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EARLY COAL SWAMP VEGETATION FROM THE SERPUKHOVIAN LOWER CLACKMANNAN GROUP OF SCOTLAND

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Abstract: The coal-bearing lower Clackmannan Group of Scotland has yielded diverse fossil floras of Serpukhovian (late Mississippian) age dominated by arborescent lycopsids, equisetopsids, ferns and lyginopteridalean pteridosperms. Similar macrofloras of the same age have been reported from coal-bearing deposits of Maine-et-Loire (NW France) and Upper Silesia (Czech Republic and Poland). These fossil floras together reflect the earliest development of the coal swamp biome in tropical Euramerica. The biome appeared on newly-exposed areas of coastal plain that formed as result of lowered sea-levels during the first major cooling phase of the Late Palaeozoic Ice Age. A new combination *Artisophyton chalmersii* is proposed based on *Megaphyton chalmersii* Goodlet.

Key words: palaeobotany, early Carboniferous, coal swamp biome, climate change

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Introduction

The Pennsylvanian (late Carboniferous) was one of the most important times for the evolution of Palaeozoic terrestrial habitats and biotas (Cleal 2018, Cleal and Thomas 2005). It was marked by the onset of a major period of ice-house conditions known as the Late Palaeozoic Ice Age (Fielding et al. 2008a, b, 2023), which resulted in a significant lowering of sea-levels and a consequential exposure of large tracts of continental shelf notably in tropical latitudes. The newly exposed areas of coastal plains became home for extensive swamps, often referred to as Coal Swamps because they produced thick peat deposits that have since changed into coal. The Coal Swamps were one of the earliest globally-significant biomes, which saw a significant diversification of plant life, notably of the arborescent lycopsids, ferns and early gymnosperms (the Palaeophytic Flora; Cleal and Cascales-Miñana 2014, 2021), as well as of insects (Jarzembowski and Ross 1996, Labandeira 2007, 2018).

The global aerial extent of the Coal Swamps shows an essentially bimodal distribution with peaks representing the late Bashkirian and Moscovian (Westphalian) coal deposits of Euramerica and the Cisuralian (early Permian) coal deposits of Cathaysian China (Cleal and Thomas 2005). These two peaks correspond to the two main intervals of icehouse conditions in the Late Palaeozoic Ice Age, separated by the Stephanian (late Pennsylvanian) interglacial (González 1990, Fielding et al. 2008a, b, 2023, Iannuzzi et al. 2023). However, there is also evidence of palaeotropical swamp development predating the first of these two peaks, most evident in the Serpukhovian (early Namurian). Although not as widespread as the Westphalian swamps, their remains are known from across North America and Europe (Mosseichik 2010) and these proto-Coal Swamps have the potential to throw light on the origins of this important biome.

The fossil biotas of these early proto-Coal Swamps have not been extensively studied in recent years, the only notable exceptions being work on the macrofloras of Upper Silesia (Purkyňová 1970, Gastaldo et al. 2009a, b) and the Maine-et-Loire area in northwestern France (Strullu-Derrien et al. 2021, 2023). There are also historical records of the vegetation of these proto Coal Swamps in the Midland Valley of Scotland, in the lower Clackmannan Group (Lower Limestone, Limestone Coal and Upper Limestone formations), mainly in the monographs by Kidston (1923,

