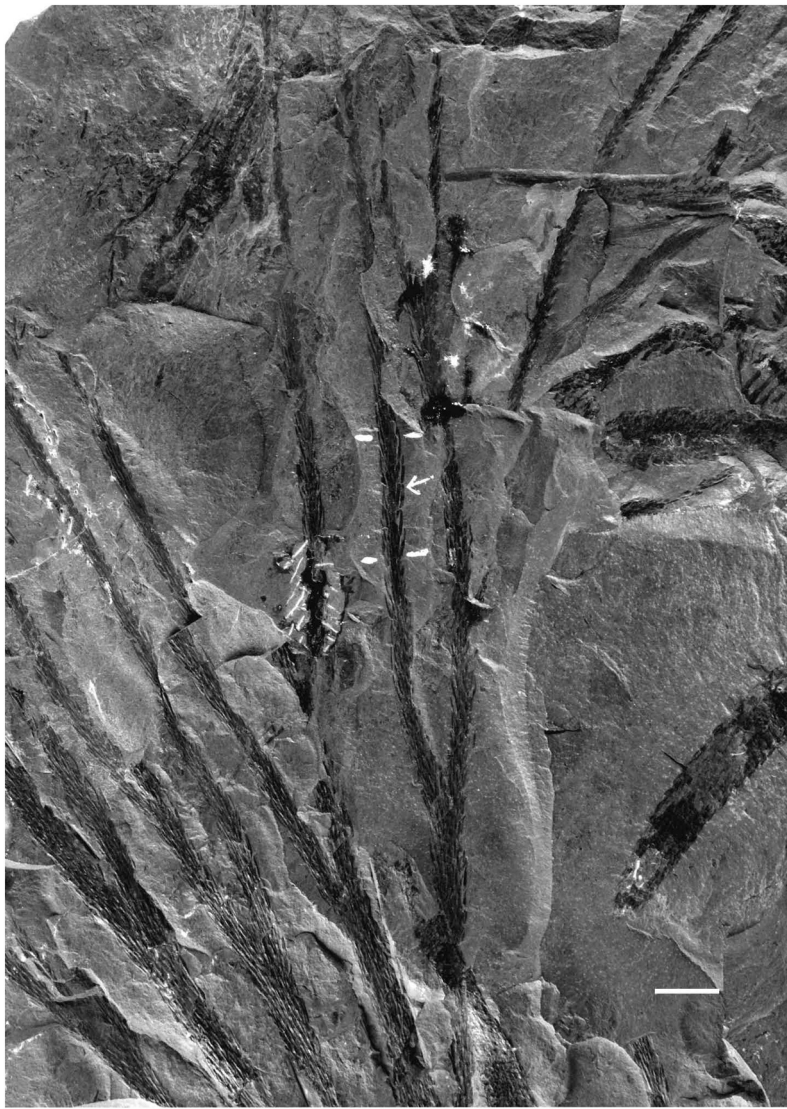


Figure 12. *Lepidodendron wingfieldense* Thomas and Seyfullah (holotype), British Geological Survey, Keyworth, Specimen 76,267, Wingfield Colliery, Derbyshire (UK); above the Kilburn Coal (Langsettian).

Britain, Sydney coalfield in Canada, Bohemia in the Czech Republic and the Dobrudzha coalfield in Bulgaria.

Lepidodendron pictoense Dawson 1863

Fig. 4b,c

- 1863 *Lepidodendron pictoense* Dawson, p. 449.
 1866 *Lepidodendron pictoense* Dawson; Dawson, p. 160, pl. 9, fig. 37.
 1868 *Lepidodendron pictoense* Dawson; Dawson, pp. 487, 453, fig. 169A.
 1880 *Lepidodendron lanceolatum* Lesquereux, p. 369 (1879, pl. 63, figs 3–5a).
 1962 *Lepidodendron pictoense* Dawson; Bell, p. 52, pl. 49, figs 1, 3, pl. 50, figs 1–3.
 1966 *Lepidodendron pictoense* Dawson; Bell, pl. 29, fig. 1.

Lectotype (designated here):

Redpath Museum, McGill University, Specimen 3478 (Figure 4c). Provenance, Sydney Coalfield, Nova Scotia (Canada); Morien Group (Asturian). Originally figured by Dawson (1866, pl. 9, fig. 37a) and Dawson, 1868, fig. 169A).

Description

Leaf cushions about four times longer than broad, with acute upper and lower angles, and broadly rounded lateral sides with the leaf scars in the upper half of the cushion. Ligule pit apertures about 1 mm above the leaf scars. The leaves are 10–25 mm long and 1.5–3 mm broad, bending out to about 45° and then straight or more generally curved upwards. (Based on Bell 1962).

Remarks

Dawson (1863) described *Lepidodendron pictoense* as a new species without illustrating types, but then later (Dawson 1866, 1868) repeated the description with accompanying drawings of a leafy shoot. Bell (1962) regarded Dawson's descriptions inadequate for a satisfactory diagnosis and gave an emended description. In our view, the relatively straight leaves attached to the stem at a narrow angle in the somewhat wider stems (e.g. Figure 4c) are quite different from the other species recognised here. As pointed out by Bell (1962) the different leaf sizes seen in the syntypes were said to relate to the size of the branches, which fits in with modern ideas of the growth pattern of the plants.

We agree with Bell (1962) that the types of *Lepidodendron lanceolatum* Lesquereux, 1879 are identical to those of *L. pictoense*.

Occurrence

Abundant in the Morien Group (Bolsovian – Cantabrian) of the Sydney and Pictou coalfields of the Canadian Maritimes (Dawson 1866); Bell's (1966) figured specimens were from the Bolsovian Clifton Formation of the Pictou Coalfield. Lesquereux's (1879) type of *L. lanceolatum* originated from the Clinton Coal of Missouri (USA).

Lepidodendrom rigens Lesquereux 1870

Fig. 10

1870 *Lepidodendron rigens* Lesquereux, p. 429, pl. 27, figs 1–3.

1880 *Lepidodendrom rigens* Lesquereux, p. 372.

1884 *Lepidodendron rigidum* Lesquereux, p. 839.

1925 *Lepidodendron rigens* Lesquereux; Noé, pl. 9.

1979 *Lepidodendron rigens* Lesquereux; Janssen, fig. 22.

Lectotype (designated here):

Smithsonian Museum of Natural History, Washington, Specimen No. 15516 (Figure 10b); Provenance, Mazon Creek, Illinois (USA); Middle Pennsylvanian (Cantabrian). Other syntypes in the Lesquereux collections are Specimen Nos. 15515 and 15517–15557.

Description

Branches with long rigid sub-cylindrical laminae, more than 200 mm long and 3 mm in diameter, gradually acuminate attached to rhomboidal, laterally enlarged leaf cushions.

Remarks

Lesquereux (1870) remarked that the leaf cushions were not visible but later (1880) described them as upraised, rhomboidal and laterally enlarged. The leaf scars covered the upper half of the cushions. This might infer that the leaf cushions were of the *Lepidophloios* type and, if Lesquereux had mistakenly inverted the specimen, this might be true. However, he does describe leaves, so he must have known which was up for the leaf cushions. For further discussion on the problem of leaf cushion inversion see Thomas (1977).

