



## Revision and significance of the Westphalian (Middle Pennsylvanian) arborescent lycopsid *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner

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Álvarez-Vázquez, C., Bek, J., Knight, J.A. & Wagner, R.H. 2018. Revision and significance of the Westphalian (Middle Pennsylvanian) arborescent lycopsid *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. [Revisión e importancia de la lycópsida arborescente del Westfaliense (Pensilvánico Medio) *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner]. *Spanish Journal of Palaeontology*, 33 (1), 5-40.

Manuscript received 31 January 2018

Manuscript accepted 12 April 2018

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### ABSTRACT

*Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner, a Middle Pennsylvanian lycopsid, is redescribed based on type material from England as well as 586 specimens from the Peñarroya-Belmez-Espiel Coalfield, Córdoba province, southern Spain. The species is characterized by longer than broad, smooth leaf cushions showing false leaf scars, and the presence of perennial, long, entire, single-veined leaves. A complete synonymy is presented and 21 new species (two of them with doubts), previously placed in 6 different genera, have been synonymized. Associated *Flemingites*-type cones, determined as *Flemingites russelianus*, yielded *in situ* spores of the *Lagenosporites rugosus* type and microspores of the *Microspinosporites* type.

**Keywords:** *Bergeria dilatata*, *Flemingites russelianus*, Lycopsida, Westphalian, Peñarroya-Belmez-Espiel Coalfield.

### RESUMEN

*Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner, una licópsida del Pensilvánico medio, es redescrita en base al material tipo inglés y a 586 ejemplares procedentes de la cuenca carbonífera de Peñarroya-Belmez-Espiel, provincia de Córdoba, sur de España. La especie se caracteriza por tener cojinetes foliares más largos que anchos, no ornamentados, con falsas cicatrices foliares, y por la presencia de hojas perennes, largas, enteras, univervias. Se presenta una sinonimia completa, incluyéndose en la misma 21 nuevas especies (dos de ellas con dudas) anteriormente atribuidas a 6 géneros diferentes. Los estróbilos asociados, de tipo *Flemingites*, han sido determinados como *Flemingites russelianus*, y contienen esporas *in situ* de tipo *Lagenosporites rugosus* y microsporas de tipo *Microspinosporites*.

**Palabras clave:** *Bergeria dilatata*, *Flemingites russelianus*, Lycopsida, Westfaliense, cuenca minera Peñarroya-Belmez-Espiel.

## 1. INTRODUCTION

The classic *Lepidodendron* Sternberg, 1820 is perhaps the most frequently quoted form-genus of Carboniferous lycopsids (see *Fossilium Catalogus Plantae* – Jongmans, 1913, 1929, 1936; Jongmans & Dijkstra, 1969; Dijkstra & van Amerom, 1991, 1994). It is characterised by spirally arranged, vertically elongated, rhomboidal to fusiform leaf cushions that are either contiguous or separated by narrow grooves; a rhomboidal to subtriangular leaf scar is normally situated near the middle of the cushion or a little above. The leaf scar exhibits the presence of three small pit-like impressions, the central one representing the vascular trace, and the two lateral ones aerating tissue (parichnos). In *Lepidodendron sensu stricto* two infrafoliar parichnos markings occur below the leaf scar. The presence of leaf scar and infrafoliar parichnos are determinative characters at the generic level. Although known (see references in Álvarez-Vázquez & Wagner, 2014, p. 172), stem remains with attached leaves are not normally preserved.

*Lepidodendron*, being a classic genus, has often been laxly interpreted. In fact, we consider that only a few of the more than 400 species recorded as *Lepidodendron* actually belong to this genus. Several different genera have been taken out of *Lepidodendron*, mainly (but not exclusively) on the basis of anatomical differences. Examples are: *Paralycopodites* (Morey & Morey, 1977), *Diaphorodendron* (DiMichele, 1985), *Hizemodendron* (Bateman & DiMichele, 1991) and *Synchysidendron* (DiMichele & Bateman, 1992, 1993).

In addition, two species initially attributed to *Lepidodendron* were transferred by Álvarez-Vázquez & Wagner (2014) to the little known form-genus *Bergeria* Presl in Sternberg, 1838: these are *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner and *Bergeria worthenii* (Lesquereux) Álvarez-Vázquez & Wagner. The former is reviewed in the present paper, based in the first place on the type specimen (*Lepidodendron dilatatum* Lindley & Hutton, 1831, pl. 7, fig. 2) from northern England. Secondly, a large collection from the Peñarroya-Belmez-Espiel Coalfield, in SW Spain, forms the basis for characterizing the range of variation recorded herein.

## 2. MATERIAL

More than 600 specimens (branches, leafy twigs and associated strobili), collected from upper Langsettian/lower Duckmantian and lower Bolsovian strata of the Peñarroya-Belmez-Espiel Coalfield (Fig. 1), have been available for examination. Specimens are preserved as

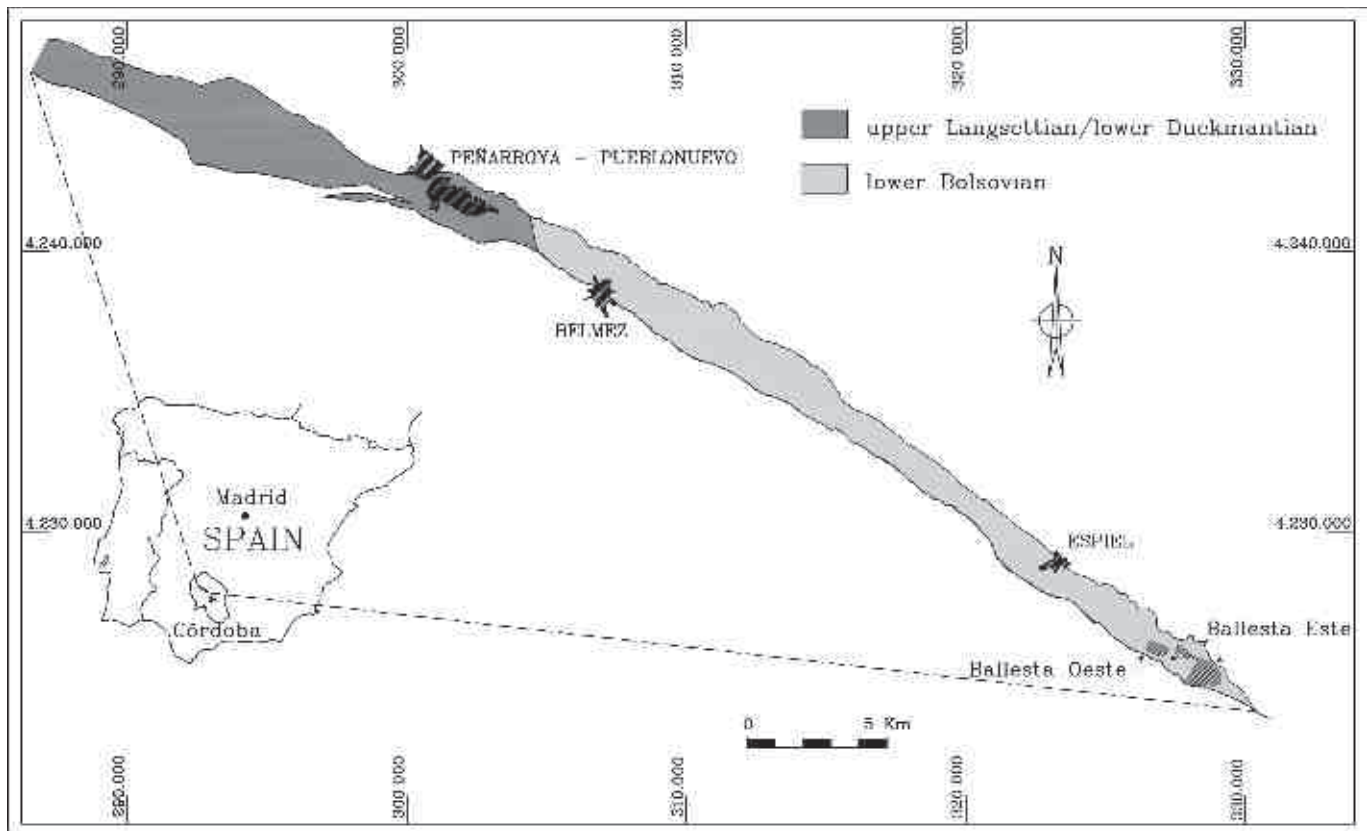
adpressions and were obtained, firstly, from boreholes and exploratory trenches made in the 1970s as part of an exploration programme by the Empresa Nacional Adaro de Investigaciones Mineras (ENADIMSA). Further material was obtained later, in the 1980s and 1990s, as a result of systematic exploration by the Geology Department of the Empresa Nacional Carbonífera del Sur, S.A. (ENCASUR) (mainly boreholes). In the years between 2003 and 2012 this collection has increased substantially by sustained sampling in the La Ballesta opencast site, at c. 5 km ESE of the village of Espiel (Fig. 1). More than half of the available specimens have come from this opencast mine (including exploratory boreholes). The large number of specimens from Peñarroya now allows morphological variation to be characterized.

The material from Spain is compared with the type material of Lindley & Hutton's *Lepidodendron dilatatum* and *Lepidodendron gracile*, both of which we regard as synonymous. The holotypes of these species are here figured photographically for the first time (Figs 2 and 3, respectively). These specimens are curated as part of the Hutton Collection, housed in the Great North Museum-Hancock, Newcastle-upon-Tyne, England.

In the collections from the Peñarroya-Belmez-Espiel Coalfield some 23 specimens of characteristic strobili have been found in close association with stems and leafy twigs of *Bergeria dilatata*. Whereas direct connection has not been unequivocally demonstrated, these are the only lycopsid fertile elements in assemblages dominated by *Bergeria dilatata*. The strobili are elongate and bisporangiate and morphologically conform to the genus *Flemingites* Carruthers emend. Brack-Hanes & Thomas. Two of these strobili have been submitted to palynological investigation in the laboratories of the Institute of Geology, Prague, Czech Republic, which also undertook bulk maceration of associated sediment from the same collection horizons. *In situ* megaspores have been identified as *Lagenosporites rugosus* type and *in situ* microspores as of *Microspinosporites orbiculus* type. These identifications are entirely consistent with *in situ* megaspores and microspores reported in strobili of *Flemingites* (Bek, 2013, 2017). The morphological characteristics of the strobili conform to *Flemingites russelianus* (Binney) Brack-Hanes & Thomas, as presented below.

## 3. GEOLOGICAL SETTING

The Peñarroya-Belmez-Espiel Coalfield occurs in a narrow NW-SE striking strip in the northwestern part of the province of Córdoba, SW Spain (Fig. 1), formed within a strike-slip controlled basin. Its preserved width nowhere exceeds 3 km and the current outcrop length is some 50 km,



**Figure 1.** Sketch map of the Peñarroya-Belmez-Espiel Coalfield showing the position of the two sub-basins and location of the Ballesta opencast site. Simplified from Álvarez-Vázquez & Cleal (2016).

although the depositional extent is estimated to have been considerably greater. The outcrop is concealed by Tertiary strata at its north-western extreme and to the south-east the outcrop wedges out against the strike-slip fault zone on the southern border of the coalfield. The coalfield has been described (Wagner, 1999, 2004, 2013) as controlled by a strike-slip fault comparable to the present-day San Andreas Fault in California, with a deduced lateral displacement of c. 150 km (Wagner, 2103).

Sub-basins have been dated as late Langsettian/early Duckmantian and (late Duckmantian?) early Bolsovian based on megafloral associations (Álvarez-Vázquez, 1995, 1999; Wagner & Álvarez-Vázquez, 2010). A full documentation of these well-sampled floras is still an ongoing process, but so far 130 taxa have been found in the two consecutive sub-basins. The total flora is based on the analysis of c. 22,000 samples with a total of some 50,000 plant fragments. This is the most complete record of a lower to middle Westphalian megaflora in the Iberian Peninsula.

The Peñarroya flora is broadly comparable with that of the well-studied Paralic Coal Belt of northern Europe, from South Wales through central and southern England into northern France, Belgium and the Ruhr District in western Germany. The fern, lycopsid and sphenopsid

species contents of the Peñarroya flora are exactly the same as in northern Europe. However, pteridosperm taxa are fewer; and, for the time being, the newly described *Wagneropteris minima* (Álvarez-Vázquez & Cleal, 2016) is the only endemic species. With regard to the Lycopsida, 19 stem taxa have been determined: *Bergeria dilatata* (the one described here), *Bergeria worthenii*, *Lepidodendron aculeatum* Sternberg, *Lepidodendron bellii* Álvarez-Vázquez & Wagner, “*Lepidodendron*” aff. *lossenii* Weiss, *Lepidophloios laricinus* (Sternberg) Sternberg, *Diaphorodendron decurtatum* (Dawson) Álvarez-Vázquez & Wagner, *Bothrodendron minutifolium* (Boulay) Zeiller, cf. *Eleutherophyllum waldenburgense* (Stur) Zimmermann, *Selaginella* sp., a new species of *Polysporia* (Álvarez-Vázquez *et al.*, in prep.), *Asolanus camptotaenia* Wood, *Sigillaria boblayi* Brongniart, *Sigillaria davreuxii* Brongniart, *Sigillaria elegans* Brongniart, *Sigillaria ovata* Sauveur, *Sigillaria polyloca* Boulay, *Sigillaria reticulata* Lesquereux, and several specimens of a still indeterminate stem with ulodendroid scars.

The above taxa are represented together by nearly 500 specimens, significantly less than the number of specimens of *Bergeria dilatata* studied here, and only about 2% of the total megaflora of the basin.



**Figure 2.** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. HM G02.16 (x 2). Holotype of *Lepidodendron dilatatum*. Figured as a drawing by Lindley & Hutton (1831, pl. 7, fig. 2). Stem fragment showing smooth, rhomboidal cushions and the characteristic long, entire, single-veined leaves inserted in the uppermost part of leaf cushions. Note the close resemblance with the stem fragment with attached leaves figured as *Lepidodendron ophiurus* by Zeiller (1886, pl. LXVIII, fig. 4); also the shape of leaf cushions with those of Presl's illustrations of *Bergeria angulata*, *Bergeria quadrata* and *Bergeria rhombica*. Origin: Low Main coal seam, Felling Colliery, near Newcastle-upon-Tyne; lower Duckmantian. Scale bar = 1 cm. Repository: Great North Museum-Hancock, Newcastle-upon-Tyne, England.

#### 4. SYSTEMATIC PALAEOLOGY

Class **LYCOPSIDA** Scott, 1909

Order **LEPIDODENDRALES**

Family **Flemingitaceae** Thomas & Brack-Hanes, 1984

Genus *Bergeria* Presl in Sternberg, 1838

Type species *Bergeria acuta* Presl in Sternberg, 1838 (a synonym of *Bergeria dilatata* – The type of the genus remains the holotype of *Bergeria acuta*).

p 1836 *Pachyphloeus* Göppert, p. 433, 468 (Göppert's *Pachyphloeus* also includes one specimen with a large ulodendroid branch scar and several decorticated, indeterminable stem fragments).

1838 *Bergeria* Presl in Sternberg, p. 138.

**Diagnosis.** After Álvarez-Vázquez & Wagner (2014). Arborescent lycopsid stems covered with spirally arranged, rhomboidal to fusiform leaf cushions, longer than broad,

contiguous or separated by narrow grooves, without a differentiated leaf scar. Leaves long, grass-like to linear-lanceolate, entire, single-veined.