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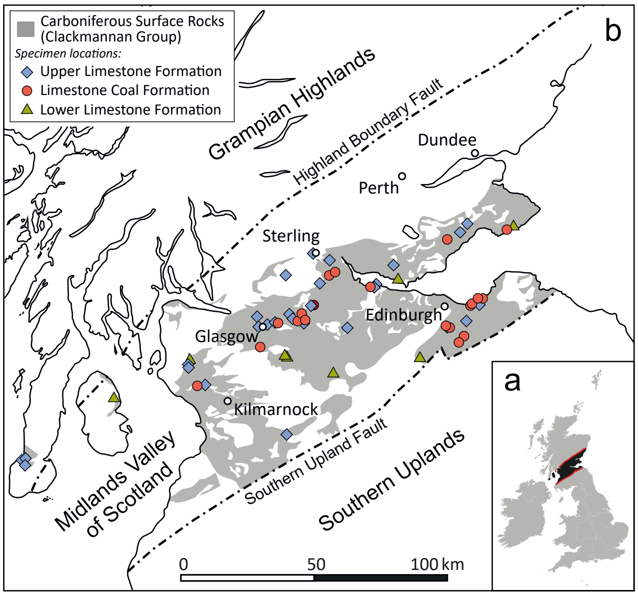
1924, 1925) and Crookall (1955, 1966, 1969, 1976), unillustrated records such as by Kidston (1901) but there has been no published attempt to look these Scottish macrofloras as a whole. In this paper we therefore review the taxonomy of the Lower Limestone, Limestone Coal and Upper Limestone formations plant adpressions, and compare them with the other documented macrofloras of this age.

Geological background

Tectonic setting

Rock of Carboniferous age occupy much of the Midland Valley of Scotland basin – an east-north-east-trending graben initiated in the Late Devonian through North-South rifting associated with the Rheno-Hercycnian back-arc basin (Text-fig. 1; Leeder 1982). The rifting created a series of large-scale grabens and half-grabens across Britain each separated by platform and tilt-block topographic highs (Leeder 1982, 1988). The Midland Valley of Scotland (~150 km long and up to ~80 km wide onshore) is the northern most of these basins. It is postulated that reactivation of pre-existing Caledonian structures controlled the basin opening, with the (eroded) Caledonian Mountains to the north-west, the Southern Uplands to the south-east, and the Highland Boundary Fault to the north (Text-fig. 1). The tectonic cause of the graben initiation however remains controversial with numerous differing interpretations having been proposed (e.g., Leeder 1982, Dewey 1982, Haszeldine 1984, Browne et al. 2003, Ritchie et al. 2003, Underhill et al. 2008). Transtensional rifting continued to affect the Midland Valley of Scotland basin during the Namurian and Stephanian, with transpression becoming dominant at the end of the Carboniferous.



Text-fig. 1. a: Overview map showing United Kingdom and Ireland with the Midland Valley of Scotland (MVS) highlighted. b: Detailed map of the MVS showing the location of the 71 localities in the Upper Limestone Formation, Limestone Coal Formation, and Lower Limestone Formation that yielded specimens discussed in this paper. Known surface geology of the Clackmannan Group is shown in grey.