Lesquereux (1884) believed the leaves of *L. rigidum* to resemble those of his *L. rigens*, but were shorter and only slightly concave towards the base. This difference in shape could be a preservation effect and the leaf length difference the result of their relative positions on the parent plants. For those reasons we regard the two species as synonyms.

The only European record that has been suggested as belonging to this species was the specimen figured by von Röhl (1868, pl. 11, fig. 2) as *Lepidodendron dichotomum* Sternberg (Jongmans 1929). However, the isodiametric leaf cushions make it more similar to *L. latifolium*.

Occurrence

Mazon Creek, near Morris, Grundy County, Illinois; Tennessee, USA (Cantabrian) (Lesquereux, 1870; Noé 1925; Janssen 1979); Pottsville, Pennsylvania from the Dade Mine, Georgia, USA (stratigraphical age uncertain) (Lesquereux 1884).

Lepidodendron selaginoides Sternberg 1821

Fig. 11

1821 *Lepidodendron selaginoides* Sternberg, p. 31, pl. 16, fig. 3; pl. 17, fig. 1.

1825 *Lycopodiolithes selaginoides* (Sternberg) Sternberg, p. viii.

1831 *Lepidodendron selaginoides* Sternberg; Lindley and Hutton, pl. 12.

1855 *Lycopodites selaginoides* (Sternberg) Geinitz, p. 33, pl. 1, figs 2–4.

1868 *Lycopodites selaginoides* (Sternberg) Geinitz; von Röhl, p. 144, pl. 6, fig. 4; pl. 7, fig. 3.

1875 *Lycopodium carbonaceum* Feistmantel, p. 183, pl. 30, figs 1, 2.

1947 "*Lepidodendron*" *selaginoides* Sternberg; Němejc, pl. 3, figs 1, 3.

1997 *Lepidodendron selaginoides* Sternberg; Kvaček and Straková, p. 138, pl. 50, figs. 1, 3.

Lectotype (designated here):

Národní muzeum (Prague), Specimen No E 4744. Provenance, Svinná, Bohemia (Czech Republic); Whetstone Horizon ash bed (upper Duckmantian) (refigured photographically Němejc 1947, pl. 3, fig. 1; Kvaček et al. 2021, pl. 50, fig. 1).

Description

Narrow stems with leaves that are linear, straight, short, and almost adpressed to the stem. Stems dichotomise at very narrow angles; largest known stem 30 mm wide (Němejc 1947).

Remarks

Kidston (1889) and Crookall (1964) described *L. selaginoides* shoots bearing the cone now known as *Flemingites olryi* (Zeiller) Brack-Hanes and Thomas 1983, but using the name *Bothrodendron minutifolium* Boulay 1876. As a consequence, Kidston (1911) regarded *B. minutifolium* as conspecific with *L. selaginoides*, quoting the figures of Lindley and Hutton (1831) and von Röhl (1868); this view was also followed by Bureau (1914) and Jongmans (1929). However, Chaloner (1953) and Thomas (1967a) showed that leafy shoots in organic connection with large non-leafy stems identifiable as *B. minutifolium* (Zeiller 1886, pl. 74, fig. 4; Lindsey 1915, pl. 2, fig. 1) have broader, more ovate and squarrose leaves than those attached to the *F. olryi* strobili; epidermal characters also serve to distinguish the two types of leafy shoot. We now believe the latter to be shoots referable to *L. selaginoides*, making this a true species.

There has also been a tradition of using this name for anatomically preserved lycopsid shoots such as found in coal balls, following Carruthers (1869) and Williamson (1872). As pointed out by Jongmans (1929), however, there is no actual evidence that these anatomically preserved shoots correspond in morphology to the adpression types of *L. selaginoides* and so the use of that name for the anatomically preserved shoots is unwarranted.

Occurrence

Langsettian – Bolsovian of Bohemia, Czech Republic (Sternberg 1821, 1825); the roof of the Low Main coal seam (Duckmantian), Felling Colliery, Gateshead, Tyne and Wear, UK (Lindley and Hutton 1831).

Lepidodendron wingfieldense* Hemingway ex Thomas and Seyfullah 2015b*Fig. 12**

2015b *Lepidodendron wingfieldense* Hemingway MS; Thomas and Seyfullah, p. 31, text figs. 4, 5, 6.

Holotype

British Geological Survey, Keyworth (UK), Specimen No. 76267. Provenance, Wingfield Colliery, Derbyshire (UK); above the Kilburn Coal (Langsettian).

Description

Stems variable in size, up to at least 62 mm in diameter with acute branching at 10–20°. The leaf cushions are up to 5.9 mm long and 4.8 mm broad with acute pointed upper and lower angles and rounded sides and are distinctly grooved along the median axis. The leaf laminae depart from about a third of the distance from the base apex, c. 4 mm long with acute apices.

Remarks

Crookall (1964) included within *L. ophiurus* some specimens that Hemingway had collected and given the manuscript name of *L. wingfieldense*. However, Thomas and Seyfullah (2015b) showed that these had leaves that were attached at a much more acute angle than in *L. ophiurus* and used Hemingway's manuscript name of *L. wingfieldense*, giving the species the description quoted above.

Striations on the leaf cushions of *L. wingfieldense* distinguish it from most other species of *Lepidodendron*. The most similar is *L. worthenii* Lesquereux, but the cushions of the latter are always elongated with much more prominent grooves running much further across the leaf cushions. The leaf laminae on *L. worthenii* are also much longer and more distinct than those of *L. wingfieldense*. The types of *L. wingfieldense* is much older (Langsettian) than *L. worthenii*, which is most commonly found in the Asturian. The slenderer shoots of *L. wingfieldense* can also resemble *L. selaginoides* but the latter lacks the striate markings on the proximal parts of the leaves; furthermore, the stems of *L. selaginoides* shoots never reach the thickness regularly seen in *L. wingfieldense*.

Occurrence

The only known occurrence of the species is from the Langsettian type locality in Derbyshire, UK

Lepidodendron worthenii* Lesquereux 1866*Fig. 13**

1866 *Lepidodendron worthenii* Lesquereux, p. 452, pl. 44, figs 4, 5.

1880 *Lepidodendron worthenii* Lesquereux; Lesquereux, p. 388 (Lesquereux 1879, pl. 64, figs 8, 9).

1880 *Lepidodendron brittsii* Lesquereux, p. 368 (Lesquereux 1879, pl. 63, figs 1, 2).