**Remarks.** As previously mentioned by Álvarez-Vázquez & Wagner (2014), *Bergeria* encompasses lycopsid specimens that lack a differentiated leaf scar. When leaves are preserved, they occupy the upper part of leaf cushions, to which they are attached by their entire width. If leaves are detached, a small, irregular scar marks the position of the leaf base at the top of leaf cushion; these would be the “false leaf scars” of Chaloner & Boureau (*in* Boureau, 1967, p. 533).

However, since the beginning of the last century, the name *Bergeria* has commonly been applied to decorticated stems of lycopsids showing lepidodendroid leaf cushions. This has been in error. While Brongniart (1838, p. 35) recognized that both *Ulodendron* (a related genus) and *Bothrodendron* only represented different states of preservation of *Lepidodendron*, the error with respect to *Bergeria* probably originated with Fischer (1905), who figured and described as *Bergeria* adpression material with subepidermal preservation, thus lacking the outline of leaf scars. Fischer (1905, figs 5, 7) seems to have confused partially decorticated remains with better-preserved specimens possessing a false leaf scar (Fischer, 1905, fig. 6). This seems to be the reason why Fischer included type specimens of *Bergeria acuta*, the type species of the genus, with decorticated remains. The error was perpetuated by later authors.

Álvarez-Vázquez & Wagner (2014) interpreted the type specimens of *Bergeria acuta* (Presl *in* Sternberg, 1838, Taf. XLVIII, figs 1a, 1b; Kvaček & Straková, 1997, pl. 2, figs 3, 4) as being well-preserved stem fragments that are not decorticated and show the outline of leaf cushions as well as an irregular, poorly defined scar at the top of the leaf cushion. Previously, Lindley & Hutton (1831, pl. 7, fig. 2; copy in Álvarez-Vázquez & Wagner, 2014, fig. 13; here Fig. 2) had introduced *Lepidodendron dilatatum*, illustrated by a drawing of a single specimen displaying the same cushion characters as Presl’s *Bergeria acuta*, and showing leaves in attachment. *Lepidodendron dilatatum* was introduced earlier than *Bergeria acuta*, so that the correct name for the species is *Bergeria dilatata*, as pointed out by Álvarez-Vázquez & Wagner (2014).

*Ulodendron* was introduced by Lindley & Hutton (1831) to include stem adpressions bearing large, subcircular branch scars showing an umbilicus in its central part; these scars are placed in vertical rows. Two species were initially distinguished, viz. *Ulodendron majus* (Lindley & Hutton, 1831, pl. 5), based on a specimen from the Bensham coal seam, Jarrow Colliery, Newcastle-upon-Tyne (Duckmantian), possessing broader than long leaf cushions and large, well-separated branch scars; and *Ulodendron minus* (Lindley & Hutton, 1831, pl. 6), with

rhomboidal, more equidimensional leaf cushions and smaller, closely spaced (separated by less than 1 cm) branch scars, originating from the High Main coal seam, South Shields Colliery, Durham (also Duckmantian). Andrews (1955) designated *Ulodendron majus* as the genotype.

References to *Ulodendron* most commonly focus on the nature of the branch scars (corresponding either to strobilar or branch detachment), and their taxonomic significance. However, *Ulodendron* has been used in very different ways, and most species are represented only by their type specimens. Kidston (1885) reviewed the various references that existed until that date and concluded that *Ulodendron majus* and *Ulodendron minus* would be synonymous with *Sigillaria discophora* (Koenig) Kidston. He also included Lindley & Hutton’s (1833) *Bothrodendron punctatum* in the synonymy. Bureau (1913-14), when figuring several specimens with ulodendroid scars, rightly regarded the absence of leaf scars (i.e. permanent leaves) as the most important difference between *Ulodendron* and *Lepidodendron*.

On the other hand, Jonker (1976) synonymized both *Ulodendron majus* and *Ulodendron minus* with *Lepidophloios larinus*. Ulodendroid scars are, in fact, rather common in *Lepidophloios*. We concur with Jonker’s attribution of *Ulodendron majus* and *Ulodendron minus* to *Lepidophloios*, as defined on adpression material, but believe that two different species are involved. Since a number of arborescent lycopsids of Pennsylvanian age possessed branch scars, occurring either singly or in vertical rows, the presence or absence of such scars cannot be used for a generic distinction.

Thomas (1967) emended the diagnosis of *Ulodendron* so as to include cuticular characteristics. His study was based on the epidermal character of specimens, which he determined as *Ulodendron majus*; he did not investigate this character in Lindley & Hutton’s type material. According to Thomas (1967), the genus *Ulodendron* would be characterised by rhomboidal leaf cushions, broader than long, the presence of persistent linear leaves and large circular scars situated in vertical rows. This redefinition of the genus, based on cuticular material from a fragmentary and incompletely illustrated specimen, appears to generate more confusion around the genus, requiring systematic analysis beyond the scope of the present work. The diagnostic characteristics used by Thomas (1967) are such as to rule out any confusion with *Bergeria*; of particular relevance are the relative dimensions of the leaf cushions and the presence of a ligule pit used as diagnostic for *Ulodendron*. However, confusion has arisen from the redesignation by Thomas (1968) of material labelled as *Lepidodendron landsburgii* Kidston to *Ulodendron*. This latter species is here considered synonymous with *Bergeria dilatata*; not surprisingly Thomas’s (1968) description of this material is closely similar to that recognised here

for the species. The assignment of Kidston's species to *Ulodendron* is here considered incorrect.

DiMichele (1980) noted the similarities between the permineralized genus *Paralycopodites*, characterized by persistent leaves, and the adpression genus *Ulodendron* (*sensu* Thomas), but kept these two genera as separate taxonomic entities in view of the absence of anatomical characters in *Ulodendron*. According to DiMichele (1980), stems of *Paralycopodites* are frequently associated with bisporangiate strobili showing microsporangia in the upper part and megasporangia in the lower part (i.e., a *Flemingites* type cone).

In contrast, Pearson (1986) synonymized both *Ulodendron* and *Paralycopodites* with *Anabathra* (Witham, 1833), a genus based on a single specimen showing both external characters and internal anatomy. The holotype of the type species, *Anabathra pulcherrima* Witham, from uppermost Tournaisian/Viséan strata of Allanbank, Berwickshire, Scotland, was fully documented by Pearson (1986), who concluded that it is conspecific with *Paralycopodites brevifolius* (Williamson) DiMichele. Since the latter is a synonym of the type species, *Paralycopodites minutissimum* Morey & Morey, Pearson placed *Paralycopodites* in synonymy with *Anabathra*, including it in the Flemingitaceae of Thomas & Brack-Hanes (1984). Subsequently, DiMichele & Phillips (1994, p. 59) restricted *Anabathra* to the type material; they regarded the type specimen of *Anabathra* as being too fragmentary to justify its synonymy with *Paralycopodites*. This may be regarded as a viable argument, but has no direct relevance to the nomenclature of material preserved as adpressions (as the one studied here).

**Comparisons.** *Lepidodendron Sternbergii* is distinguished by its vertically elongate, rhomboidal or fusiform leaf cushions. Leaf scars are situated either centrally or on the upper half of the cushions, and show a leaf trace as well as two foliar parichnos; two infrafoliar parichnos are also present, as is a ligule pit above the scar. It is rare to find specimens with attached leaves.

The Namurian genus *Meyenodendron* (Thomas & Spicer, 1986) possesses persistent leaves attached to the upper part of leaf cushions. However, cushions are obovate, with rounded upper and lateral angles and an infrafoliar bladder in the upper half of the cushion. There is no parichnos, and a ligule is visible in its upper part.

The Mississippian genus *Tomiodendron* (Radczenko, 1956; Meyen, 1972, 1976), initially described from Angaraland, includes ligulate stems with longitudinally elongate leaf cushions showing a small, subtriangular leaf scar in its upper part and a vascular trace in the centre. Attached, spirally arranged, short, falcate leaves have been reported for the Viséan *Tomiodendron variabilis* by Thomas & Purdy (1982).

The Permian, Gondwanaland genus *Brasilodendron* (Chaloner *et al.*, 1979; Spiekermann *et al.*, 2018) is characterized by persistent leaves attached to fusiform leaf cushions. *Brasilodendron* leaves are attached to the middle part of the cushions, not at the cushion apex as in *Bergeria*. Also, leaves have a sigmoidal profile: they are first attached perpendicularly to the stem, then turning parallel to the axis, and the distal part is finally directed away from the stem. In addition, leaf margins show irregular fimbriae.

*Bergeria dilatata* (Lindley & Hutton, 1831) Álvarez-Vázquez & Wagner, 2014  
(Figs 2-10b)

\* v 1831 *Lepidodendron dilatatum* Lindley & Hutton, p. 27, pl. 7, fig. 2 (here Fig. 2).

\* 1831 *Lepidodendron gracile* Lindley & Hutton, p. 30, pl. 9, figs 1, 2 (included in *Lepidodendron ophiurus* by Kidston, 1891, and in *Bergeria dilatata* by Álvarez-Vázquez & Wagner, 2014).

1831 *Lepidodendron Sternbergii*, Lindley & Hutton, p. 15-21, pl. 4.

p 1834 *Lepidodendron Sternbergii*, Lindley & Hutton, p. 83, pl. 112, figs B, C; non pl. 112, fig. A (= *Lepidophloios laricinus*).

v p 1834 *Lepidodendron selaginoides*, Lindley & Hutton, p. 85-86, pl. 113 (the specimen figured as *Lepidodendron selaginoides* by Lindley & Hutton, 1831, pl. 12 has not been included in our list of synonymy since its revision in the collections of the Hancock Museum has allowed verification that it must be included in *Bothrodendron minutifolium*).

v 1834 *Lepidodendron elegans*, Lindley & Hutton, p. 99-100, pl. 118 (included in the synonymy of *Lepidodendron similis* by Kidston in Jongmans, 1909) (see Figs 3, 4).

p 1834 *Lepidodendron Sternbergii*, Mammatt, pl. 63, fig. 144a; non pl. A9 (cushions with leaf scars).

? 1834 *Lepidodendron Dilatatum*, Mammatt, pl. 75, fig. 8; pl. 77, fig. 10; pl. A2 (cannot be judged correctly from the diagrammatic drawings).

? 1834 *Lepidodendron Dichotomum*, Mammatt, pl. A3.

p 1836 *Pachyphloeus tetragonus* Göppert, p. 433, 468, Tab. XLIII (cited as Tab. XLI in the text), fig. 2 (figured upside down); non Tab. XLIII, figs 1, 3, 4 (decorticated, indeterminable stems?); non Tab. XLIII, fig. 5 (ulodendroid branch scar).

\* 1838 *Bergeria acuta* Presl in Sternberg, p. 184, Taf. XLVIII, figs 1a, 1b (acc. to Álvarez-Vázquez & Wagner, 2014).

- \* 1838 *Bergeria angulata* Presl in Sternberg, p. 184, Taf. LXVIII, fig. 17 (synonym of *Lepidodendron acutum*, acc. to Němejc, 1947; to *Bergeria dilatata* acc. to Álvarez-Vázquez & Wagner, 2014).
- \* 1838 *Bergeria marginata* Presl in Sternberg, p. 184, Taf. LXVIII, fig. 16 (synonym of *Lepidodendron acutum*, acc. to Němejc, 1947; to *Bergeria dilatata* acc. to Álvarez-Vázquez & Wagner, 2014).
- \* 1838 *Bergeria quadrata* Presl in Sternberg, p. 184, Taf. LXVIII, fig. 19 (*Lepidodendron acutum*, acc. to Němejc, 1947; to *Bergeria dilatata* acc. to Álvarez-Vázquez & Wagner, 2014).
- \* 1838 *Bergeria rhombica* Presl in Sternberg, p. 184, Taf. LXVIII, fig. 18 (synonym of *Lepidodendron acutum*, acc. to Němejc, 1947; to *Bergeria dilatata* acc. to Álvarez-Vázquez & Wagner, 2014).
- ? 1838 *Lepidodendron elegans*, Brongniart, p. 85, pl. 14, figs 1-2A (two specimens with medium-sized, repeatedly dichotomized, leafy branches. The enlarged image shows leaf scars, so a revision of the original material would be needed).
- 1838 *Lepidodendron*, Brongniart, pl. 30, figs 1-2A (two specimens with attached leaves).
- 1848 *Lepidodendron dilatatum*, Sauveur, pl. LX, fig. 3 (stem fragment with obovate cushions and long leaves similar to holotype).
- \* 1848 *Lepidodendron gibbosum* Sauveur, pl. LX, fig. 4.
- 1848 *Lepidodendron sternbergii*, Sauveur, pl. LIX, fig. 1 (dichotomized branches).
- 1852 *Lepidodendron dilatatum*, Owen, Tab. VI, fig. 5.
- 1852 *Lepidodendron obovatum*, Owen, Tab. VI, fig. 2.
- \* 1854 *Lepidodendron Haidingeri* von Ettingshausen, p. 55, Taf. 22; Taf. 23, figs 1, 2 (acc. to Álvarez-Vázquez & Wagner, 2014).
- ? 1855 *Lepidodendron elegans*, Phillips, p. 235, fig. 115.
- \* 1859-60 *Knorria apicalis* Eichwald, p. 154-155, pl. XII, fig. 1.
- \* p 1859-60 *Sagenaria Glincana* Eichwald, p. 127-130, pl. V, fig. 21 (dichotomized branches); pl. Va, figs 6, 7; non pl. V, fig. 22 (decorticated); non pl. Va, figs 1-3, 5 (= "*Lepidodendron*" *rimosum*); non pl. Va, fig. 4 (decorticated).
- p 1859-60 *Sagenaria undulata*, Eichwald, p. 126-127, pl. VIII, fig. 8; non pl. IX, fig. 1 (difficult to judge).
- \* 1859-60 *Ulodendron pumilum* Eichwald, p. 144-146, pl. X, fig. 5 (with ulodendroid branch scar).
- \* p 1859-60 *Ulodendron transversum* Eichwald, p. 139-140, pl. IX, fig. 8 (with ulodendroid branch scar); non pl. VI, fig. 13 (decorticated).
- \* 1860 *Lepidodendron Oweni* Wood, p. 239, pl. 5, fig. 1 (acc. to Álvarez-Vázquez & Wagner, 2014).
- 1868 *Lepidodendron dilatatum*, von Roehl, p. 134, Taf. VIII, fig. 4.
- 1870-74 *Lepidodendron Sternbergii*, Schimper, p. 19, pl. LVIII, figs 1-4.
- 1875 *Sagenaria elegans*, Feistmantel, p. 203-204, Taf. XXXVII, fig. 3.
- 1875 *Bergeria rhombica*, Feistmantel, p. 200-201, Taf. XLI, figs 3-4a.
- 1878 *Lepidodendron lycopodioides*, Zeiller, pl. CLXXI (large stem fragment and small leafy branches, isotomously forked, similar to that figured as *Lepidodendron elegans* by Lindley & Hutton, 1834, pl. 118).
- \* 1879-80 *Lepidodendron lanceolatum* Lesquereux, p. 369, pl. LXIII, figs 3-5.
- \* ? 1879-80 *Lepidodendron Scutatatum* Lesquereux, p. 369, pl. LXIII, figs 6-6c (presence or absence of leaf scars is not clear from the drawings – acc. to Álvarez-Vázquez & Wagner, 2014).
- 1879-80 *Lepidodendron rhombicum*, Lesquereux, p. 382, pl. LXII, figs 4, 4a; pl. LXIV, fig. 18.
- ? 1884 *Lepidodendron (Bergeria) marginatum*, Lesquereux, p. 784, pl. CVII, fig. 3.
- p 1886-88 *Lepidodendron Haidingeri*, Zeiller, p. 461-463, pl. LXIX, fig. 1; non pl. LXIX, fig. 1A (drawing which shows a leaf scar).
- 1886-88 *Lepidodendron lycopodioides*, Zeiller, p. 464-467, pl. LXIX, figs 2-3A; pl. LXX, fig. 1 (same as Zeiller, 1878, pl. CLXXI; included by Kidston, 1911 in his *Lepidodendron simile*).
- p 1886-88 *Lepidodendron ophiurus*, Zeiller, p. 458-461, pl. LXVIII, figs 1-1A, figs 4-6A; non pl. LXVIII, figs 2, 3 (strobili).
- ? 1886-88 *Ulodendron majus*, Zeiller, p. 481-483, pl. LXXIII, fig. 1 (although leaf cushions shape and other features seem to correspond those of *Bergeria dilatata*, Zeiller mentioned leaves 250 mm long, much longer than those in our specimens).
- ? 1887 *Lepidodendron lanceolatum*, Kidston, p. 394, pl. XXVII, fig. 5 (small branch with strobilus); pl. XXVIII, figs 3, 4.





p 1888 *Lepidodendron Sternbergii*, Howse, p. 78, 79, 80, 81 (*Lepidodendron dilatatum* quoted as a synonym).