Basin filling

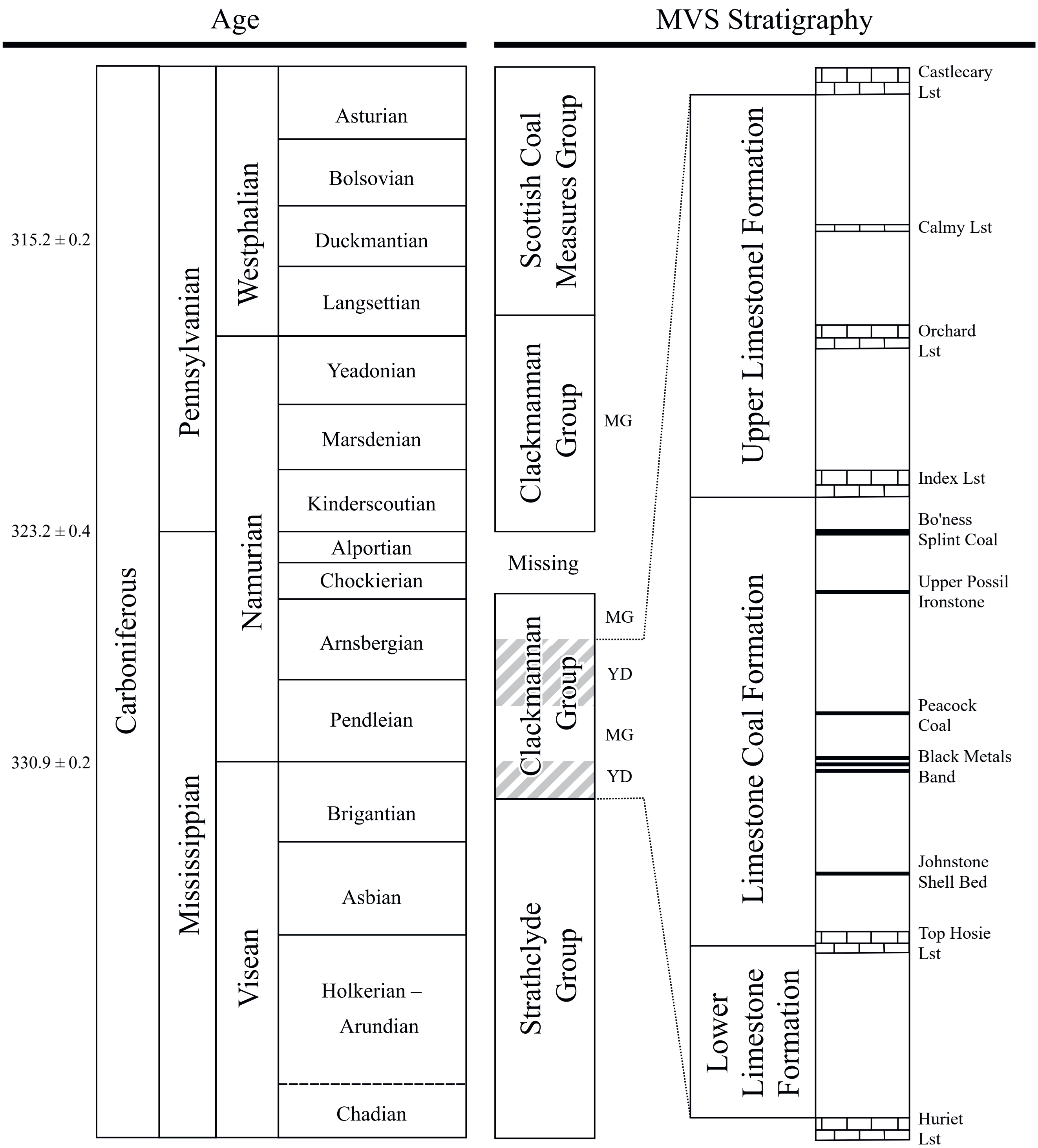
The Midland Valley has a distinctive Carboniferous sedimentary fill compared to the more southernly basins. Minimal temporal and spatial facies changes are seen, with the depocenters dominated by shallow-marine, deltaic and alluvial environments. No alluvial fans are recorded along basin margins implying deposition kept pace with accommodation generation for a prolonged period (Hooper 2003).

Lithofacies

The Clackmannan Group is a 1,800 m thick succession of variable facies containing the Lower Limestone, Limestone Coal, Upper Limestone, and Passage formations (Text-fig. 2). The base of the group is The Hurlet Limestone which sits conformably on the underlying Stathclyde Group. The upper boundary of the group is marked by the Lowstone Marine Band of the overlying Scottish Coal Measures. The Clackmannan Group shows a variable succession of facies that are predominantly characterised by the Yoredale and Millstone Grit facies. The Yoredale lithofacies comprises of grey mudstones, siltstones, sandstones and marine limestones, with minor coal seams and seat-earths or ganisters. While the Millstone Grit facies contains darker black and grey mudstones, siltstone, ironstones and very coarse-grained sandstones, with minor seat-earths and relatively thin coal seams. Both the Yoredale and Millstone Grit facies predominantly show upwards-coarsening cycles. The depositional environment for lower parts of the cycles in the Yoredale has been described as a mixture of marine environments as represented by the limestone, mudstone, and some sandstones. While the upper parts of the Yoredale cycles show progradational lobate deltas as represented by most sandstones and the coal seams. Whereas the Millstone Grit shows a change to a fluviodeltaic environment with cycles of delta progradation associated with black mudstones followed by channel abandonment. The first cycle of Yoredale-Millstone Grit-Yoredale of the Clackmannan Group correlates to Lower Limestone Formation, Limestone Coal Formation, and Upper Limestone Formation (Text-fig. 2). It is within these three formations that the fossiliferous plant material described herein was collected.