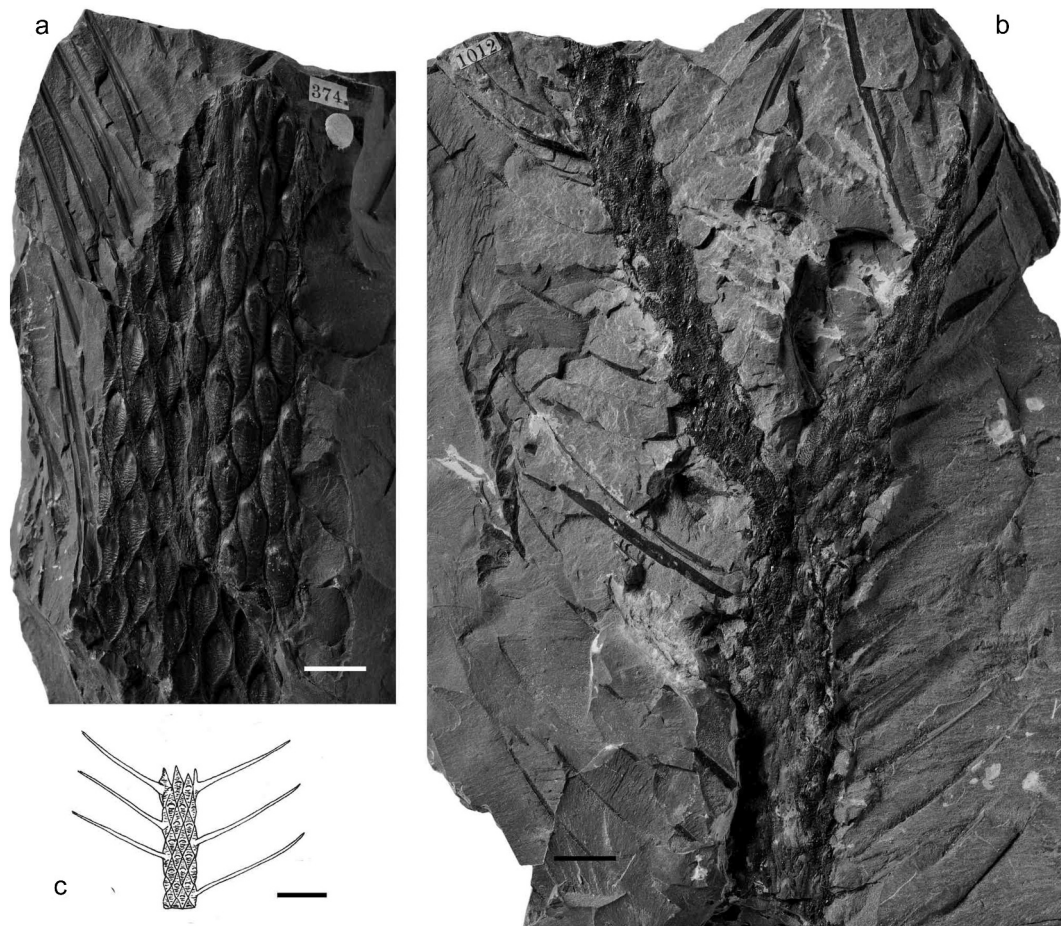


Figure 13. *Lepidodendron worthenii* Lesquereux. (a), British Geological Survey, Kidston Collection Specimen 379, unknown locality in UK; Coal Measures (Westphalian). (b), British Geological Survey, Kidston Collection Specimen 1012, Gawber Colliery, Barnsley, Yorkshire (UK); Middle Coal Measures (Duckmantian). (c), Drawing of leafy shoot by Deborah Spillards (from Cleal and Thomas 1994). All scale bars = 10 mm.

1938 *Lepidodendron worthenii* Lesquereux; Bell, p. 94, pl. 96, figs 4–7.

1940 *Lepidodendron worthenii* Lesquereux; Janssen, p. 13, pl. 1, figs 3, 4.

1979 *Lepidodendron worthenii* Lesquereux; Janssen, p. 43, fig. 19.

1964 *Lepidodendron worthenii* Lesquereux; Crookall, p. 275, pl. 51, figs. 2, 7.

Holotype

Illinois State Museum, Springfield IL, Specimen No. 1730. Provenance, Murphysboro IL (USA); from above coal no. 1B (photographically refigured by Janssen 1940, pl. 1, fig. 3, 4; 1979, fig. 19)

Description

Leaf cushions with deep horizontal grooves, both above and below the leaf scars. The characteristic cushions can be seen on leafy shoots where the leaf laminae are straight and attached at c. 45–50° from the vertical. Individual laminae are about 20–60 mm long,

presumably varying in length reflecting their relative positions on the branches and narrowing upwards to a sharp point.

Remarks

The taxonomy of this species has been discussed by Thomas et al. (2019) including its relationship with *Lepidodendron brittsii* Lesquereux, 1880. See also the comments above on *L. wingfieldense*.

Occurrence

Most of the records of this species come from the Asturian and has been recorded from the Pennsylvanian of Illinois, Pennsylvania, Indiana; Oklahoma, New Mexico in the USA; Nova Scotia in Canada (for further details of the American records see Álvarez-Vásquez and Wagner 2014); South Wales, Forest of Dean, Bristol & Somerset the Forest of Wyre and South Staffordshire in the UK; the Donetz Basin in the Ukraine; Dobrudzha Coalfield, Bulgaria and in Spain and Portugal (Thomas 2007). Josten (1991, fig. 76, pl. 43 fig. 1,

1a, 2) described and figure specimens from north-west Germany that we can accept. The figured specimens are from the Duckmantian although Josten also recorded it from the Langsettian and the Bolsovian of the Ruhr coalfield, the Langsettian and Duckmantian of the Aachen coalfield. Van Ameron (1975) recorded the species from the Netherlands. Crookall (1964) recorded and figured (pl. 61) a specimen of this species from the Bench Coal of Warwickshire, U.K. Close examination of the specimen shows its leaf cushions to be completely covered with horizontal striations, but they have distinct triangular leaf scars with three foliar prints a feature never seen on Asturian specimens of *L. worthenii*.

Genus: *Lepidophloios* ("Lepidofloyos")
Sternberg 1825 nom. cons.

Remarks

The nomenclatural status and conservation of the name *Lepidophloios* has been discussed by Wang (2007a, 2007b) and Doweld (2013). The genus is

characterised by having downward bulging leaf cushions where the leaf scar occurs at the base of the bulge. Leafy stems can only be attributed to one species, *L. acerosus*.

***Lepidophloios acerosus* (Lindley and Hutton)**
Kidston 1890

Fig. 14

- 1831 *Lepidodendron acerosum* Lindley and Hutton, p. 29, pl. 7, fig. 1; pl. 8.
 1837 *Lepidostrobus pinaster* Lindley and Hutton, p. 129, pl. 198.
 1838 *Lycopodites acerosus* (Lindley and Hutton) Presl in Sternberg, p. 176.
 1890 *Lepidophloios acerosus* (Lindley and Hutton) Kidston, p. 49.
 1893a *Lepidophloios acerosus* (Lindley and Hutton) Kidston; Kidston, p. 558, pl. 1, fig. 1; pl. 2, fig. 9.
 1904 *Lepidophloios acerosus* (Lindley and Hutton) Kidston; Kidston, text-fig7c.
 1914 *Lepidophloios acerosus* (Lindley and Hutton) Kidston; Arber, p. 414, pl. 28, fig. 20.