\* 1893 *Lepidodendron Landsburgii* Kidston, p. 338-339, pl. III, figs 9-9a; pl. III, figs 10-10b (transferred to *Ulodendron* by Thomas, 1968; to *Anabathra* by Pearson, 1986; and regarded as synonymous with *Bergeria dilatata* by Álvarez-Vázquez & Wagner, 2014).

1899 *Lepidodendron lanceolatum*, White, p. 192-195, pl. LIII, figs 2-2a.

1903a *Lepidodendron lycopodioides*, Arber, p. 12, pl. II, fig. 5.

1903b *Lepidodendron lycopodioides*, Arber, p. 19, text-fig. (without number).

p 1903 *Lepidodendron Glincanum*, Kidston, pl. III, figs 27, 28; non p. 762-765, pl. II, figs 20, 21 (= *Lepidodendron canobianum* Crookall acc. to Crookall, 1964); pl. IV, figs 37-40 (= *Lepidodendron canobianum*); pl. V, figs 41-31 (= *Lepidodendron canobianum*).

1904 *Lepidodendron ophiurus*, Zalessky, p. 23-25 [95-96], pl. V, figs 1-3, fig. 4 (leafy twigs), figs 6-7.

1904 *Ulodendron* sp., Zalessky, p. 36-37 [101-102], pl. VI, fig. 5 (medium-sized branch with attached leaves); text-figs 7-8.

\* ? 1907 *Lepidodendron Tonderae* Zalessky, p. 28-29 [60-61], Taf. I, fig. 7 (cushions with a well-marked keel); text-fig. 6 (drawing).

1907 *Ulodendron* sp., Zalessky, p. 29-30 [61], text-figs 7, 8.

p 1909 *Lepidodendron similis* Kidston in Jongmans, p. 174, 201, 215 (*nomen nudum* – Although *Lepidodendron simile* is very often cited and figured as a separate species, the specific name *similis* was published without a proper diagnosis, description or figuration. Only a list of synonymy was provided: 1) *Lepidodendron elegans*, Lindley & Hutton, 1834, pl. 118 – here included in *Bergeria dilatata*; 2) *Lepidodendron elegans*, Brongniart, 1838, pl. 14, figs 1-2A – also included here, with doubt, in *Bergeria dilatata*; 3) *Lepidodendron lycopodioides*, Zeiller, 1878, pl. CLXXI – here included in *Bergeria dilatata*; 4) *Lepidodendron lycopodioides*,

Renault, 1882, pl. 5, fig. 8 – cushions with leaf scars and short, well-marked transverse lines in the lower part of leaf cushions; and 5) *Lepidodendron lycopodioides*, Zeiller, 1886, pl. LXIX, figs 2-3A; pl. LXX, fig. 1 – here included in *Bergeria dilatata*).

p 1911 *Lepidodendron simile* Kidston, p. 137-138 (excluding Renault's 1882, pl. 5, fig. 8 – Kidston repeated his 1909 list of synonymy, except Lindley & Hutton's illustration of *Lepidodendron elegans* which he compared at that time with *Lepidodendron lycopodioides*. A proper diagnosis, description or illustration is lacking).

? 1912 *Lepidodendron lanceolatum*, Arber, p. 250, pl. 12, fig. 14 (with short, well-marked transverse lines in lower part of leaf cushions).

\* 1913-14 *Lycopodites foliosus* Bureau, p. 160, pl. XXIX, figs 1-3.

p ? 1913-14 *Lepidodendron lycopodioides*, Bureau, p. 118-121; pl. XXXI, fig. 1; pl. XXXII, fig. 1; pl. XXXIII, figs 1-2 (small branches bearing strobili); pl. XXXIV, figs 1-2 (leafy twigs); non pl. XXVIII, fig. 5 (?); non pl. XXXIII, fig. 3 (strobilus); non pl. XXXIV, figs 3-6 (strobili).

p 1913-14 *Lepidodendron Veltheimianum*, Bureau, p. 136-142, pl. XXX<sup>BIS</sup>, figs 1-1B (leafy twigs isotomously forked at acute angles – Bureau also mentioned *Lepidodendron lycopodioides* in association); pl. XXXI, figs 2-3 (leafy twigs); non pl. II, fig. 6 (decorticated specimen resembling *Lepidodendron lossenii* Weiss); non pl. IV, fig. 1 (to be compared with *Lepidodendron lossenii*); non pl. XXXIX, figs 4-4A (= *Lepidodendron veltheimii* Sternberg); non pl. XL, figs 4-4A (= *Lepidodendron veltheimii*); non pl. XLIII, figs 1-1B (= *Lepidodendron lossenii*), fig. 2 (indeterminable, decorticated specimen); non pl. XLIV, figs 1-2 (decorticated), fig. 3 (too fragmentary to be identified specifically); ? non pl. XLV, figs 1-2 (ulodendroid branch scars).

? 1914 *Lepidodendron lanceolatum*, Arber, p. 402, pl. 28, fig. 26 (short transverse markings in the lower part of leaf cushions).

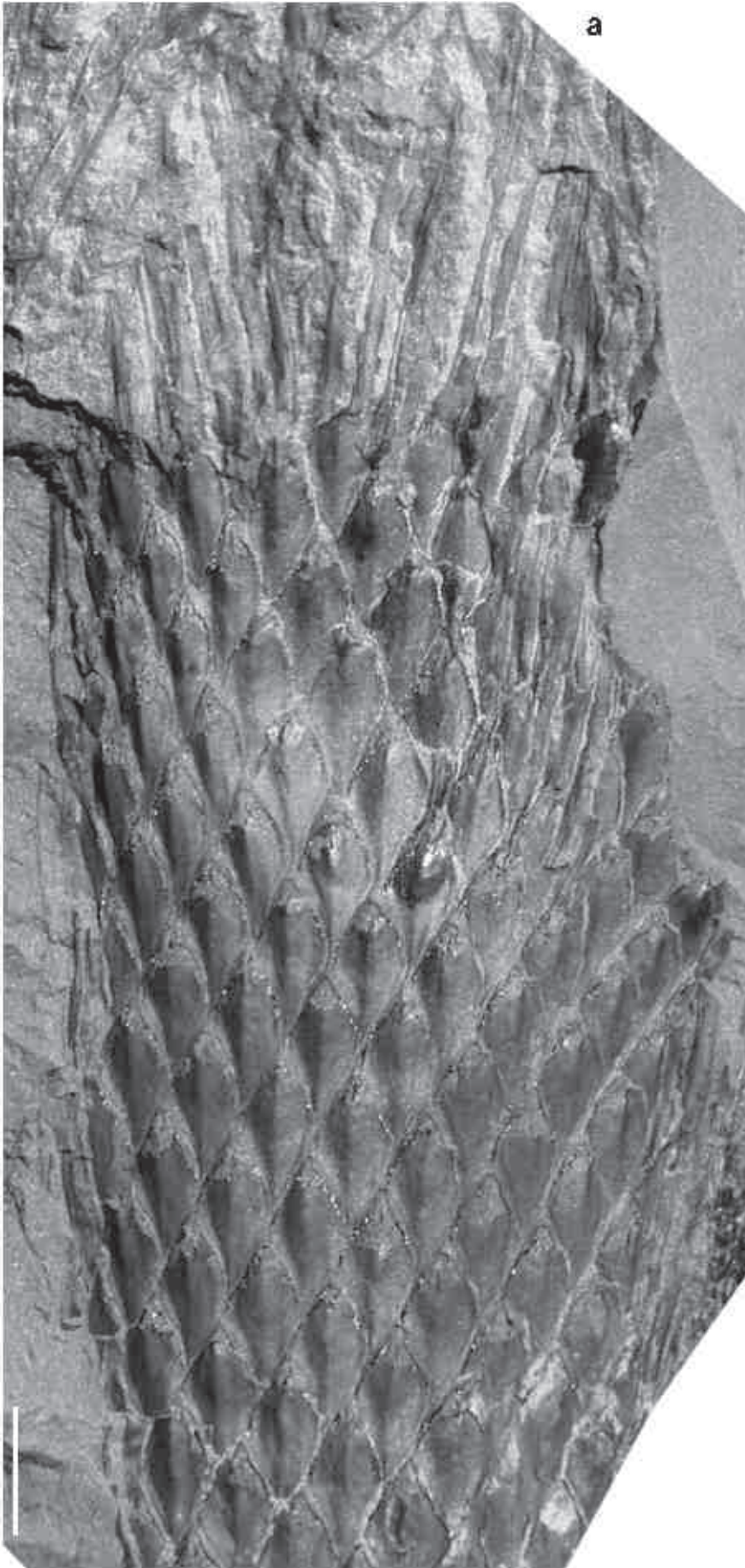
1916 *Bergeria angulata*, Hörich, p. 428, fig. 3 (photograph of Presl's 1838, Taf. LXVIII, fig. 17).

**Figure 3.** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. HM G02.17 (x 0.75). Large stem (lower left corner) with leafy twigs branching isotomously at acute angle. Part of the specimen figured as *Lepidodendron elegans* by Lindley & Hutton (1834, pl. 118 – Fig. 4 here). Note the resemblance with the stem fragment with attached leaves and small leafy branches figured as *Lepidodendron lycopodioides* by Zeiller (1878, pl. CLXXI; 1886, pl. LXX, fig. 1). Origin: Low Main coal seam, Felling Colliery, Newcastle-upon-Tyne; lower Duckmantian. Scale bar = 1 cm. Repository: Great North Museum-Hancock, Newcastle upon Tyne, England.



**Figure 4.** Copy, reduced to less than half, of the original figure published by Lindley & Hutton (1834, pl. 118) as *Lepidodendron elegans*.

- 1922 *Lepidodendron lycopodioides*, Arber, p. 191-195, pl. 10, figs 1-9; pl. 11, figs 10, 11, fig. 12 (cf.), fig. 13, fig. 14 (with doubt), figs 15A-16.
- 1922 *Lepidodendron lanceolatum* (= *L. lycopodioides*), Arber, p. 195-196, pl. 11, fig. 17; pl. 12, figs 18-22.
- 1925 *Lepidodendron simile*, Crookall, p. 391, pl. XVI, fig. 2.
- 1928 *Lepidodendron* sp., Šusta, Taf. VIII, Abb. 2 (small branches with associated strobili); Taf. LVIII, Abb. 4; Taf. LXII, Abb. 1.
- 1929 *Lepidodendron lanceolatum*, Crookall, pl. XX, fig. a.
- ? 1929 *Lepidodendron acutum*, Crookall, pl. XX, fig. f (small branches with strobili – difficult to judge from the illustration).
- 1929 *Lepidodendron simile*, Crookall, pl. XX, fig. d (same as Crookall, 1925, pl. XVI, fig. 2).
- 1929 *Lepidodendron lycopodioides*, Gothan & Franke, p. 73, Taf. 30.2 (drawing).
- 1932 *Lepidodendron lycopodioides*, Crookall, pl. VI, fig. 5.
- 1932 *Lepidodendron ophiurus*, Crookall, pl. VII, fig. 4 (leafy twigs; difficult to judge from the illustration at natural size).
- \* ? 1934 *Lepidodendron adygense* Zalessky, p. 4-5 (16-17), 20, 21, pl. II, fig. 5; pl. IX, figs 2-2a.
- 1937 *Lepidodendron ophiurus*, Jongmans, p. 397, pl. 15, figs 23-24.
- 1938 *Ulodendron lycopodioides*, Renier & Stockmans in Renier *et al.*, p. 63, pl. 15 (in association with one strobilus attributed to *Ulostrobos geinitzii*).
- ? 1938 *Lepidodendron lycopodioides*, Bell, p. 93-94, pl. XCVI, fig. 2, fig. 3 (presence or absence of leaf scars is unclear); pl. XCVII, figs 1-3 (small leafy branches).
- p 1940 *Lepidodendron ophiurus*, Bell, p. 123, pl. VII, figs 5, 7; non pl. VII, fig. 6 (indeterminable; single leaf cushion with attached leaf).
- 1942 *Lepidodendron simile*, Němejc, p. 140, Tab. IV, fig. 2; Tab. IV, figs 3, 4 (with doubt – difficult to judge from the illustration).
- v 1944 *Lepidodendron lanceolatum*, Bell, p. 88-89, pl. XLVIII, fig. 3 (leafy twigs with terminal strobili).
- p 1947 *Lepidodendron simile*, Němejc, p. 68-72, Tab. I, figs 9-10; non Tab. I, fig. 1 (= “*Lepidodendron*” *ophiurus*), figs 2-3 (= “*Lepidodendron*” *ophiurus*?).
- 1949 *Lepidodendron lanceolatum*, Arnold, p. 165-167, pl. V; pl. VI, figs 4-6.
- p 1949 *Lepidodendron ophiurioides*?, Arnold, pl. IV, fig. 5; non p. 162-165, pl. III, fig. 4 (= *Lepidodendron ophiurioides*); pl. IV, figs 1-3 (= *Lepidodendron ophiurioides*) (Arnold compared with “*Lepidodendron*” *ophiurus* and *Lepidodendron lycopodioides*).
- 1949 *Lepidodendron vestitum*, Arnold, p. 168-169, pl. II, fig. 5.
- 1949 *Lepidodendron ophiurus*, Jongmans, p. 41, Afb. 1.25 (profusely branched specimen).
- 1951 *Lepidodendron* cf. *ophiurus*, Jongmans, p. 11, 12, pl. III, figs 22-22a, 29-29a.
- 1951 *Lepidodendron* groupe *ophiurus*, Jongmans, p. 21, 23, pl. XI, fig. 97; pl. XII, figs 98-99a (leafy branches); pl. XV, fig. 133.
- ? 1951 *Lepidodendron ophiurus*, Jongmans, p. 22, pl. XIV, fig. 123 (leafy twigs which cannot be judged adequately from the illustration).
- 1952 *Lepidodendron acutum*, Jongmans, p. 8, pl. II, figs 13-16 (leafy branches); pl. XIII, fig. 97 (leafy branches).
- p 1952 *Lepidodendron obovatum*, Jongmans, p. 8, pl. II, figs 17, 18; non pl. XVII, figs 136-136a (= *Lepidophloios*?); non pl. XX, fig. 151 (= *Lepidodendron bellii*).
- p 1952 *Lepidodendron obovatum*, Novik, Tab. XXV, fig. 1; non Tab. XXV, fig. 2 (difficult to judge), fig. 3 (resembles *Lepidodendron bellii*).
- 1952 *Lepidodendron adygense*, Novik, p. 187, 459, pl. XXIX, figs 1, 2 (same as Zalessky, 1934, pl. IX, figs 2-2a).
- \* 1952 *Ulodendron Goodei* Stockmans & Willière, pl. E, fig. 1 (associated with *Ulostrobos goodei*), pl. E, fig. 3 (three times isotomously forked leafy twigs); pl. F, fig. 2 (leafy twigs associated with *Ulostrobos goodei*). (Although Stockmans & Willière’s specimens are leafy twigs, which are difficult to judge properly from the illustrations, all originate from a locality that also yielded two specimens with small cushions identified as *Ulodendron* sp. by Stockmans & Willière and which we here assigned to *Bergeria dilatata* – see below).
- 1952 *Ulodendron* sp., Stockmans & Willière, pl. E, figs 4, 5.
- 1953 *Lepidodendron ophiurus*, Jongmans, p. 39, pl. 2, figs 9-10a; pl. 3, figs 11-11a (leaf cushions with short wrinkles in the lower part), figs 12-12a.
- 1953 *Ulodendron* sp., Stockmans & Willière, pl. XXIV, fig. 7.
- 1954 *Lepidodendron lycopodioides*, Novik, p. 50-51, 134, Tab. X, fig. 1.