Sources of data

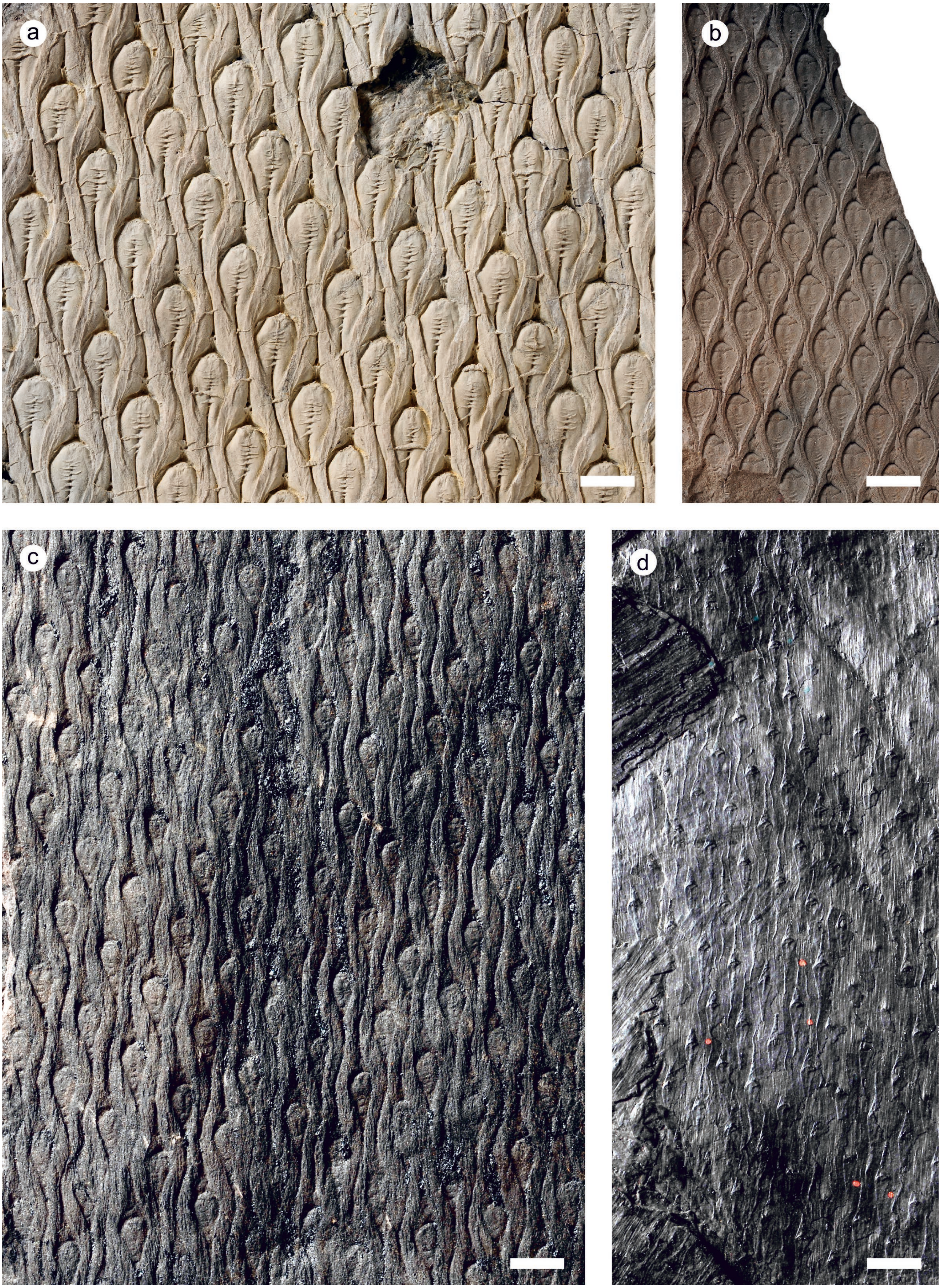
This study is based mainly on a reassessment of the Kidston Collection at the British Geological Survey (Keyworth, UK), this being the most extensive assemblage of specimens from these deposits. These specimens came from 70 localities listed in the Appendix at the end of the paper and the species occurrences are shown in Table 1. Many of these specimens were acquired through fieldwork by the Geological Survey, together with specimens donated by local geologists Henry Moubray Cadell of Bo'ness, West Lothian (Mendum 2010), James Coutts and Andrew Patton of East Kilbride, Lanarkshire (Coutts 1886, Young 1886), John Smith of Dalry, Ayrshire (Macgregor 1945, Wilson 1995), Robert Dunlop of Airdrie (Ford 1988), Peter Macnair of Kelvingrove Museum Glasgow (Gregory 1930) and John Kirsop of Glasgow.