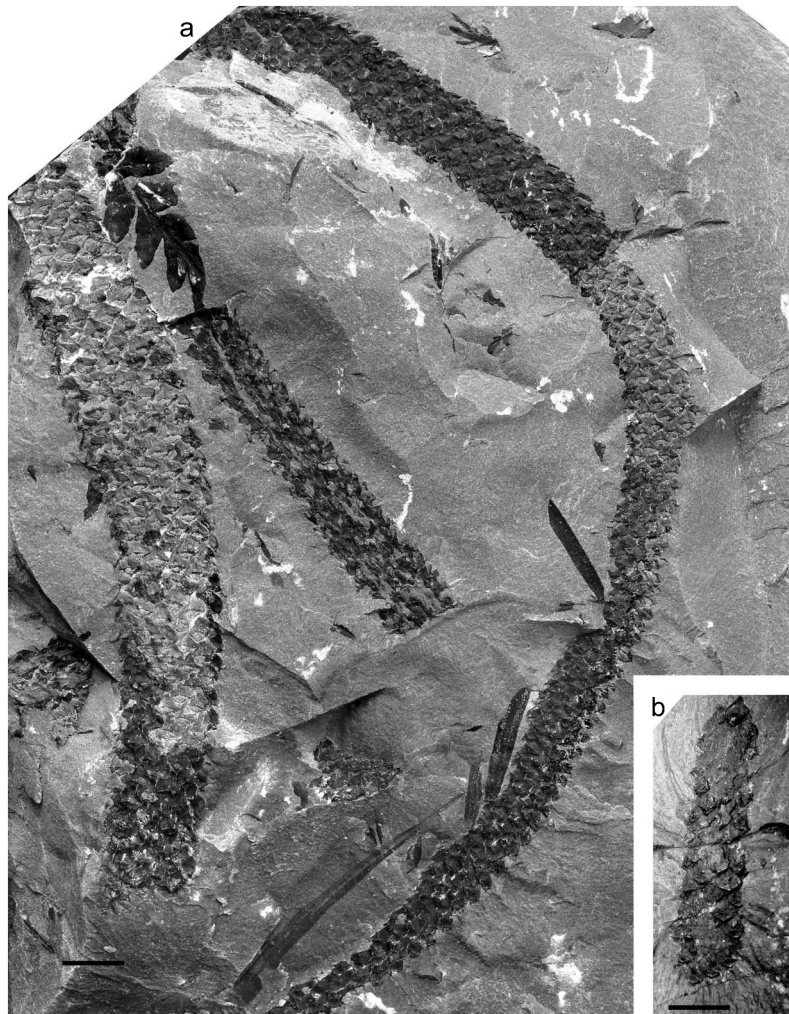


Figure 14. *Lepidophloios acerosus* (Lindley and Hutton) Kidston, National Museum Wales, Specimen NMW 2013.43 G.136; Brymbo Opencast near Wrexham, Denbigh Coalfield, north Wales, UK (photo by P. Appleton); Middle Coal Measures (Duckmantian).

- 1917 *Lepidophloios acerosus* (Lindley and Hutton)
Kidston; Kidston, pl. 2, fig. 5.
- 1929 *Lepidodendron acerosus* Lindley and Hutton;
Crookall, p. 26, pl. 3, fig. 50; pl. 22, fig. k.
- 1964 *Lepidophloios acerosus* (Lindley and Hutton)
Kidston; Crookall, p. 313, pl. 75 fig. 7; pl. 76, fig. 2.
- 1977 *Lepidophloios acerosus* (Lindley and Hutton)
Kidston; Thomas, p. 280, pl. 35, fig. 1, 2; text-fig. 4.

Syntypes

Lindley and Hutton (1831, pl. 7, fig. 1; pl. 8). Provenance, Bensham Colliery, roof of the Bensham Seam (pl. 7, fig. 1) and Felling Colliery, Low Main Seam (pl. 8); both of Duckmantian age, and located at Gateshead, Tyne and Wear (UK). According to Kidston (1891, 1893a) all syntypes are lost.

Description

Stems with downturned and overlapping leaf cushions whose exposed parts are longer than broad. The cushions have clear keels that are usually slightly raised. The leaf scars are at the base of the downturned leaf cushions and ligule pit apertures occur just above them. Leaves are 40–50 mm long and ascend from the cushions at narrow angles. Epidermal structure different on the exposed upper surface of the leaf cushion and its lower hidden surface.

Remarks

The interpretation of this species is problematic as all of the syntypes are reported lost and the figures provided by Lindley and Hutton (1831) are somewhat diagrammatic. We have provisionally followed the interpretation of the species by Kidston (1893a) and Thomas (1977) as a more complete taxonomic analysis will be required of stems in all growth stages will be needed before a neotype can be selected.

Lindley and Hutton (1837) figured what they interpreted as a strobilus as *Lepidostrobus pinaster* (Figure 14b). However, this is clearly a stem with downturned leaf cushions and attached leaves, and belongs to *L. acerosus*.

The leaf cushions on the smallest shoots of this species are not downturned and resemble those of *Lepidodendron*. Thomas (1977) has shown that some stems (e.g. Nos 764 and 4947 in the Kidston collection, British Geological Survey) show a progression from smaller un-downturned to larger downturned cushions and suggested that this was subsequent growth possibly to increase photosynthesis. Leaves were shed before the expansion of the leaf cushions.

Occurrence

This has been recorded from the Langsettian to the Bolsovian of England and Wales (Crookall 1964), the Duckmantian of North Wales and the Asturian of Southern Britain by Thomas (2007); Cucuiova Formation of the Sirinia Basin, Danubian Units, in Almăj Mountains, South Carpathians (Bolsovian – Cantabrian) in Romania (Popa 2016); Bolsovian of the Czech Republic (Opluštil et al. 2009b).

Genus: *Ulodendron* Lindley and Hutton 1831

Type: *Ulodendron majus* Lindley and Hutton 1831

Remarks

Jongmans (1913) attributed the publication of this genus name to Rhode (1823), mainly following Lindley and Hutton (1831) who regarded the specimen figured by Rhode as being conspecific with their *Ulodendron majus*. However, Rhode never actually used the name, whose first valid use was by Lindley and Hutton (1831).

Ulodendron is characterised by having rhomboidal leaf cushions separated by narrow grooves and narrow areas of flat stem above each cushion. The leaves were retained so no true leaf scars occur. Ligule pits are present at the base of the adaxial leaf lamina (Thomas 1967b, fig. 2). The large round so-called ulodendroid branch-abscission scars illustrated by Lindley and Hutton (1831) are not diagnostic features for *Ulodendron*, having also been found on stems with leaf scars referable to other fossil-genera including *Lepidodendron* and *Synchysidendron* (e.g. Bureau 1913; DiMichele et al 2013).

Renier (1926) used *Ulodendron* for all lycopod leafy shoots, and this was followed by Moore and Cox (1943), and Moore (1945). Stockmans and Willière (1953) described cones attached to lycopod leafy shoots as *Ulostrobus*, but there was no evidence that the shoots were in fact *Ulodendron* and these strobili are indistinguishable from *Lepidostrobus* and *Flemingites*.