1957 *Lepidodendron lycopodioides*, Gothan & Remy, p. 67, Abb. 57.

v 1959 *Lepidodendron ophiurus*, Jongmans in Wagner, p. 399.

1959 *Sublepidodendron lycopodioides*, Remy & Remy, p. 100, 103, Abb. 79a-79b.

v 1960 *Lepidodendron simile*, Wagner, p. 82, 84-86, figs 22c, 23a, 24a-24f.

p 1962 *Lepidodendron bretonense*, Bell, pl. XLIX, fig. 2; non p. 53-54, pl. XLVII, fig. 5 (= *Diaphorodendron decurtatum* acc. to Álvarez-Vázquez & Wagner, 2014), fig. 6 (decorticated specimen comparable with "*Lepidodendron*" *rimosum* acc. to Álvarez-Vázquez & Wagner, 2014); non pl. XLVIII, fig. 4 (= *Diaphorodendron decurtatum*), fig. 6 (specimen with elongate, fusiform leaf cushions comparable with "*Lepidodendron*" *rimosum*).

p 1962 *Lepidodendron pictoense*, Bell, p. 52-53, pl. XLVI, fig. 1; pl. XLIX, fig. 3; pl. L, figs 1-3; non pl. XLIX, fig. 1.

1964 *Lepidodendron acutum*, Crookall, p. 285-287, pl. LX, fig. 2 (leaf cushions with barely distinct keels crossed with short wrinkles, showing also attached leaves); text-fig. 92 (copy of Presl in Sternberg, 1838, Taf. XLVIII, fig. 1b).

p 1964 *Lepidodendron ophiurus*, Crookall, pl. LXI, fig. 4 (several times dichotomized leafy twigs); pl. LXI, fig. 9 (same as Crookall, 1932, pl. VI, fig. 5); pl. LXIII, figs 1, 2 (syntypes of *Lepidodendron landsburgii*); non p. 287-294, pl. LXII, fig. 5 (= "*Lepidodendron*" *ophiurus*); non pl. LXX, fig. 7 (compared with "*Lepidodendron*" *volkmannianum* by Álvarez-Vázquez & Wagner, 2014); non pl. LXXIII, fig. 4 (branchlet with terminal strobilus); non text-fig. 93 (copy of "*Lepidodendron*" *ophiurus* Brongniart, 1822).

1964 *Ulodendron* sp., Dräger, p. 69, Taf. 12, fig. 1.

v 1965 *Lepidodendron simile*, Wagner, p. 17, pl. 9, fig. 11 (same as Wagner, 1960, fig. 24b).

1966 *Lepidodendron ophiurus*, Bell, pl. XX, fig. 1 (same as Bell, 1940, pl. VII, fig. 7).

1966 *Lepidodendron pictoense* (= ? *L. ophiurus*), Bell, pl. IV, fig. 13 (leafy twigs); pl. XXIX, fig. 1.

p 1966 *Lepidodendron lycopodioides*, Greber, p. 108-109, pl. XLVI, figs 1-1a; non pl. XLVI, figs 4-5 (cannot be judged from the illustration).

1967 *Lepidodendron acutum*, Chaloner & Boureau in Boureau, p. 537.

p 1967 *Lepidodendron simile*, Chaloner & Boureau in Boureau, p. 549, figs 377A-377B, fig. 379; non fig. 378 (leafy branches several times dichotomized associated with *Flemingites dubius* cones; previously figured in Chaloner, 1953).

k 1968 *Ulodendron landsburgii*, Thomas, p. 426-428, text-fig. A (drawing), text-figs C-D (drawings of cuticle).

? 1969 *Lepidodendron*, Daber, Taf. VIII, figs 1, 1a (difficult to judge).

1972a *Lepidodendron obovatum*, Bițoianu, pl. I, fig. 1 (figured upside down).

1972a *Lepidodendron ophiurus*, Bițoianu, pl. I, fig. 2.

1972a *Lepidostrobos* sp., Bițoianu, pl. III, fig. 26.

1972b *Lepidodendron acutum*, Bițoianu, pl. I, fig. 1 (same as Bițoianu, 1972a, pl. I, fig. 1).

? 1972b *Lepidodendron obovatum*, Bițoianu, pl. I, fig. 2 (difficult to judge from the poor illustration).

1972b *Lepidostrobos* sp., Bițoianu, pl. I, fig. 3 (same as Bițoianu, 1972a, pl. III, fig. 26).

1972 *Lepidodendron subdichotomum*, Maithy, p. 85, pl. 49, fig. 1; text-fig. 2A.

? 1972 *Lepidodendron ophiurus*, Maithy, p. 86, pl. 49, fig. 2; text-fig. 2B (specimen with short transverse marks in lower part of cushions).

1972 *Lepidodendron lycopodioides*, Migier, Tab. I, fig. 2.

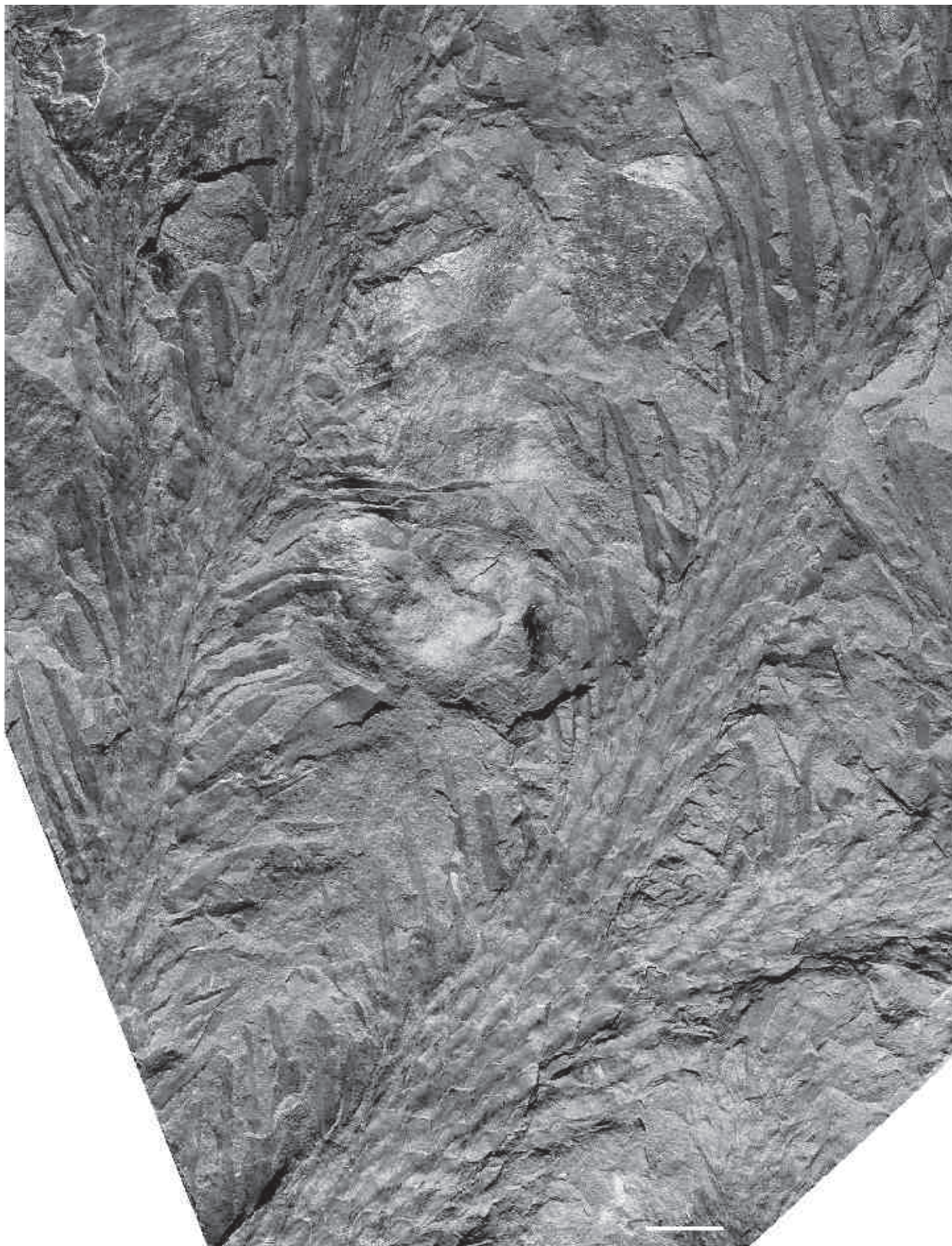
1973 *Lepidodendron acutum*, Bassett & Edwards, p. 14 (figure).

? 1973 *Lepidodendron* cf. *lanceolatum*, Bassett & Edwards, p. 21 (figure below).

? 1973 *Lepidodendron acutum*, Bițoianu, pl. I, fig. 1 (same as Bițoianu, 1972b, pl. I, fig. 2).

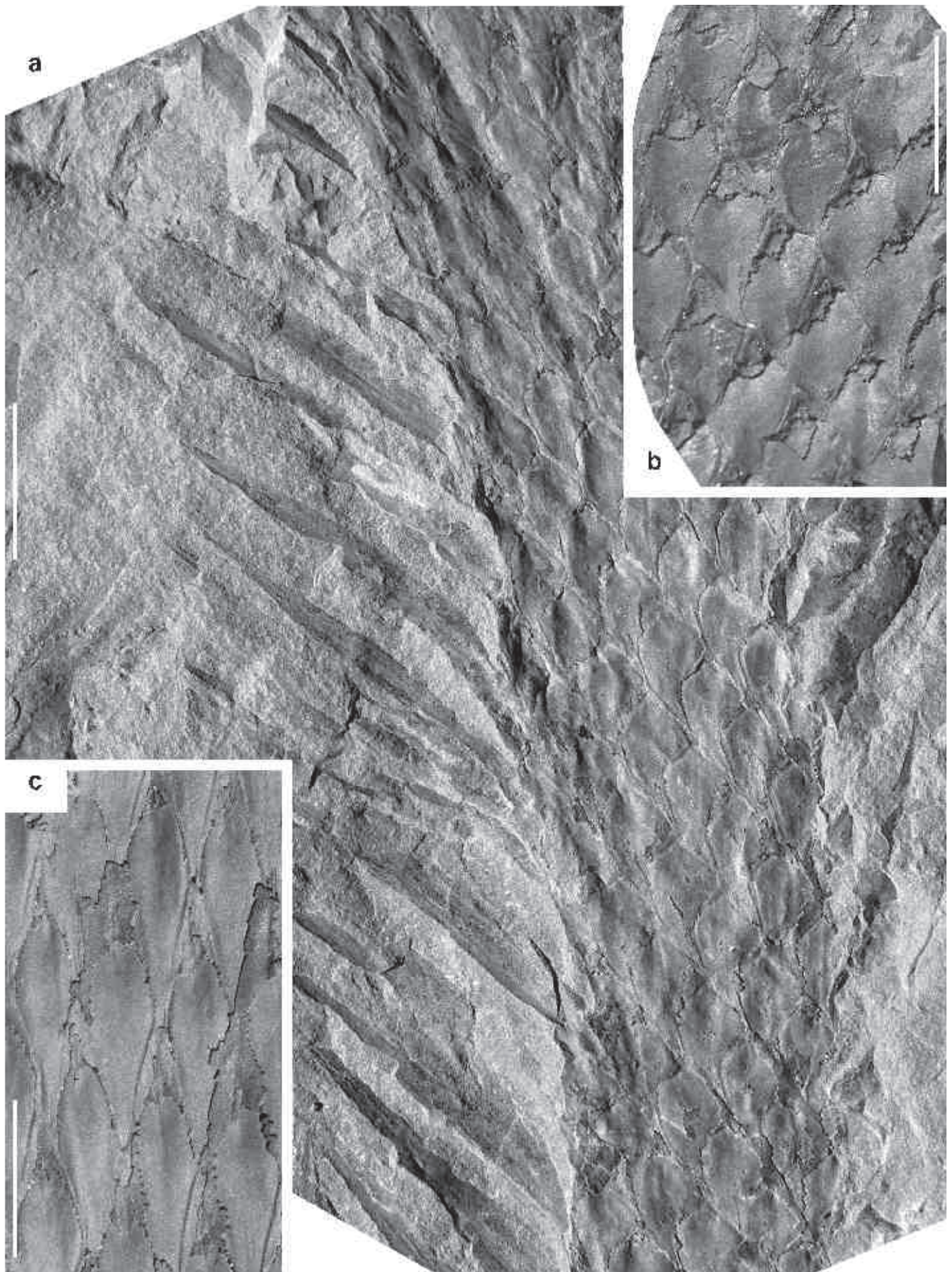
1976 *Ulodendroid* scars of *Lepidodendron aculeatum*, Jonker, p. 111, pl. 1, figs 1, 2.

**Figure 5.** *Bergeria dilatata* (Lindey & Hutton) Álvarez-Vázquez & Wagner. **a)** PBE11000 (x 2). Large stem showing obovate, smooth cushions and long, entire, grass-like leaves inserted at the top. Figured (partly) as *Ulodendron acutum* by Wagner & Álvarez-Vázquez (2010, pl. XI, fig. 2). Origin: Corta Ballesta; 2 m above Capa (Seam) 7 (locality 10251); lower Bolsovian. **b)** Another enlargement (x 3) of the upper part of the same specimen. Note the insertion of leaves in the uppermost part of leaf cushions. **c)** PBE09515 (x 2). Origin: borehole B4 in Aurora area, at 265,40 m depth (locality GIV-B4-M46); lower Bolsovian. Scale bars = 1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.