Text-fig. 2. Generalized stratigraphy of the Midland Valley of Scotland. For ages, ISC System and Subsystem names are given along with NW Europe ("Heerlen") Stage and Substages. The main lithological groups (Strathclyde Grp., Clackmannan Grp., and Scottish Coal Measures Grp.) are given, with lithofacies indicated for the Clackmannan Grp.: YD = Yoredale facies; MG = Millstone Grit. Additionally, the stratigraphy for the lower Clackmannan Grp. is given to the left comprising the Lower Limestone formation, Limestone Coal Fr., and Upper Limestone Fr. Note the Passage Fr. that overlies these units is not shown.

The plant fossils from the Lower Limestone Formation were very scattered and no locality or even area stands out as having yielded an important macroflora. Many of the Limestone Coal Formation macrofloras originated from:

a) Midlothian near Edinburgh, especially from the lower part of the formation between the Johnstone Shell Bed and Black Metals Marine Band;
b) Stirlingshire in central Scotland, especially from the interval of coal seams in the middle part of the formation, above the Black Metals Marine Band;
c) Lanarkshire in central Scotland, especially in the upper part of the formation below the Index Limestone;
d) Ayrshire in southwest Scotland, especially the interval above the Johnstone Shell Bed, such as at Dalry;
e) Machrihanish Coalfield in western Scotland.



Text-fig. 3. **a–b:** ***Lepidodendron veltheimii*** **Sternb. a: Specimen showing larger leaf cushions; New Braidbar Quarry, Giffnock, East Renfrewshire; below Orchard Limestone, Upper Limestone Formation; BGS Kidst.248. b: Specimen showing smaller cushions; No 1 Pit, Polmaise Colliery, Fallin, Stirlingshire; Knott Coal, Limestone Coal Formation; BGS Kidst.5115. c–d:** ***Lepidodendron jaschei*** **J.Roem. c: Specimen showing prominent intercushion areas; Woodyett Pit, Denny, Stirlingshire; above Blackband Ironstone,**

Table 1. Species distributions in the lower Clackmannan Group of southern Scotland. Numbers refer to localities as listed in the Appendix.