Pearson (1986) interpreted *Ulodendron* as a synonym of the genus of anatomically preserved stems *Anabathra*, and proposed new combinations and species previously assigned to *Ulodendron*. However, this is an example of the confusion that can occur when attempts are made to integrate the fossil-taxa in different states of preservation (see comments by Thomas and Cleal 2020). *Anabathra* was based on a Tournaisian fossil from Scotland (Witham 1833). Pearson suggested that they had a similar anatomy to Viséan stems now named *Paralycopodites brevifolium* (Williamson) DiMichele 1980 and that the latter species is

equivalent to the Pennsylvanian-age *Ulodendron* adpressions based on the presence of large branch scars on the stems (DiMichele 1980). However, these scars are now known not to be a reliable indicator of that genus (see above). There is, moreover, now doubt that *Anabathra* and *Paralycopdites* are generically the same (DiMichele and Bateman 1996). Since there is no clear evidence that the types of either *Anabathra* or *Paralycopodioides* have the same diagnostic morphological features as the rather younger *Ulodendron* adpressions, and there is similarly little evidence that the type of *Ulodendron* had the *Anabathra/Paralycopodites* anatomy, combining these fossil-genera merely introduces confusion and lack of clarity into the taxonomy, and should be rejected.

Ulodendron majus Lindley and Hutton 1831

Fig. 15

1825 *Lepidodendron discophorum* König (nomen nudum), pl. 16, fig. 194.

1831 *Ulodendron majus* Lindley and Hutton, p. 22, pl. 5.

1831 *Ulodendron minus* Lindley and Hutton, p. 25, pl. 6.

1885a *Sigillaria discophora* (König) Kidston (nom. illegit.), p. 251, pl. 4, fig. 5; pl. 5, fig. 8; pl. 7, figs 12, 13.

1886 *Ulodendron majus* Lindley and Hutton; Zeiller, pl. 73.

1966 *Ulodendron majus* Lindley and Hutton; Crookall, p. 486, pl. 99, fig. 3; pl. 100, figs 1–3,

1967b *Ulodendron majus* Lindley and Hutton; Thomas, p. 778, fig. 1.

1986 *Anabathra thomasiana* Pearson, p. 280.

Holotype

Lindley and Hutton (1831, pl. 5). Provenance, Jarrow Colliery, near Newcastle-upon-Tyne (UK); Bensham Seam (Duckmantian). The holotype has been reported lost but there are 13 other specimens in the Hutton Collection from the same locality from which a neotype might be selected (Lebour 1878). However, such a selection would need the specimens to be investigated.

Description

Leaf cushions rhomboidal and slightly broader than long, and separated by narrow grooves. The laminae are c. 30 mm long and 1.5 mm broad at their attachment points.

Remarks

The holotype is lost and the illustration accompanying protologue in Lindley and Hutton (1831) is somewhat unclear. However, the latter seems to suggest that the stems had rhomboidal leaf cushions, slightly broader than long, and lacking leaf scars, and this was the basis of the interpretation of this species by Thomas (1967b) and which we have followed here. Thomas (1967b, fig. 1A)

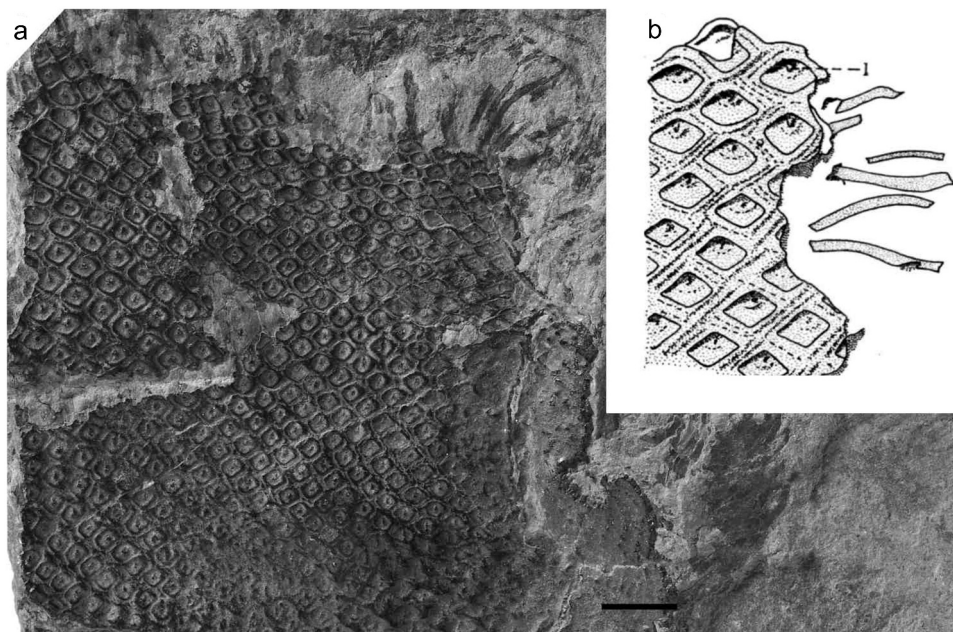


Figure 15. *Ulodendron majus* Lindley and Hutton. (a), British Geological Survey, Kidston Collection Specimen 19, Devonside, Tillicoultry, Clackmannanshire (UK); Lower Coal Measures (Duckmantian); scale bar = 10 mm. (b), Drawing of leaf cushions with associated leaves (from Thomas 1967b).

showed a stem with associated elongated leaves, and a similar specimen has been found in the Kidston Collection (Figure 15). A specimen with attached leaves was figured by Zeiller (1886); Álvarez-Vásquez et al. (2018) identified the latter as *Lepidodendron dilatata* but the leaves are much longer and straighter than in that species, and the squat, rhomboidal leaf cushions clearly correspond to those of *U. majus*.

Ulodendron minus was mainly differentiated by having smaller leaves and leaf scars (Lindley and Hutton 1831; Zeiller 1888). However, this almost certainly represents parts of the same plant species (Thomas 1967b).

Kidston (1885a, 1885b) named the species *Sigillaria discophora* (König) Kidston (\equiv *Lepidodendron discophora* König 1825). However, the basionym was only given as a label on a figure, with no accompanying description or text, and so was not validly published.

Pearson (1986) proposed that the species as interpreted by Thomas (1967b) should be re-named *Anabathra thomasiana* as the *U. majus* type is lost and it is not certain that the latter is conspecific with Thomas's material. However, we regard this as premature as there are paratypes in the Hutton Collection that could be used to establish the true nature of *U. majus*. We have therefore continued to use the epithet *majus* as proposed by Lindley and Hutton.

Occurrence

U. majus has been recorded from above the Bensham Seam, Jarrow colliery, Tyne and Wear, UK; and above the High Main coal South Shields colliery Tyne and Wier, UK; also from Kilmarnock, Ayrshire, Scotland, UK (Thomas 1967b); the Duckmantian of North Wales (Thomas et al. 2019).