- 1977 *Lepidodendron simile*, Remy & Remy, p. 315, Bild 184 (same as Gothan & Remy, 1957, Abb. 57).
- 1978 *Lepidodendron* cf. *wortheni*, Gillespie *et al.*, p. 52, pl. 12, fig. 2.
- ? 1978 *Lepidodendron* with attached *Lepidophylloides*, Gillespie *et al.*, p. 45, 52, pl. 12, fig. 4; pl. 13, figs 3-5 (small branches with attached leaves; poorly figured).
- 1979 *Lepidodendron lycopodioides*, van Amerom & Lambrecht, p. 153, Taf. VIII, figs 1a-1b (?), fig. 7.
- 1979 *Lepidodendron adygense*, Anisimova, p. 32-33, Tab. I, fig. 2.
- ? 1979 *Lepidodendron lycopodioides*, Anisimova, Tab. I, fig. 4 (poorly figured).
- 1979 *Lepidodendron worthenii*, Anisimova, Tab. II, fig. 3.
- 1981 *Lepidodendron ophiurus*, van Amerom, fig. 2.D.
- ? 1979 *Lepidodendron simile*, Purkyňová, p. 188, Tab. II, fig. 4.
- 1982 *Lepidodendron acutum*, Bassett & Edwards, p. 18 (figure without number – associated with terminal strobili) (same as Bassett & Edwards, 1973, p. 14).
- ? 1982 *Lepidodendron* cf. *lanceolatum*, Bassett & Edwards, p. 26 (right) (same as partially reproduced by Bassett & Edwards, 1973, p. 21).
- ? p 1982 *Lepidodendron ophiurus*, Migier, p. 38, 67, Tab. I, fig. 1, fig. 2; non Tab I, fig. 3 (= *Asterophyllites*?); non Tab. I, fig. 6 (difficult to judge).
- 1983 *Lepidodendron acutum*, Chaloner & Meyer-Berthaud, p. 138, 142, fig. 2.
- ? 1983 *Lepidodendron* cf. *acutum*, Chaloner & Meyer-Berthaud, fig. 4 (difficult to judge from the illustration).
- 1983 *Lepidodendron simile*, Chaloner & Meyer-Berthaud, p. 138, 141, 142, fig. 3 (same as Chaloner & Boureau *in* Boureau, 1967, fig. 379).
- 1983 *Lepidodendron simile*, Rex & Chaloner, p. 237, text-fig. 3D; text-fig. 3E (drawing of the previous specimen).
- ? 1983 *Lepidodendron* cf. *aculeatum*, Josten, Taf. 22, figs 1, 2 (difficult to judge from illustrations at natural size).
- ? 1983 *Lepidodendron aculeatum*, Josten, p. 71 (excluding synonymy), Taf. 22, fig. 3.
- v 1983 *Lepidodendron simile*, Wagner, p. 158.
- v 1983 *Lepidodendron simile*, Wagner *in* Wagner & Bowman, p. 154.
- v 1983 *Lepidodendron simile*, Wagner *in* Wagner *et al.*, p. 61.
- v 1984 *Lepidodendron simile*, Wagner *in* Wagner *et al.*, p. 35.
- ? 1985 *Lepidodendron acutum*, Gillespie & Crawford, p. 250, pl. I, fig. 3 (poorly figured).
- ? 1985 *Lepidodendron* cf. *rimosum*, Gillespie & Crawford, p. 250, pl. I, fig. 6 (presence or absence of leaf scars is unclear).
- ? 1985 *Lepidodendron acutum*, Gillespie & Rheams, p. 200, pl. III, fig. 9 (presence or absence of leaf scars is unclear).
- 1986 *Lepidodendron acutum*, Purkyňová, p. 59, Tab. III, figs 1-2.
- 1986 *Lepidodendron*, Thomas, p. 26, top figure.
- 1987 *Lepidodendron acutum*, Tenchov, p. 58, pl. XXI, figs 1-2.
- p 1987 *Lepidodendron lycopodioides*, Tenchov, p. 60, pl. XXIV, figs 7, 9; non pl. XXIV, figs 6, 8 (= *Diaphorodendron decurtatum*).
- p 1987 *Lepidodendron obovatum*, Tenchov, pl. XXIII, fig. 3; non p. 60, pl. XXIII, figs 1, 5, 6 (= *Lepidodendron bellii*); non pl. XXIII, fig. 2 (= *Lepidodendron aculeatum*), fig. 4 (= *Lepidodendron aculeatum*).
- 1988 *Lepidodendron lycopodioides*, Cleal & Thomas, p. 418, pl. 3, fig. 1.
- 1989 *Lepidodendron simile*, Laveine, p. 30, pl. 4, figs 2-2a; text-fig. 20 (drawings).
- 1992 *Lepidodendron acutum*, Kvaček & Kvaček, Tab. I, fig. 3 (partial illustration of *Bergeria acuta* Presl, 1838, Taf. XLVIII, fig. 1a).
- 1994 *Lepidodendron acutum*, Cleal & Thomas, p. 103, tex-fig. 48 (drawing); text-fig. 49 (dichotomized medium-sized branches with attached leaves).

**Figure 6.** *Bergeria dilatata* (Lindey & Hutton) Álvarez-Vázquez & Wagner. PBE11001 (x 1.5). Medium-sized branches forked at acute angles. Note the strong resemblance with *Lepidodendron haidingeri* as figured by Ettingshausen (1854, Taf. 22) and Zeiller (1886, pl. LXIX, fig. 1), with Bureau's *Lycopodites foliosus* (1913, pl. LXXIX, figs 1-3), with the magnificent specimen figured as *Lepidodendron acutum* by Bassett & Edwards (1973, 1982), and with the specimen figured as *Lepidodendron* by Thomas (1986). Origin: Corta Ballesta; 1,80 m above Capa (Seam) 13 (locality 10257); lower Bolsovian. Scale bar = 1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.

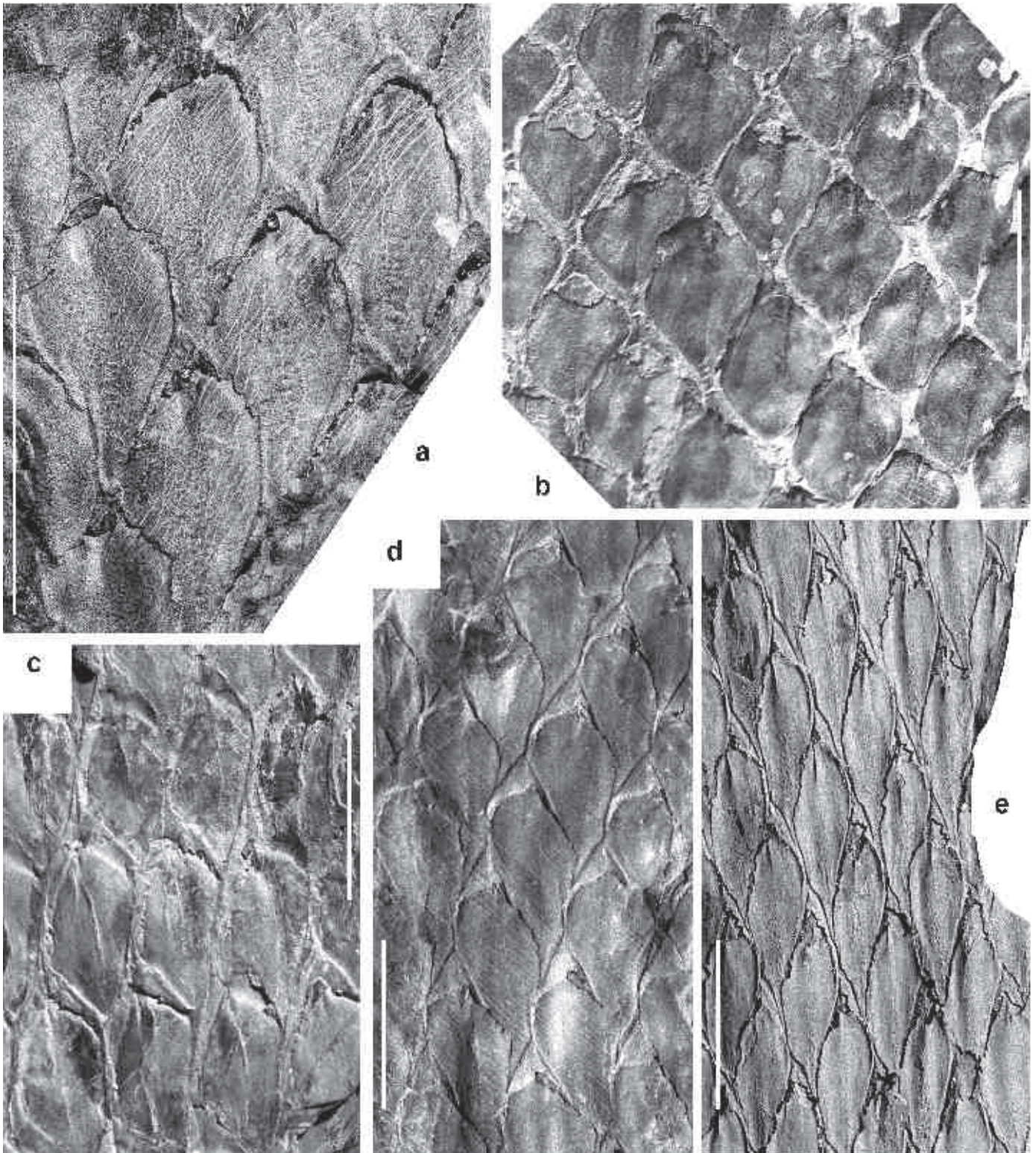




- 1994 *Lepidodendron lycopodioides*, Cleal & Thomas, p. 103, pl. 4, fig. 4; pl. 15, fig. 4 (leafy twig); text-fig. 48E.
- p 1994 *Lepidodendron ophiurus*, Cleal & Thomas, p. 103, pl. 6, fig. 5; non text-fig. 48C (= "*Lepidodendron*" *ophiurus*).
- v 1995 *Ulodendron acutum*, Álvarez-Vázquez, p. 218-221, lám. 73, figs 1-2; lám. 74, figs 1, 2; lám. 75, figs 1, 2 (together with *Flemingites russelianus*); lám. 76, figs 1, 6.
- v 1995 *Lepidodendron acutum*, Wagner & Álvarez-Vázquez, p. 161, 168.
- 1996 ?*Tomiodendron*, Brousmiche Delcambre *et al.*, p. 88, 104, pl. 6, figs 4-5a.
- 1996 *Lepidodendron lycopodioides*, Brousmiche Delcambre *et al.*, p. 105, pl. 6, fig. 7.
- ? 1996 *Lycopodites*, Cross *et al.*, p. 478, fig. 23-30.2 (leafy twigs with long leaves that cannot be judged with certainty from the illustration).
- ? 1997 *Lepidodendraceae* sp., Brousmiche Delcambre *et al.*, p. 173, pl. I, fig. 2 (poorly preserved).
- 1997 *Lepidodendron acutum*, Kvaček & Straková, p. 28, 34, 100, 126, 130, pl. 2, figs 3, 4 (holotype of *Bergeria acuta*); pl. 4, fig. 3 (holotype of *Bergeria angulata*); pl. 33, fig. 5 (holotype of *Bergeria marginata*); pl. 45, fig. 4 (holotype of *Bergeria quadrata*); pl. 46, fig. 4 (holotype of *Bergeria rhombica*).
- p 1997 *Lepidodendron ophiurus*, Migier, p. 261, pl. I, fig. 13; non pl. I, fig. 10 (same as Migier, 1982, Tab. I, fig. 6).
- 1997 *Lepidodendron* sp., Migier, pl. I, fig. 19 (together with strobilus).
- 1998 *Lépidodendrale incertae sedis*, Brousmiche Delcambre *et al.*, p. 91, 116, pl. 1, figs 3-3a.
- v 1999 *Ulodendron acutum*, Álvarez-Vázquez, figs 2, 4 (name only).
- v 2001 *Ulodendron acutum*, Wagner, p. 95.
- ? 2003 *Lepidodendron* species (cf. *L. lycopodioides*), van Amerom & Kabon, p. 535, Taf. 4, fig. 1.
- ? 2007 *Lepidodendron acutum*, Opluštil *et al.*, pl. VII, fig. 2 (leafy twig difficult to judge from the illustration at reduced size).
- p 2008 *Lepidodendron lycopodioides*, van der Veldt, p. 63, fig. 3; non fig. 4 (= "*Lepidodendron*" *ophiurus*).
- 2009 *Lepidodendron acutum*-*L. simile* type branches, Opluštil & Bek, p. 217, fig. 6A (leafy branches associated with strobilus), fig. 6C.
- ? 2009a "*Lepidodendron*" *simile*, Opluštil *et al.*, p. 244-245, 252, pl. I, figs 1-6 (difficult to judge from the illustration).
- 2009b *Lepidodendron simile*, Opluštil *et al.*, p. 729, 731, 735, 736, 744, fig. 7C (leafy twigs with long leaves), fig. 7D.
- v 2010 *Ulodendron acutum*, Wagner & Álvarez-Vázquez, p. 257, 262, 264, 266, 270, 307, pl. XI, fig. 2 (here Figs 5a-5b).
- 2011 *Lepidodendron acutum*, Pšenička & Opluštil, p. 65, pl. I, figs 1-3, 5, 7.
- ? 2011 *Lepidodendron simile*, Pšenička & Opluštil, p. 65, pl. I, figs 4, 6 (difficult to judge from the illustration).
- ? 2012 *Lepidodendron* cf. *acutum*, Pšenička *et al.*, p. 41, pl. V, fig. 4 (difficult to judge from the illustration).
- § v 2014 *Bergeria dilatata*, Álvarez-Vázquez & Wagner, p. 201-204, fig. 13 (copy, at reduced size, of Lindley Hutton's drawing); figs 14a-14h; figs 16g-16h (leafy twigs).
- 2016 *Bergeria dilatata*, Opluštil *et al.*, figs 10G, 11D.
- 2017 *Bergeria dilatata*, Opluštil *et al.*, p. 268, 274, pl. I, fig. 3.
- ? 2017 *Bergeria* sp., Pšenička *et al.*, p. 16-17, pl. 1, fig. 2 (leafy twig – cannot be judged properly from the illustration).
- 2017 *Synchysidendron*, DiMichele *et al.*, p. 5, fig. 4B (*Synchysidendron*, as described by DiMichele & Bateman, 1992, possesses differentiated leaf scars and a marked lower keel with distinct plications; none of these characteristics are visible in the specimens figured by DiMichele *et al.*).

*N.B.* System of annotations as follows: \* Protologue; § first publication of currently accepted combination; ? references to doubtful specimens due to poor preservation or illustration; p *pars*: only part of the specimens published belong to the species; v *vide*: the authors have seen the

**Figure 7.** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. **a**) PBE11001 (x 3). Enlargement of lower part of specimen in Fig. 6. Origin: same as for Fig. 6 (locality 10257). **b**) PBE09352 (x 3). Origin: borehole SBA-92-33, at 29,50 m depth (locality 8203); lower Bolsovian. **c**) PBE09508 (x 3). Detail of smooth, obovate cushions, with acute apices and bases. Origin: borehole SEP-10, at 39,10 m depth (locality 6738); lower Bolsovian. Scale bars = 1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.



**Figure 8.** *Bergeria dilatata* (Lindey & Hutton) Álvarez-Vázquez & Wagner. **a)** PBE11002. Obovate leaf cushions showing barely distinct keels crossed with short wrinkles. Origin: Corta Ballesta; 1,10 m above Capa (Seam) 9 (locality 10344); lower Bolsovian. **b)** PBE09573. Rhomboidal leaf cushions separated by narrow grooves. Origin: borehole SB-11, at 60,25 m depth (locality 7266); lower Bolsovian. **c)** PBE11005. Origin: same as Fig. 8a (locality 10344). **d)** PBE09510. Note the slightly inflected bases. Origin: borehole SEP-5bis, at 324,70 m depth (locality 5632); lower Bolsovian. **e)** PBE11003. Note the similarity with one of the types of *Lepidodendron lanceolatum* (Lesquereux, 1879, pl. LXIII, figs 5-5a). Origin: same as Figs 8a and 8c (locality 10344). Scale bars =1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.

specimen(s); k: reference includes cuticular evidence; acc.: according to. We have tried to compose a complete list of synonymy, ignoring only mere textual citations unless these have been reviewed by the present authors.