Taxon	Lower Limestone Formation	Limestone Coal Formation	Upper Limestone Formation
Spathulopteris clavigera	5		
Rhacopteris transitionis	5, 6	15	
Archaeopteridium tschermakii	2, 3, 5	14	
Calymmotheca distans	8		46
Sphenopteridium dissectum	1, 4, 7	13	
Sigillaria youngiana		27	
Artisophyton chalmersii		19	
Lepidophloios grangeri		36	
Sphenopteris dicksonioides		17, 30, 39	
Lepidodendron veltheimii		9, 26, 33, 34, 35, 37, 38, 40, 44, 45, 46	66
Lepidodendron rhodianum		35	66
Lepidodendron jaschei		16, 37, 40, 41, 44	66
Sublepidophloios ventricosus		26	
Lepidostrobophyllum veltheimianum		42, 43	66
Stigmaria stellata		29, 35, 40, 44	56
Mesocalamites taitianus		32, 40	63, 71
Zeilleria moravica		17	49, 50, 56, 66, 67
Sphenopteris elegans		9, 10, 11, 12, 18, 20, 21, 22, 23, 24, 25, 28, 31, 36, 37	48, 53, 54, 57, 59, 61, 63, 64, 66, 68, 70
Calymmotheca divaricata		9, 10, 11	52, 53, 54, 56, 59, 60, 63
Mesocalamites haueri			63, 69, 70
Sphenophyllum tenerrimum			56
Pecopteris aspera			53
Sphenopteris taitiana			51, 53
Sphenopteris mira			66
Eusphenopteris foliolata			50, 65
Calymmotheca stangeri			56, 66

For the Upper Limestone Formation, the best macrofloras were associated with the Orchard Limestone in the middle of the formation, notably the coastal exposures near Prestonpans (East Lothian), Robroyston Colliery (Lanarkshire), and New Braidbar Quarry (Renfrewshire).

There have been records from the Isle of Arran off the west coast of Scotland that have been assigned to the Upper Limestone Formation (e.g., Lochrim Burn, Sliddery Water Head; Kidston 1901). However, the stratigraphy of these beds is problematic and their exact age is uncertain (e.g., Young and Caldwell 2012) and so these records have been omitted from this review.

Systematic palaeobotany

Order Lepidodendrales Haeckel, 1868

Remarks. The family classification of the Lepidodendrales used here is based on Thomas and Branck-Hanes (1984).

Family Lepidodendraceae Sternb., 1820

Fossil-genus *Lepidodendron* Sternb., 1820

Remarks. Crookall (1964) suggested that *Lepidodendron volkmannianum* Sternb. from the Lower Limestone Formation occurs in the Kidston Collection, but this could not be verified, and there are no records listed in the relevant Fossilium Catalogus (Jongmans 1929). What appears to be the axis of a lycopsid cone from Swinless Glen was misattributed to *Cyclostigma*? *hercynium* C.E.Weiss by Crookall (1964: pl. 79, fig. 4). Another lycopsid stem fragment was made the type of *Cyclostigma majus* Crookall (Crookall 1955: pl. 79, fig. 2) but this specimen is indeterminate.

***Lepidodendron veltheimii* Sternb., 1825**
Text-fig. 3a, b

1825 *Lepidodendron veltheimii* Sternb., p. 43, pl. 52, fig. 3.
1885 *Lepidodendron veltheimianum* Sternb.; Kidston, p. 243, pl. 3.

Limestone Coal Formation; BGS Kidst.2452. d: Specimen with shallower intercushion areas; Stripside Pit, Herbertshire Colliery, near Denny, Stirlingshire; Steam Coal, Limestone Coal Formation; BGS Kidst.4287. All scale bars = 10 mm.

1964 *Lepidodendron veltheimii* Sternb.; Crookall, pl. 64, fig. 5, pl. 70, fig. 8.
1970 *Lepidodendron veltheimii* Sternb.; Thomas, p. 153, pl. 33, figs 4–6.
1973 *Lepidodendron veltheimii* Sternb.; Chaloner and Gay, pl. 79, fig. 5.
1974 *Lepidodendron veltheimii* Sternb.; Thomas, p. 526, pl. 78, figs 3, 5, pls 79, 80, pl. 81, figs 1, 3.

Description. Helically-arranged, protuberant leaf cushions usually 5–30 mm long, 2–10 mm wide (rarely up to 40 mm long, 20 mm wide). Cushions subrhomboidal, with acute, often sinuous upper and lower angles, and rounded lateral angles. Leaf scar rounded or rhomboidal occurs in upper part of cushion; scars slightly elongate laterally, occupying over half the cushion width, and with prominent vascular cicatrix in middle. Prominent ligule pit occurs adjacent to leaf scar, and the cushion surface above the leaf scar shows distinct striae. Prominent keel extends down from the scar to base of cushion, often with prominent lateral wrinkles. Large, round ulodendroid branch scars sometimes occur in longitudinal rows along stem.