Ulodendron landsburgii (Kidston) Thomas 1968.

Fig. 16

1893b *Lepidodendron landsburgii* Kidston, p. 338, pl. 3, figs 9, 10.

1964 *Lepidodendron ophiurus* Brongniart; Crookall (pars, non Brongniart), p. 287, pl. 63, figs 1, 2.

1968 *Ulodendron landsburgii* (Kidston) Thomas, p. 425, fig. 1.

1986 *Anabathra landsburgii* (Kidston) Pearson, p. 280.

Holotype

British Geological Survey, Keyworth (UK), Kidston Collection, Specimen No. 1546. Provenance, Bonnington pit, Kilmarnock, Ayrshire (UK); from above the Whistler seam (Bolsovian).

Description

Leaf cushions longer than broad and separated by narrow grooves. Laminae are c. 25–30 mm long and 2 mm broad at their attachment points.

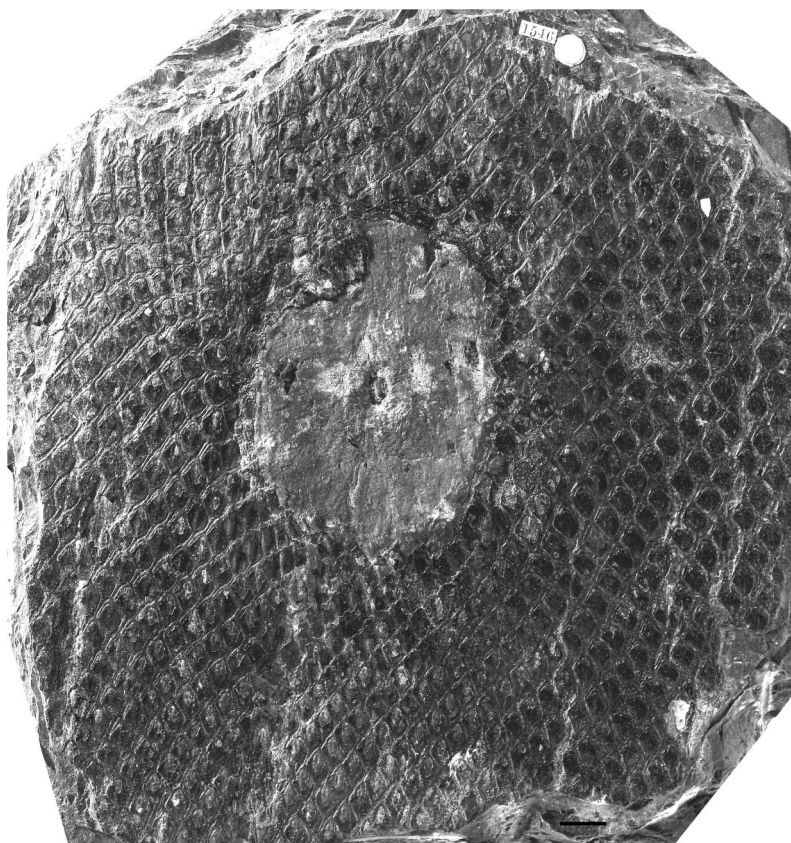


Figure 16. *Ulodendron landsburgii* (Kidston) Thomas. British Geological Survey, Kidston Collection Specimen 4546 (lectotype), Bonnington pit, Kilmarnock, Ayrshire (UK); above the Whistler seam (Bolsovian). Scale bar = 10 mm.

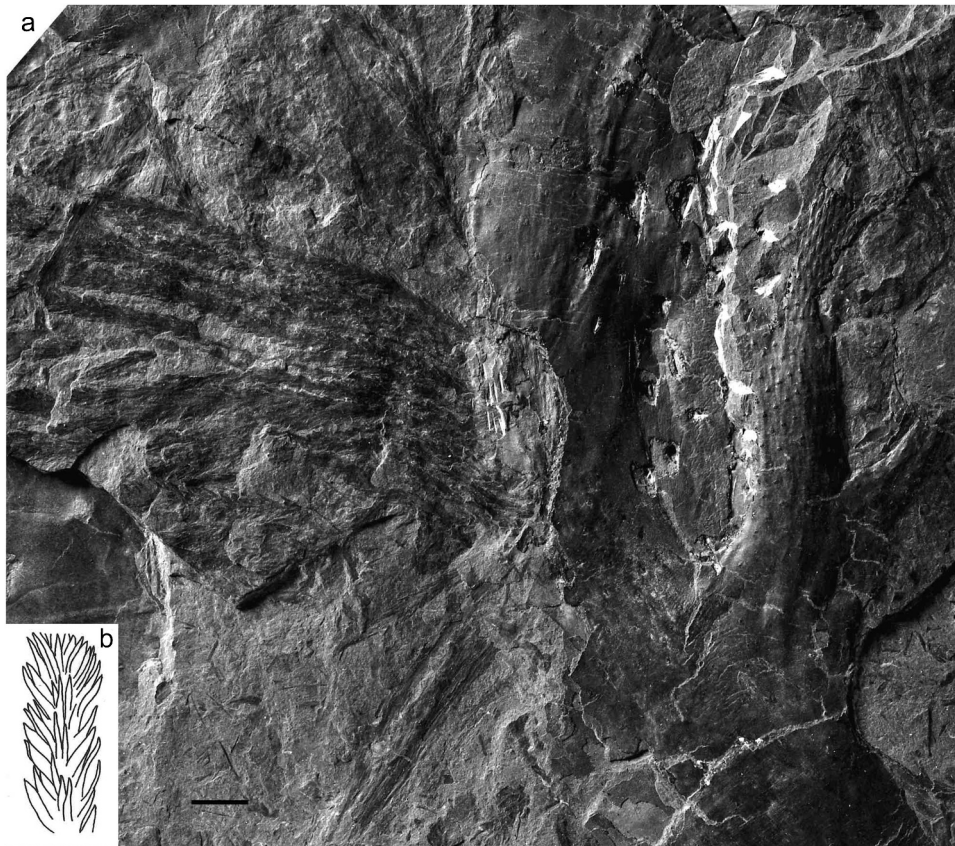


Figure 17. *Bothrodendron minutifolium* (Boulay) Zeiller. (a), British Geological Survey, Kidston Collection Specimen 1546 (lectotype), Bonnington pit, Kilmarnock, Ayrshire (UK); above the Whistler seam (Bolsovia). Scale bar = 10 mm. (b), Drawing of leafy shoot by Deborah Spillards (from Cleal and Thomas 1994; based on Thomas 1967a)

Remarks

Crookall (1964) assigned the type of this species to *L. ophiurus* but it is clearly a *Ulodendron* based on both morphological and epidermal characters (Thomas 1967b). Thomas (1968) showed that it differed from *U. majus* by having more elongate cushions and the larger, sunken stomata.

Álvarez-Vásquez and Wagner (2014) regarded *U. landsburgii* as a synonym of *Bergeria dilatata*, but in our view they have different shaped leaves.