**Material and preservation.** An extensive collection from 78 localities in the Peñarroya-Belmez-Espiel Coalfield comprises a total of 586 specimens; these include a few large stem fragments (up to 30 cm long and 8 cm wide) as well as numerous medium-sized leafy branches (the most frequent: up to 25 cm long and 2 cm wide), and small leafy twigs. Several tens of them are one to four times dichotomized at an acute angle. Specimens are preserved as adpressions on siltstones. They are identified by engraved locality numbers and a catalogue number preceded by PBE (identifying the coalfield). All material was photographed dry and with natural lighting.

Lindley & Hutton's material consists of three specimens that originated from the roof of the Low Main coal seam, Felling Colliery, Newcastle-upon-Tyne, England. Catalogue numbers are HM G02.16 (Lindley & Hutton, 1831, pl. 7, fig. 2 – holotype of *Lepidodendron dilatatum*), HM G02.17 (Lindley & Hutton, 1834, pl. 118) and HM G02.20 (Lindley & Hutton, 1834, pl. 113).

**Age.** Late Langsettian/early Duckmantian and early Bolsovian for the material from Spain. Lindley & Hutton specimens originated from lower Duckmantian strata (see Ramsbottom *et al.*, 1978).

**Repository.** Spanish material is stored in the Fossil Plant Collection of the Centro Paleobotánico, Real Jardín Botánico de Córdoba, Córdoba, Spain. Lindley & Hutton's specimens are in the collections of the Great North Museum-Hancock, Newcastle-upon-Tyne, England.

**Diagnosis.** Lycopsid stems, branches and leafy twigs covered with spirally arranged leaf cushions. Branches isotomously forked at acute angles. Leaf cushions contiguous or separated by narrow grooves; smooth, obovate to rhomboidal, longer than broad, broadest in the upper part of cushion; straight or slightly inflected acuminate base, acute apex and rounded lateral angles. Parichnos markings absent. Keel absent or very faintly marked. Long, grass-like leaves, single-veined, inserted at acute angles. A very small, irregular scar marks the position of leaf base at the top of the cushion where leaves have been detached.

**Description.** Stem and branch fragments up to 55 cm long and 11 cm wide, straight, covered with closely spaced, helicoidally disposed leaf cushions; these are longer than broad, contiguous in the smaller branches and separated by very narrow grooves (less than 1.2 mm broad) in the larger ones. Distal, leafy stems up to 38 cm long and 2

cm wide, branching isotomously at acute angles (30–60° – Figs 3, 4, 6). Gradual change in size and shape of leaf cushions below and above dichotomies.

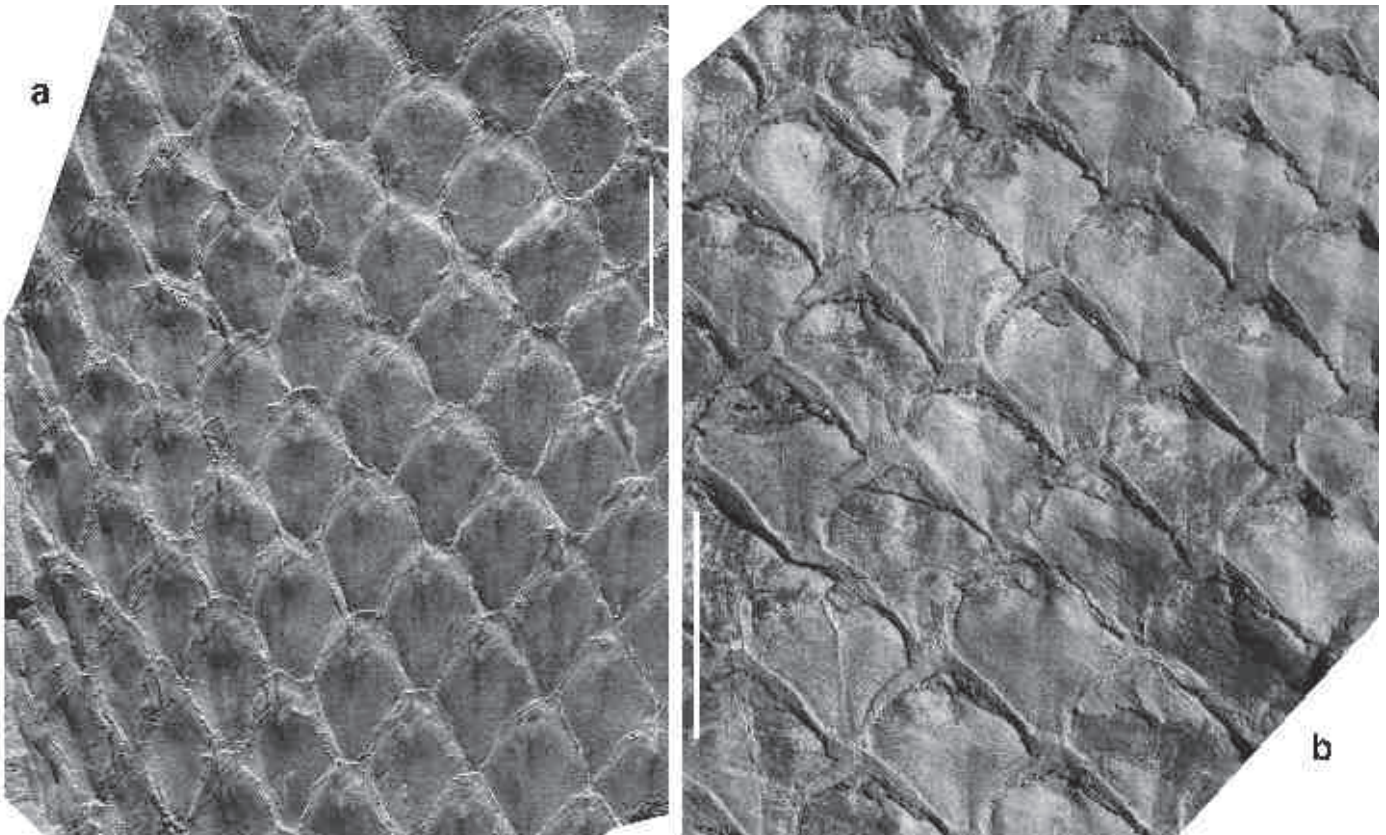
Neither the specimens in the Peñarroya-Belmez-Espiel collection nor those of Lindley & Hutton show ulodendroid branch scars, but the two syntypes of the synonymous *Lepidodendron landsburgii* Kidston (1893, pl. III, figs 9, 10; also Crookall, 1964, pl. LXIII, figs 1, 2) show large, oval scars. Kidston's specimens are larger than those described here; although only partly figured, the specimen in his pl. III, fig. 9 measures 28.5 cm long and 25 cm wide and possesses two branch scars separated by 18.5 cm (Kidston, 1893, p. 338). This specimen also shows more distant leaf cushions, separated by slightly wider grooves (up to 2 mm) ornamented with flexuous, irregular markings.

Leaf cushions slightly asymmetrical vertically and horizontally, flat and smooth in the medium-sized and smaller branches (e.g. Figs 6, 7a, 7b, 8d), more convex, smooth (Figs 5a, 5b, 9a) or with a very faintly marked, occasionally ornamented keel (Fig. 8a), in the larger ones. Rhomboidal (Figs 2, 8b, 8c, 9a, 9b) to obovate (e.g. Figs 5a, 5b, 5c, 8d, 8e), broadest in the upper third or upper half of cushion, straight or very slightly inflected in opposite directions; apex acute in obovate cushions (e.g. Figs 7c, 8d, 8e), broadly acute to obtuse in rhomboidal ones (Figs 2, 9a, 9b); base acute (Figs 7c, 8d, 8e) or truncate due to slight overlapping between rows of leaf cushions (Figs 9a, 9b); lateral angles more or less rounded in all cases. Dimensions: 3–18 mm long and 1.5–8 mm broad; length/breadth ratio = 2 to 6 (most commonly 2.5–3.5). (True) leaf scar absent; when leaves are detached, a small, irregular scar is seen to mark the position of the leaf base at the top of the leaf cushion (e.g. Figs 7b, 8e, 9b). There is no evidence of either a ligule pit or parichnos markings.

Long, single-veined, straight, entire, grass-like leaves (Figs 2, 5a, 5b, 6, 7a, 10, 10b); they are slightly curved near the base and inserted in total continuity in the uppermost part of leaf cushion at narrow, acute angles (20–40°), tapering gradually to an acuminate apex. Dimensions: up to 80 mm long and 2–5 mm width at the base; leaf length at least five times that of the leaf cushions.

**Comparisons.** The presence of rhomboidal, smooth, longer than broad leaf cushions with small, irregular (false) leaf scars at the top of the cushion, and (when preserved) the long, grass-like leaves make *Bergeria dilatata* a distinctive taxon.

*Bergeria worthenii* (Lesquereux) Álvarez-Vázquez & Wagner (Lesquereux, 1866, pl. XLIV, figs 4, 5; Janssen, 1940, pl. I, figs 3, 4; Bell, 1944, pl. XLVII, figs 2, 4; pl. L, fig. 2; pl. LIV, fig. 4; Janssen, 1957, fig. 19; Laveine *et al.*, 2003, pl. VII, figs 1, 2; Wagner & Álvarez-Vázquez, 2010, pl. XI, figs 3–3a; Álvarez-Vázquez & Wagner, 2014, figs 15a–15e) shows smaller, fusiform to obovate leaf cushions with a markedly convex surface. In addition, the narrow,



**Figure 9.** *Bergeria dilatata* (Lindey & Hutton) Álvarez-Vázquez & Wagner. **a)** PBE09458 (x 2). Stem fragment with rhomboidal leaf cushions showing obtuse apex and truncate base. Origin: Pozo (shaft) Espiel, Rampa 4W, 3ª Traviesa, 6 m below Capa (Seam) Candelaria (locality 6769); lower Bolsovian. **b)** PBE11004 (x 3). Truncate bases due to overlapping between rows of leaf cushions. Origin: Corta Ballesta; 1,10 m above Capa (Seam) 9 (locality 10344); lower Bolsovian. Scale bars = 1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.

irregular, transversally oval to punctiform (false) leaf scar is placed in the upper third of the leaf cushion and occupies almost the entire cushion width. There is no keel; the field area above and below the leaf scar is almost totally covered by relatively coarse, transverse, discontinuous wrinkles. *Bergeria worthenii* ranges through the entire Westphalian.

The Langsettian species *Bergeria wingfieldense* (Thomas & Seyfullah, 2015) comb. nov. [Basionym: *Lepidodendron wingfieldense* Thomas & Seyfullah, 2015, *Palaeontographica*, Abt. B, 292 (1-3), p. 31, text-figs 4A-5D, text-fig. 5E (strobilii), text-fig. 5F (megaspore), text-figs 6A-6F (cuticles)] is characterized by rhomboidal, shorter and more equidimensional cushions, with a length/breadth ratio of ~ 1.2. Since no proper leaf scar is seen, we exclude this species from *Lepidodendron*. Thomas & Seyfullah (2015) only described seven specimens (together with two strobili), which seems insufficient to show the intraspecific variability. However, apart from the size and shape, the well-marked, ornamented keel with short transverse wrinkles allows *Bergeria wingfieldense* to be easily distinguished from *Bergeria dilatata*. Associated strobili possess *Lagenosporites*-type megaspores and were

compared by Thomas & Seyfullah (2015) with *Flemingites olryi* (Zeiller) Brack-Hanes & Thomas.

Also similar is the Westphalian species *Bergeria lycopodioides* (Sternberg, 1821) comb. nov. [Basionym: *Lepidodendron lycopodioides* Sternberg, 1821, *Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt*, p. 26, Taf. XVI, figs 1, 2, 4 – refigured by Kvaček & Straková, 1997, pl. 32, and as “*Lepidodendron*” *selaginoides* by Němejc, 1947, Tab. II, fig. 6, Tab. III, fig. 2] and its synonym “*Lepidodendron*” *selaginoides* (Sternberg, 1821, Taf. XVI, fig. 3, Taf. XVII, fig. 1; copy of the original drawing in Cleal *et al.*, 2005, p. 47, fig. 5 (1); and refigured by Němejc, 1947, Tab. III, figs 1, 3; Kvaček & Straková, 1997, pl. 50, figs 1, 3; and Opluštil *et al.*, 2007, pl. V, fig. 9). *Bergeria lycopodioides* possesses contiguous, fusiform, elongate leaf cushions with upper and lower ends that are slightly inflected in opposite directions. Leaves are apparently linear, and much shorter than in *Bergeria dilatata*. Opluštil *et al.* (2009b, fig. 7A) illustrated a large specimen (more than 70 cm long) showing a wide stem fragment as well as numerous medium-sized branches and small twigs, several times dichotomized at acute angles.

The detail of leaf cushions (*op. cit.*, fig. 7B) shows no proper leaf scars, but a small, irregular, punctiform scar in the upper third of the leaf cushions. A well-marked keel, crossed by relatively coarse, transverse wrinkles (similar to those seen in *Bergeria worthenii*) is seen in the field below the false leaf scars. There is no parichnos. As in the case of *Lepidodendron wingfieldense*, *Lepidodendron lycopodioides* must be excluded from *Lepidodendron*.

Comparison can also be made with “*Lepidodendron*” *ophiurus* (Brongniart) Brongniart (Brongniart, 1822, pl. IV, figs 1a-1b – drawings reproduced in Crookall, 1964, text-fig. 93; Thomas & Seyfullah, 2015, text-figs 1A, 1B; text-figs 2A-D), but this species shows much smaller, fusiform leaf cushions, with acute upper and lower angles and rounded laterals, showing a well-marked, unornamented keel. There is no parichnos. Leaves are much shorter than those of *Bergeria dilatata* and are attached at about one third down the leaf cushion at near right angles, curving upwards more or less parallel to the stem. Although this species should be excluded from *Lepidodendron*, the presence of small, rhomboidal leaf scars when leaves are not preserved, confirms that it can not be included in *Bergeria*.

The lower Westphalian species “*Lepidodendron*” *belgicum* (Kidston, 1911, pl. XVII, figs 1-3) shows similar, contiguous, longer than broad, obovate to rhomboidal leaf cushions. Poorly-defined, relatively short leaves are observed in some areas of the type material (three larger stems and two twigs in the same slab), but leaf cushions possess a well-defined, rhomboidal leaf scar located in the upper part. This excludes “*Lepidodendron*” *belgicum* from *Bergeria*. Additionally, there is a distinctive keel crossed by well-marked, short, transverse wrinkles in the lower field; a large branch scar is seen in one of the specimens. Although a revision of the original material would be necessary, Kidston’s specimens do not show parichnos, so this species should also be excluded from *Lepidodendron*.

Small branches with attached leaves of *Bergeria dilatata* are distinguished from those of *Bothrodendron minutifolium* (Boulay) Zeiller (Boulay, 1876, pl. III, figs 1-1bis; Zeiller, 1879, p. 117-118; Zeiller, 1886, pl. LXXIV, figs 2-4C) by the presence, in the latter, of more tightly adpressed, shorter (always less than 10 mm long), linear-lanceolate leaves with a sharply pointed apex. Moreover, *Bothrodendron minutifolium* leaves are attached to the middle part of the very small, rhomboidal-elongated leaf cushions, not at the top as in *Bergeria dilatata*.

Genus *Flemingites* Carruthers, 1865 emend. Brack-Hanes & Thomas, 1983

Type-species *Flemingites gracilis* Carruthers, 1865

**Remarks.** Flemingitacean cones are characterized by the occurrence of megasporangia in the basal part and

microsporangia near the apex. Brack-Hanes & Thomas (1983) restricted *Lepidostrobus* to monosporangiate cones with cingulizone and cingulate *Lycospora* type microspores, and *Flemingites* to bisporangiate strobili with megaspores of the *Lagenicula* and *Lagenoisporites* types and microspores of *Microspinosporites* type. Not all flemingitacean cones yield both *in situ* micro- and megaspores. It is not unusual to find flemingitacean specimens (preserved as fragments) that yield only micro- or megaspores, but if the *in situ* spores are identified to these characteristic types, this is strong confirmation of the generic classification of the strobilus (see Bek, 2017). *In situ* flemingitacean microspores have been referred to *Lycospora* (Schopf, Wilson & Bentall) Potonié & Kremp, mostly to the dispersed microspore species *Lycospora orbicula* (Potonié & Kremp) Smith & Butterworth or *Lycospora granulata* Kosanke (Bek, 2017). These microspores were originally interpreted as cingulate (Potonié & Kremp, 1955; Smith & Butterworth, 1967), but Bek (2013) re-defined these spores as monopseudosaccate, excluding them from *Lycospora*, and proposed a new genus, *Microspinosporites*. Flemingitacean cone species with megaspores of the *Lagenoisporites* type (see Bek, 2017) are significantly more numerous than those that produced *Lagenicula*.

This group of flemingitacean cones includes not only true *Flemingites* but also two uppermost Devonian *Sublepidodendron* species (Bek, 2017). The genus *Thomasostrobus* Opluštil *et al.* appears to represent a special position among Pennsylvanian bisporangiate cones, being bisporangiate but probably close to some sigillarians that are monosporangiate.

*Flemingites russelianus* (Binney, 1871) Brack-Hanes & Thomas, 1983  
(Figs 11a-11j)

\* p 1871 *Lepidostrobus Russelianus* Binney, p. 51, pl. IX, figs 1, 1a; non pl. IX, figs 2, 2a (*Lepidostrobus dubius* Binney acc. to Chaloner, 1953).

\* 1871 *Lepidostrobus Hibbertianus* Binney, p. 55, pl. X, figs 2-2b (acc. to Chaloner, 1953).

1928 *Lepidostrobus* sp., Šusta, Taf. VIII, Abb. 2 (associated with small branches that have been included here in the synonymy of *Bergeria dilatata*).

1937 *Lepidostrobus* cf. *Goodei*, Jongmans, 397, pl. 15, fig. 25.

1949 *Lepidostrobus* sp., Arnold, p. 172-173, pl. VII, figs 1, 3, 4 (acc. to Chaloner, 1953).

? 1952 *Ulostrobus Goodei*, Stockmans & Willièrè, pl. E, fig. 1 (in association with *Ulodendron goodei*, here included in *Bergeria dilatata*); pl. F, figs 1, 1a, fig. 2 (together with *Ulodendron goodei*), figs 3-5a.



**Figure 10.** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. **a)** PBE11007 (x 3). Detail of the long, entire, single-veined leaves. Origin: Corta Ballesta; 1,10 m above Capa (Seam) 9 (locality 10344); lower Bolsovian. **b)** PBE11006 (x 2). Leafy twig. Origin: same as Fig. 10a (locality 10344). Scale bars = 1 cm. Repository: Centro Paleobotánico, Real Jardín Botánico de Córdoba, Spain.

1953 *Lepidostrobus russelianus*, Chaloner, p. 277 (emended diagnosis), text-figs 13-16 (megaspores), 17A-E (microspores).

\* 1966 *Lepidostrobus russelianus*, Crookall, p. 500, text-fig. 147 (copy of Binney's figures).

§ 1983 *Flemingites russelianus*, Brack-Hanes & Thomas, p. 132.

v 1995 *Flemingites russelianus*, Álvarez-Vázquez, p. 222, lám. 74, fig. 3; lám. 75, fig. 2; lám. 77, figs 1-3.

1998 *Lepidostrobus* sp. 1, Brousniche Delcambre *et al.*, p. 92, 117, pl. 2, figs 1-1a.

v 1999 *Flemingites russelianus*, Álvarez-Vázquez, fig. 4 (name only).

v 2001 *Flemingites russelianus*, Wagner, p. 98.

p 2009 *Flemingites* cf. *russelianus*, Opluštil & Bek, p. 216-218, fig. 6A (together with *Bergeria dilatata*), fig. 6B; figs 6D-6G (spores).

v 2010 *Flemingites russelianus*, Wagner & Álvarez-Vázquez, p. 266.

**Material.** Twenty-three specimens found in association with stem and leafy twigs of *Bergeria dilatata*. Two specimens, from localities 6789 (Pozo Espiel) and 10251 (Corta Ballesta), were macerated for palynology. Megaspores were macerated in nitric acid (24 hours), treated in potassium hydroxide (20 minutes) and washed in distilled water. Microspores and dispersed miospores and pollen were macerated in hydrofluoric acid (5 days), nitric acid (24 hours) and treated in potassium hydroxide (20 minutes). Descriptive terms for the spores follow the latest edition of the Glossary of Pollen and Spore Terminology (Punt *et al.*, 2007). Megaspores are classified based on Dybová-Jachowicz *et al.* (1979, 1982, 1987a, 1987b). Microspores are classified according to the system of dispersed spores suggested by Potonié & Kremp (1954, 1955), Smith & Butterworth (1967) and Bek (2013). *In situ* spores were compared directly with the original diagnoses, type specimens, description, and illustrations of dispersed spore species. Species determinations are based solely on the original diagnoses, not on the interpretations of subsequent authors.

**Diagnosis.** Strobilus cylindrical, slightly tapering from base to apex; axis wide, with perpendicular or nearly perpendicular, closely adpressed sporophylls. Megasporangia concentrated in lower part of strobilus and microsporangia in apical part. *In situ* megaspores of the *Lagenosporites rugosus* type and microspores of the *Microspinosporites orbiculus* type.

**Description.** Strobilus cylindrical, elongate, slightly tapering from base to apex, at least 120 mm long (incomplete) and 18-20 mm wide. Axis 2-2.5 mm wide, with perpendicular or nearly perpendicular sporophylls arranged in pseudowhirls and separated by c. 1 mm. Sporophyll pedicel up to 15 mm long, inserted perpendicular to the axis; upper part of the sporophyll closely adpressed and abruptly ascending parallel to the axis, with a relatively thick, subtriangular and single-veined lamina; margins entire. Sporophyll dimensions: up to 12 mm long and 25 mm width.

Megasporangia concentrated in the lower part of strobilus and microsporangia in the apical part. Sporangia 5-7 mm long (measured radially) and 1.5-2 mm wide (parallel to the axis). Trilete megaspores flattened laterally, more or less oval; those in proximal-distal direction, round or oval (Figs 11b, 11f-j). Apical prominence distinct. Arcuate ridges distinctly marked in well-preserved specimens. Megaspores 550 (883) 1210 µm in diameter, gula 240 (310) 400 µm high and 180 (226) 300 µm wide (Figs 11b, 11g, 11i). Exine punctate to rugose, 10-20 µm thick. Many megaspores have small globules called ubisch bodies (or their imprints) on the surface (Fig. 11h). Trilete pseudosaccate miospores, 23-36 µm in diameter (Figs 11a, 11c-e). Amb circular

to oval, margin microspinate. Laesurae simple, equal to the radius of the inner body, sometimes indistinct. Distal surface microspinate, proximal surface microspinate except for laevigate contact area. *In situ* megaspores of the *Lagenosporites rugosus* type and microspores of the *Microspinosporites orbiculus* type.

**Comparisons.** Although containing both megaspores of the *Lagenosporites* type and microspores of the *Microspinosporites* type, cones of the lower to middle Westphalian species *Flemingites olryi* (Zeiller) Brack-Hanes & Thomas are smaller (less than 12 mm wide) and have a higher length/breadth ratio than those of *Flemingites russelianus*.

Cones of *Lepidostrobus ornatus* Brongniart are also large, long and cylindrical. However, they are microsporangiate, with microspores of the *Lycospora* type.

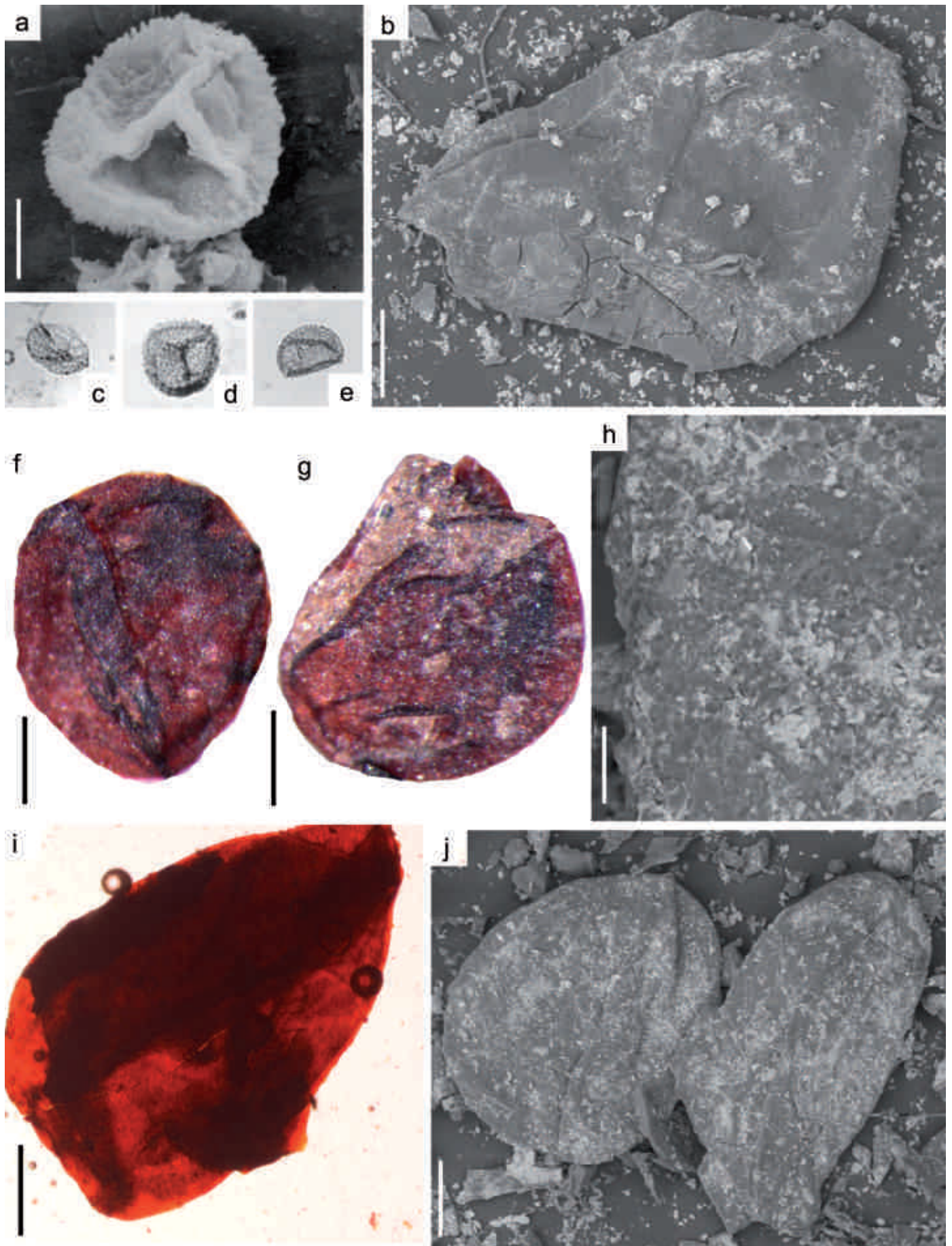
The lower Westphalian, monosporangiate cones of *Lepidostrobus spinosus* Kidston are smaller, oval, with an obtuse apex. Microspores are of the *Lycospora* type (Opluštil & Bek, 2009).

**Remarks.** There are at least 17 Paleozoic flemingitacean strobilus form-species that are recorded to have produced miospores of the *Microspinosporites* type (Bek, 2017) and 16 species that yielded megaspores of the *Lagenosporites rugosus* type. All these *in situ* micro- and megaspores are closely similar and differ only slightly in diameter. All other morphological features are identical, i.e. sculpture, cingulum, gula, rays of trilete mark, etc. As such, it is not possible to distinguish parent plants of *Microspinosporites orbiculus* and *Lagenosporites rugosus* based solely on their *in situ* spores. Comparisons can be made based on the morphology/anatomy of the cones and the whole parent plant, if cones are in connection.

**Stratigraphic distribution.** *Flemingites russelianus* has been recorded from Langsettian to Bolsovian strata. The type specimens came from the Blackband Ironstone, Airdrie, Lanarkshire, Scotland, from upper Langsettian strata. Chaloner (1953) noted the association of *Flemingites russelianus* cones with *Lepidodendron acutum* (= *Bergeria dilatata*).

## 5. DISPERSED MIOSPORE AND POLLEN ASSEMBLAGE

A small piece of the matrix (4x4x1 cm) was macerated to obtain a dispersed miospore and pollen assemblage associated with studied specimens of *Bergeria dilatata*; based on our knowledge of *in situ* spores and pollen (e.g. Balme, 1995), this provides insight into the vegetation





growing in the same general area as *Bergeria dilatata*. The dispersed miospore and pollen assemblage consists of 37 species belonging to 22 genera. The most abundant were arborescent lycopsids (attributed to *Lepidodendron*, *Lepidophloios* and *Sigillaria* types). They are represented mainly by several species of the genus *Lycospora* and the flemingitacean microspore genus *Microspinosporites*, i.e. the same species as macerated *in situ* from the cones. The second most abundant miospore type is that attributed to marattialean and botryopterid ferns; less abundant miospore types are attributed to zygopterid and gleicheniacean fern taxa. The miospore record of other groups, including herbaceous lycopsids, *Calamites*, sphenophylls, cordaitaleans, conifers and pteridosperms, is poorly represented.

The predominance of miospores of arborescent lycopsids of the *Lepidodendron* and *Lepidophloios* type points to typical peat-forming vegetation of a Pennsylvanian rheotrophic peatland.

## 6. HABITAT

As mentioned above, *Bergeria dilatata* is the most common species of lycopsid in the Peñarroya-Belmez-Espiel Coalfield. It is noted that it never appears in direct association with a coal seam, and that it is frequently associated (28 localities; almost a third of the total localities) with sphenopsids: mainly *Calamites suckowii* Brongniart and *Calamites cistii* Brongniart, and less commonly *Sphenophyllum cuneifolium* (Sternberg) Zeiller, *Annularia* sp., *Asterophyllites* sp. and *Calamostachys* sp. Another frequent association is with pteridosperms: *Neuropteris guadiatensis* Wagner emend. Álvarez-Vázquez, *Laveineopteris tenuifolia* (Schlotheim ex Sternberg) Cleal, Shute & Zoderow, *Paripteris linguaefolia* Bertrand and *Mariopteris muricata* (Schlotheim) Zeiller. Less commonly (only at one locality in each case), it is associated with *Bothrodendron minutifolium* (Boulay) Zeiller, *Wagneropteris minima* Álvarez-Vázquez & Cleal, *Lonchopteris rugosa*

Brongniart, *Palmatopteris furcata* (Brongniart) Potonié, *Senftenbergia plumosa* (Artis) Stur, *Sturia amoena* (Stur) Němejc, *Renaultia* sp. and *Pecopteris* sp.

It is further noted that *Bergeria dilatata* occurs in siltstones above coal seams, forming part of the fining upward sequences of alluvial plain facies (see Fig. 12 containing localities 8203, 10251, 10257 and 10344 in Corta Ballesta, which contributed more than 300 of the 586 specimens assigned to *Bergeria dilatata* in the Peñarroya-Belmez-Espiel Coalfield). It may be interpreted that, in contrast to other lycopsids, this species inhabited open flooded areas with higher clastic input; in effect, a pioneer species.