Occurrence

This species is known only from the type locality in Ayrshire.

Bothrodendron Lindley and Hutton 1833a

Type: *Bothrodendron punctatum* Lindley and Hutton 1833a.

Remarks

Being the name of an initially monotypic genus, it was validated by the protologue of the type species. Lindley and Hutton (1834, p. 97) later gave a generic diagnosis (“Stem not furrowed, covered with dots. Scars of cones, obliquely oval”) but this definition was ambiguous. Following Presl (in Sternberg 1838) many authors

regarded it simply as a decorticated form of *Ulodendron*, but Zeiller (1885) and Kidston (1904) showed that this was in error and that the stems were not decorticated, but were simply lacking leaf cushions. Zeiller (1885) also pointed out that a stem figured by Boulay (1876, pl. 3, fig 1) under the genus *Rhytidodendron* also belonged to *Bothrodendron* as he was then defining it.

We are here using the fossil-genus with the emended diagnosis given by Thomas (1967a): stems with small leaf scars with three foliar scars that are level with the wrinkled stem surface; ligule pit apertures are immediately above or slightly separated from the leaf scars; smaller leafy branches covered with small acutely pointed leaves.

Bothrodendron is distinguished from the similar fossil-genera *Cyclostigma* Haughton 1859 and *Pinakodendron* Weiss 1893 which show no ligule pits, and from *Lepidobothrodendron* Daber 1959 which has two external parichnos.

Bothrodendron minutifolium (Boulay) Zeiller 1880

Fig. 17

1876 *Rhytidodendron minutifolium* Boulay, p. 39, pl. 3, fig. 1, 1bis.



Figure 18. *Bothrodendron punctatum* Lindley and Hutton. Nova Scotia Museum, Halifax NS, Specimen 990–281, Pioneer Coal Mine at Sydney Airport, Nova Scotia (Canada); Gardiner Seam, Morien Group (middle Asturian) (from Thomas et al. 2010, fig. 2b; photo by E.L. Zodrow). Scale bar = 10 mm.

1880 *Bothrodendron minutifolium* (Boulay) Zeiller, p. 117.

1915 *Bothrodendron minutifolium* (Boulay) Zeiller; Lindsey, pl. 11.

1967a *Bothrodendron minutifolium* (Boulay) Zeiller; Thomas, fig. 2, 3.

Lectotype (designated here):

Boulay (1876, pl. 3, fig. 1bis). The specimen was probably in the collections of the Muséum national d'Histoire naturelle (Paris), but has not been located. Provenance, Bonne-Part pit, Fresnes, north of Valenciennes (France).

Description

Large shoots with oval, laterally elongated leaf scars level with the stem surface and ligule pit apertures just above them. The stem surface is divided into small areas by fine,

irregular and undulating grooves with each area containing groups of small puncti (probably stomata – Thomas 1967a) in horizontal rows. Smaller shoots have leaf scars on raised leaf cushions whose surface features are like those on the largest shoot, while the smallest, leafy twigs have ovate-lanceolate, leaves that are about 5 mm long with acute pointed apices. The midrib is about 150 µm broad narrowing rapidly towards the leaf apex.

Remarks

Some authors have reported leafy shoots attached to the identifiable stems of *B. minutifolium* (e.g. Zeiller 1880; Weiss 1893; Kidston 1902; Lindsey 1915); the Kidston specimen is refigured here as Figure 17a. However, it is difficult to identify the isolated leafy shoots of *B. minutifolium* unless they are found attached to diagnostic, wider stems.

Occurrence

B. minutifolium has been recorded by Crookall (1964) as a common and widespread species from the Langsettian to the Duckmantian in many coalfields in England, Scotland and Wales; Thomas (2007) recorded it from the Asturian of Iberia and Bulgaria.

***Bothrodendron punctatum* Lindley and Hutton**

1833a
Fig. 18

1833a *Bothrodendron punctatum* Lindley and Hutton, pls 80, 81.

1967a *Bothrodendron punctatum* Lindley and Hutton; Thomas, p. 53, fig. 1.

2010 *Bothrodendron punctatum* Lindley and Hutton; Thomas et al., p. 2, fig. 1–3.

Lectotype

British Geological Survey, Keyworth (UK), Specimen No. 5257. Provenance, Jarrow Colliery, near Newcastle-upon-Tyne (UK); from the roof of the High Main Seam (Duckmantian) (1964). The whereabouts of the other syntype figured by Lindley and Hutton (1833a, pl. 81), from the Percy Main Colliery, Newcastle-upon-Tyne, is unknown.

Description

Stems with oval leaf scars up to 2 mm long with ligule pits contiguous with the top of the leaf scar. The stem surface is covered with fine, sinuous, vertical striations, and the epidermis has uniformly elongated epidermal cells and evenly scattered stomata. The side shoot departs upwards at an angle of about 20° with a decurrent upper surface. Side shoots are about 10 mm across a little way from its broader point of attachment and for the first 20 mm bear no leaves. The surface of this basal portion of the branch is like that of

the main stem. The leaves are in tight spirals decurrent and then spreading out at angles of 30–40° before curving upwards again. Individual leaves are lanceolate, about 0.6 mm long and about 0.2 mm across at their broadest point and their apices are shortly acuminate.

Remarks

The above description of a leafy side shoot is based on a specimen from above the middle Asturian Gardiner Seam of the Sydney Coalfield, Nova Scotia, described by (Thomas et al. 2010). The leaves of *B. punctatum* are very similar to those of *B. minutifolium* but are less densely packed together on the shoots.

Occurrence

The type specimen came from the Duckmantian of the UK; Crookall records the species from the UK, from the Langsettian (Yorkshire, Derbyshire, Lancashire, and Lanarkshire), and Bolsovian to Asturian (South Wales, Yorkshire, Derbyshire, Nottinghamshire, Northumberland and Durham, North Ayrshire, Clackmannanshire and Fife. Thomas (2007) recorded it from the Asturian of Nova Scotia, Canada and Bulgaria.

Key for distinguishing species of leafy shoots

1. Large stems with small leaf scars level with the stem surface that is wrinkled. The smaller branches are leafy and covered with small acutely pointed leaves..... 2
Stems with leaf cushions 3
2. Main stems horizontally wrinkled. Leaves on smaller branches ovate-lanceolate about 5 mm long with acute pointed apices *Bothrodendron minutifolium*
Main stems vertical striated. Leaves on smaller branches lanceolate, about 0.6 mm long and shortly acuminate *Bothrodendron punctatum*
3. Leaf cushions rhomboidal separated by narrow grooves and areas of flat stem 1 mm broad above each leaf cushion. Leaf laminar broadly attached and never shed 4
Leaf cushions elongated or not visible being covered by narrow laminae 5
4. Leaf cushions slightly broader than long, laminae c. 30 mm long and 1.5 mm broad at their attachment points *Ulodendron majus*
Leaf cushions slightly longer than broad, laminae 25–30 mm long and 2 mm broad at their attachment points *Ulodendron landsburgii*.
5. Leaves attached at right angles to the leaf cushions 6
Leaves attached at acute angles to the leaf cushions 7