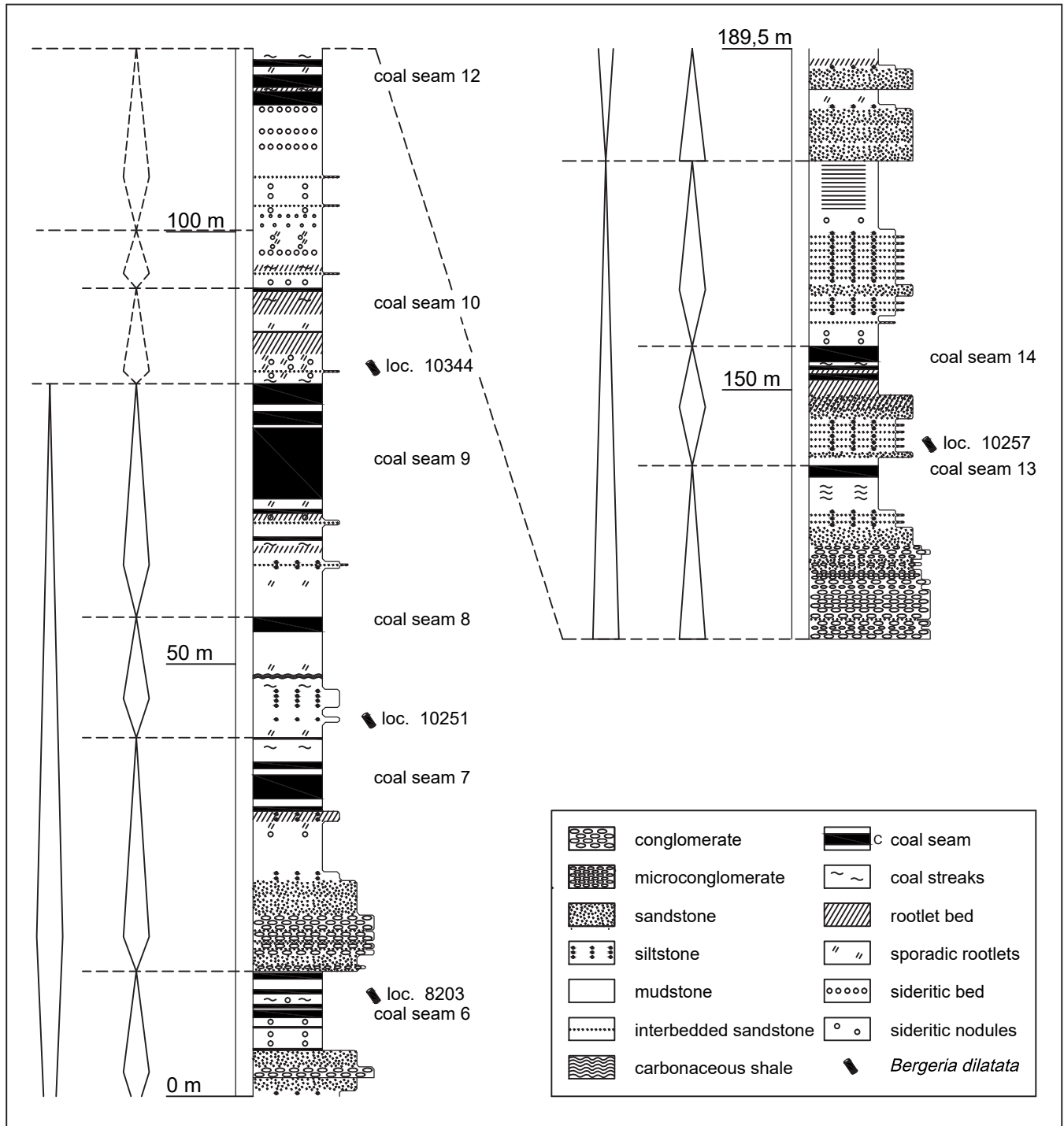
It is considered relevant to compare with the interpretation of DiMichele & Phillips (1985, 1994) and Phillips & DiMichele (1992) of the anatomically preserved *Paralycopodites*, which was a small (less than 10 m tall), straight tree with two opposite rows of deciduous lateral branches of relatively small size. Its leaves also remained attached to lateral branches and to the main trunk. *Paralycopodites* would appear also to have been a pioneer element living in open, clastic, disturbed parts of swamp areas, probably not subjected to long-term flooding.

## 7. GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The only specimen (holotype) figured by Lindley & Hutton (1831, pl. 7, fig. 2) as *Lepidodendron dilatatum* originated from the roof of the Low Main coal seam, Felling Colliery, near Newcastle-upon-Tyne, England, from strata of early Duckmantian age. Lindley & Hutton's *Lepidodendron gracile*, and the specimens figured by them as *Lepidodendron sternbergii* Brongniart, *Lepidodendron selaginoides* Sternberg, and *Lepidodendron elegans* all came from the same horizon.

In Great Britain, *Bergeria dilatata* has been repeatedly recorded, under various names, throughout the Westphalian; i.e. Kidston's *Lepidodendron landsburgii*, which originated

**Figure 11.** Palynomorphs. **a)** *In situ* microspore of the *Microspinosporites orbiculus* type. Note laevigate proximal surface and a part of densely microspinate distal sculpture and elevated rays of the trilete mark. SEM. Scale bar = 10 µm. **b)** Lateral view on *in situ* megaspore of the *Lagenoisporites rugosus* type. Note laevigate sculpture and developed gula (left). SEM. Scale bar = 150 µm. **c)** Semi-lateral view of *in situ* microspore of the *Microspinosporites orbiculus* type (x 500). Note difference between microspinate sculpture of the distal surface (lower) and laevigate proximal surface (upper). **d)** Proximal view of *in situ* microspore of the *Microspinosporites orbiculus* type (x 500). **e)** Partial semi-lateral view of *in situ* microspore of the *Microspinosporites orbiculus* type (x 500). **f)** *In situ* megaspore of the *Lagenoisporites rugosus* type without gula. Scale bar = 260 µm. **g)** *In situ* megaspore of the *Lagenoisporites rugosus* type with gula. Scale bar = 260 µm. **h)** Detail of the surface of an *in situ* megaspore of the *Lagenoisporites rugosus* type. Note negative imprints of ubish bodies and small circular ubish bodies (upper edge). SEM. Scale bar = 22 µm. **i)** Semi-lateral view on *in situ* megaspores of the *Lagenoisporites rugosus* type with gula. Scale bar = 180 µm. **j)** Two *in situ* megaspores of the *Lagenoisporites rugosus* type. SEM. Scale bar = 200 µm. Repository: Institute of Geology, Academy of Sciences, Prague, Czech Republic.



**Figure 12.** Stratigraphic column of part of the succession in Corta Ballesta showing the position of localities 8203, 10251, 10257 and 10344, from which most of the specimens figured here originated.

from the roof shales of the Whistler Seam, Kilmarnock, Ayrshire, Scotland, of lower Duckmantian age; the two specimens figured as *Lepidodendron simile* by Chaloner & Boureau in Boureau (1967) also from lower Westphalian strata of Scotland (Clackmannanshire); the specimens figured as *Lepidodendron ophiurus* by Crookall (1964) from the Barnsley Coal, Yorkshire Coalfield, early Duckmantian, and from Hanley, North Staffordshire,

upper Bolsovian; Cleal & Thomas's (1988) *Lepidodendron lycopodioides* from the Cattybrook Claypit, on Bristol-Somerset Coalfield, upper Langsetian; or those figured by Crookall (1964) as *Lepidodendron acutum*, and as *Lepidodendron acutum* and *Lepidodendron cf. lanceolatum* by Bassett & Edwards (1973, 1982), from the upper Bolsovian of Glamorgan, Wales.

The westernmost occurrence of *Bergeria dilatata* is in the Michigan Basin, the United States of America, where Arnold (1949) figured it as *Lepidodendron lanceolatum*, *Lepidodendron ophiuroides* and *Lepidodendron vestitum* from upper Langsettian/upper Duckmantian strata. The species has also been recorded in the Warrior Basin, Alabama (Gillespie & Rheams, 1985) and the Crab Orchard Mountains Formation, Georgia (Gillespie & Crawford, 1985), from Langsettian strata. The records from West Virginia are those of Jongmans (1937) from Seam No. 3 of the Pocahontas Formation (lower Langsettian), Gillespie *et al.* (1978), who do not provide an exact locality, and Cross *et al.* (1996) from strata above the Eagle Coal of the Kanawha Formation, lower Duckmantian according to Blake *et al.* (2002). Lesquereux (1879-84) recorded the species at different levels in Illinois, Kentucky, Missouri and Pennsylvania. Lesquereux's types of *Lepidodendron lanceolatum* and *Lepidodendron scutatum* came from the Clinton Coal, Missouri, of early Asturian age. DiMichele *et al.*'s (2017) record as *Synchysidendron* originated in the roof shales of the Springfield Coal, Illinois Basin, of Asturian age.

Although Bell (1944) only figured one specimen of *Bergeria dilatata* (as *Lepidodendron lanceolatum*) from the Minas Basin, Nova Scotia, Canada, the review of the original collection by Álvarez-Vázquez & Wagner (2014) indicates that it is a relatively frequent species in the upper Langsettian of the Cumberland Basin. Bell's (1938) records (under *Lepidodendron lycopodioides*) from the Sydney Basin, Nova Scotia, and those from the Minto Coalfield, New Brunswick (Bell, 1940, 1966 – as *Lepidodendron ophiurus*) came from (lower?) Bolsovian strata.

Records from the Nord/Pas-de-Calais Coalfield, northwestern France (Zeiller, 1886-88 – under *Lepidodendron haidingeri*, *Lepidodendron lycopodioides*, *Lepidodendron ophiurus* and *Ulodendron majus*) are from Duckmantian strata.

*Lepidodendron gibbosum* Sauveur (1848), and the specimens figured by him as *Lepidodendron dilatatum* and *Lepidodendron sternbergii*, originated from lower Westphalian strata of Belgium. Stockmans & Willière's (1952) *Ulodendron goodei* came from Yeadonian strata. Van Amerom & Lambrecht's (1979) *Lepidodendron lycopodioides* originated from lower Westphalian strata.

Records from South Limburg, the Netherlands, include material from Langsettian and Duckmantian strata (Jongmans, 1949, 1953; van der Veldt, 2008).

In the Ruhr Basin, western Germany, there are records of *Bergeria dilatata* (under different names) from Langsettian to Bolsovian (e.g. Gothan & Remy, 1957; Dräger, 1964; Remy & Remy, 1977).

*Bergeria dilatata* has been repeatedly recorded (under various names) from the Czech Republic. The two syntypes of *Bergeria acuta* (Presl in Sternberg, 1838; Kvaček & Straková, 1997) originated from the Nýřany Member of the Kladno Formation, Central Bohemia, of Asturian age.

Presl's *Bergeria angulata*, *Bergeria marginata*, *Bergeria quadrata* and *Bergeria rhombica* also came from the same horizon. In the Radnice Basin there are records from the base of the Whetstone Horizon (Opluštil *et al.*, 2009a) and from different levels of the Upper Radnice Coal (Ettingshausen, 1854; Pšenička & Opluštil, 2011; Opluštil *et al.*, 2016), of late Duckmantian age.

Romanian material from the Sirina Basin was initially regarded by Bițoiu (1972a, 1972b) as Westphalian D (= Asturian), but Wagner & Álvarez-Vázquez (2008) indicate a Langsettian age.

In Bulgaria, *Bergeria dilatata* was recorded by Tenchov (1987) from Duckmantian and Bolsovian strata of the Svoje Basin.

Records published from South Briançonnais, French Alps, by Greber (1966) and Brousmiche-Delcambre *et al.* (1996, 1997) show *Bergeria dilatata* (under *Lepidodendron lycopodioides* and ?*Tomiodendron*) to range from Yeadonian to lower Langsettian.

Pšenička *et al.* (2012) ascribed the fossil plant collection (including *Lepidodendron cf. acutum*) from Val Sanagra, western Southern Alps, Italy, to the Duckmantian/Bolsovian transition.

Bureau's (1913-14) *Lycopodites foliosus* and the other records from the Vendée, southwest France, refer to lower Westphalian strata.

According to Wagner & Álvarez-Vázquez (2010), *Bergeria dilatata* ranges from Langsettian to lower Asturian in the Iberian Peninsula. In the Cantabrian Mountains of NW Spain, the sparse records are from uppermost Langsettian strata of La Camocha, Asturias (Wagner & Álvarez-Vázquez, 1995) and San Emiliano, León (Wagner & Bowman, 1983), and from lower Asturian strata of the Central Asturian Coalfield. In SW Spain, the species has been widely sampled in upper Langsettian/lower Duckmantian and lower Bolsovian strata of the Peñarroya-Belmez-Espiel Coalfield (Álvarez-Vázquez, 1995; Wagner & Álvarez-Vázquez, 2010; this paper).

*Bergeria dilatata* has also been published under different names from Bolsovian strata in Djerada, Morocco (Jongmans, 1952) and the Sud-Oranais, Algeria (Jongmans, 1951; Migier, 1982, 1997).

*Bergeria dilatata* is, therefore, a common, widespread and long-ranging species that has been recorded (under various names) from Yeadonian to Asturian strata. It has been reported most often from the Langsettian, Duckmantian and Bolsovian substages.

## 8. GENERAL CONCLUSIONS

This work recognizes the widespread presence of the arborescent lycopsid *Bergeria dilatata* in the Westphalian successions of North America, Europe and North Africa.

Considerable confusion has surrounded identification of this species. The very abundant material from the Peñarroya-Belmez-Espiel Coalfield has allowed for a well-documented record of the variability of the species and the recognition of extensive synonymous records.

The priority of the genus *Bergeria* for lycopsid stem adpressions characterized by false leaf scars was noted by Álvarez-Vázquez & Wagner (2014). The present work documents the range of the Spanish material from the Peñarroya-Belmez-Espiel Coalfield and provides for the first time a photograph of the type of Lindley & Hutton's *Lepidodendron dilatatum*, housed in the Hutton Collection, Newcastle-upon-Tyne. In conjunction, it has also been possible to recognize further illustrations attributable to the genus *Bergeria* and to designate two new combinations: *Bergeria lycopodioides* and *Bergeria wingfieldense*.

Palynological study of strobili closely associated with *Bergeria dilatata* has confirmed their identification as *Flemingites russelianus*, a bisporangiate cone taxon; this has also been previously recognized in the literature (Chaloner, 1953) as corresponding to adpression material identifiable as *Bergeria dilatata*. The present work strongly supports the whole-plant relationship between *Bergeria dilatata* and *Flemingites russelianus*.

## ACKNOWLEDGEMENTS

The authors are particularly pleased to present this work in a volume dedicated to recognise the life work of Dr M.L. Martínez Chacón (Lis) and Dr L.C. Sánchez de Posada (Suco); for those of the authors working in Spain, they have consistently been inspiring and supportive friends and colleagues, and all the authors recognise the importance of their open welcome and helpfulness to fellow workers. The curatorial staff, and in particular Ms. Sylvia Humphrey, of the Great North Museum-Hancock, Newcastle-upon-Tyne, England, are thanked for enthusiastic assistance in making the Hutton collection available for inspection. Juan I. Peláez and mining engineers at ENCASUR Company have been most helpful in providing access to boreholes and collecting sites. Carmen Álvarez-Vázquez wishes to acknowledge unconditional field support from Juan Peláez and Eva Peláez Álvarez. The authors acknowledge with thanks the helpful and well-focused corrections and suggestions of the two referees, Bill DiMichele and Arden Bashforth. Jiří Bek acknowledges financial support from the Research Program of the Institute of Geology AS CR, v.v.i. (RVO67985831).

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