6. Leaves turned upwards to be more or less parallel to shoot axis *Lepidodendron ophiurus*.
Leaves curved upwards and outwards *Lepidodendron dawsonii*.
7. Leaves S-shaped at their base and curved in the upper parts often reaching 50–70 mm in length. If laminae are missing a curved lines visible near the apices are pseudoscars *Lepidodendron dilatatum*.
Leaves straight or curved and departing from leaf cushions 8
8. Leaves attached at c. 45° to leaf cushions *Lepidodendron pictoense*.
Leaves attached at less than 45° to leaf cushions 9
9. Leaves over 40 mm long 10
Leaves 35 mm long or less 13
10. Leaves cylindrical, >200 mm long, 3 mm in diameter *Lepidodendron rigens*.
Leaves flat not cylindrical 11
11. Leaves 40–50 mm long, attached to diamond-shaped cushions at narrow angles *Lepidophloios acerosus*
Leaves attached to shoots with no obvious leaf cushions 12
12. Leaves less than 5 mm broad *Lepidodendron longifolium*.
Leaves 7 mm broad *Lepidodendron latifolium*.
13. Leaves 10–25 mm long, 1.5–3 mm wide, bending outwards to about 45° and then curving upwards *Lepidodendron pictoense*
Leaves less than 10 mm long 14
14. Narrow stems with closely arranged leaves and no obvious leaf cushions 15
Broad stems with leaf cushions with a striate surface, and leaves c. 4 mm long with acute apices *Lepidodendron wingfieldense*
15. Leaves spreading, 5–9 mm long and 1 mm wide, lanceolate and gradually narrowing *Lepidodendron lycopodioides*
Leaves straight, up to 5 mm long, less than 1 mm wide and closely adpressed to the stem *Lepidodendron selaginoides*

Discussion

We have shown that leafy shoots of arborescent lycopods can be identified using leaf size and shape. Then, considering the growth patterns of the plant, it is possible to interpret very similar species as synonyms. For example, we have synonymised *Bergeria acuta* into *Lepidodendron dilatatum*, and *Ulodendron minus* into *U. majus*,

regarding both pairs of species as expressions of different sized stems. It has also been possible to untangle the taxonomic confusion over leafy shoots sometimes described as *Bothrodendron minutifolium* with those having terminal cones of *Flemingites olryi*; the latter have been shown to be identical with, and better described as, *Lepidodendron selaginoides*.

We have not attempted to integrate the adpression taxa of leafy lycopod shoots with taxa of the anatomically preserved leaves described by Graham (1935); the latter species tended to be differentiated on characters, such as the relative distribution of tissue-types and of stomatal furrows seen in transverse sections, which are virtually impossible to recognise in adpressions. Similarly, the morphological characters used to differentiate the leaf adpression species would be very difficult to recognise in anatomically preserved fossils.

As with the stems, trying to integrate the taxonomies for the adpressions and anatomically preserved floras will only cause confusion (Thomas and Cleal 2020); see, for instance, the discussion under *Ulodendron majus* in the present paper. We have never tried to promote the idea of a “preservational apartheid” when developing taxonomies for such fossils, as suggested by Bateman and DiMichele (2021). Neither do we deny the significant advances that can be made in understanding the parent plants by integrating data from different types of fossils (e.g. DiMichele and Bateman 1996, 2020; DiMichele et al. 2013). But palaeobotanical taxonomy should not be used as a hierarchical system imposing patterns on the empirical data based on hypothetical phylogenetic models; rather, it should be regarded as a practical and therefore flexible tool for naming and classifying plant fossils (Cleal and Thomas 2021), which was the underlying philosophy behind our proposals made in Cleal and Thomas (2010) and which became incorporated into the International Code of Nomenclature (Turland et al. 2018). In the case of the arborescent lycopods, combining the fossil-taxa based on adpressions and anatomically preserved remains of stems and leafy shoots does no favours to the study of the fossils in either preservation state, nor does it provide any additional clarity to our understanding of plant phylogeny.

Conclusions

Palaeobotany relies on a secure taxonomic foundation for, without it, chaos will ensue. Today, this is achieved through the use of fossil-taxa that allow different taxonomic names to be given to fossils representing different plant parts, life history stages and preservation states (Cleal and Thomas 2010, 2021); as pointed out by Bateman and DiMichele (2021), fossil-taxa provide a flexible and practical

tool for recording plant fossils that few palaeobotanists would want to jettison. How the fossil-taxa are circumscribed can be subjective and can often be influenced by what the palaeobotanist is trying to achieve.

For those whose primary interest is plant phylogeny, there is a temptation to merge the fossil-taxa from different plant parts and/or preservation states, with the aim of making them as near to whole-plant taxa as possible; trying to develop cladistic phylogenies will rarely be successful if based on just a small subset of the plant parts and preservation states. But this ignores the fact that taxonomy has a dual role: it is not only to classify things (in this case plant fossils, or even the fossil plants) but it is also to record things (Williams and Ebach 2020). For those interested in floristic or palaeoecological studies the recording aspect can be a higher priority than simple classification. For such studies, it is essential that the distribution of the plants is analysed and this is often based on fossils that in themselves would provide incomplete data for a phylogenetic analysis. Bateman and DiMichele (2021) ask if “decayed pieces . . . found on the floors of woodlands be given a Linnaean binomial”? We would suggest that, in some cases, yes: it might not help with determining the cladistic relationships of the parent plants but it may give vital evidence as to vegetation patterns, and historical experience has shown us that this is best recorded using a Linnaean-style binomial system of fossil-taxa.

How to structure the taxonomy of the fossils has to be a practical decision: what will be most useful to all palaeobotanists (not just those concerned with plant phylogeny). Ideally, the two imperatives should be accommodated; a taxonomy will be more useful in floristic and palaeoecological studies if it at least partly reflects the phylogenetic relationship of the parent plants; but equally, plant phylogeny will be better understood if we have an understanding of vegetation patterns and therefore plant fossil distribution. Ideally, the two functions of taxonomy need to be brought together to provide the most useful tool for all palaeobotanists. It must be recognised, however, that different types of fossils are used for different purposes and therefore need to be named and classified in different ways.

The classification outlined in the present paper should make it possible to identify leafy shoots of arborescent lycopods with more confidence and allow the stratigraphical and geographical ranges of the taxa to be recorded for use in palaeogeographical and palaeoecological interpretations. The taxa are not completely “natural” in a phylogenetic sense, but neither are they totally artificial and hopefully, as more data become available (e.g. from cuticles), it may be possible to refine the fossil-taxa so they become more congruent with the taxonomic structure

of the parent plants. But this is “a work in progress” and in the meantime it is vital that we have a working taxonomy to fulfil the various demands of all of today’s palaeobotanical community.

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Author contributions

Both co-authors have been involved in the writing of this paper.

Data availability

All of the fossils documented in this paper are in publicly available collections, as recorded in the descriptions of each species.

Disclosure statement

The authors have had no financial interest or benefit arising from the direct applications of this research.

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