Remarks. This is the most abundant lepidodendrid species in these floras and is clearly the same as the *L. veltheimii* specimens found in the Maine-et-Loire floras. Kidston (1885) gave an extensive comparative analysis of other similar species found in Mississippian age floras, as well as providing a list of localities in the Limestone Coal Formation that have yielded *L. veltheimii*. It can also be compared with the abundant Westphalian-age species *Lepidodendron aculeatum* Sternb. except that the leaf scars are much larger and are higher on the cushion, and there are striae on the leaf cushion surface above the scar. Cuticles of this species prepared from specimens from the Upper Limestone Formation (Thomas 1970, 1974, Chaloner and Gay 1973) differed from *L. aculeatum* in having elongate epidermal cells on the cushion below the leaf scar.

The unillustrated record of *Sigillaria taylorii* (Carruth.) Kidst. from the Upper Limestone Formation at New Braidbar Quarry in Kidston (1901) probably referred to a stem of *L. veltheimii* with ulodendroid branch scars.

There has been disagreement as to the orthography of this species epithet as Sternberg (1825) referred to both *Veltheimii* and *Veltheimianum*. However, his first reference to the fossil-species (on his p. 43) was as *L. Veltheimii* where it is accompanied by a very brief diagnosis, and so we have used this spelling here.

Occurrences. Widespread in Limestone Coal Formation above the Johnstone Shell Bed notably at Todholes, and in the Upper Limestone Formation just below the Orchard Limestone notably at New Braidbar Quarry and Lochrim Burn, Arran.

Lepidodendron jaschei A.Roem., 1866
Text-fig. 3c,d

1866 *Lepidodendron jaschei* A.Roem., p. 213, pl. 35, fig. 6.
1885 *Lepidodendron lossenii* C.E.Weiss, p. 169, pl. 6, figs 6, 7.
1964 *Lepidodendron jaschei* A.Roem.; Crookall, pl. 64, figs 1, 2, pl. 69, figs 3–7.
1964 *Lepidodendron lossenii* C.E.Weiss; Crookall, pl. 63, figs 3, 4.
1964 *Lepidodendron* cf. *nathorstii* Kidst.; Crookall, pl. 66, fig. 1.
2021 *Lepidodendron* cf. *nathorstii* Kidst.; Strullu-Derrien et al., fig. 3C.

Description. Leaf cushions helically-arranged, sometimes laterally contiguous, sometimes separated by prominent 1–2 mm wide inter-cushion areas. Cushions subrhomboidal, slender, straight, 15–20 mm long, 3 mm wide, with narrow, thread-like prolongations at upper and lower ends. Round to laterally oval leaf scar located just above middle of cushion, showing clear vascular and two foliar parichnos cicatrixes. Cushion surfaces both above and below scar have prominent lateral ridges, but no parichnos visible below scar. Ligule pit visible above scar.

Remarks. These distinctive, slender leaf cushions have often been referred to two separate fossil-species depending on whether the cushions are laterally contiguous (*L. lossenii*) or are separated by a wide inter-cushion area (*L. jaschei*). As pointed out by Potonié (1901), however, the types of these two species originated from the same locality (Kammerberg, Harz, Germany), and the two morphologies of stem are regularly found associated, and it is likely that they merely represent different growth stages of the same stems.

Similar fragments from the Maine-et-Loire flora were reported by Strullu-Derrien et al. (2021) and provisionally named *L.* cf. *nathorstii* Kidst. However, having now had the opportunity to examine the more extensive material from the lower Clackmannan Group, we now regard these French specimens as being conspecific with *L. jaschei*.

The unillustrated record of *Lepidodendron spetsbergense* Nath. from the Upper Limestone Formation of New Braidbar Quarry (Kidston 1901) probably represents *L. jaschei*.

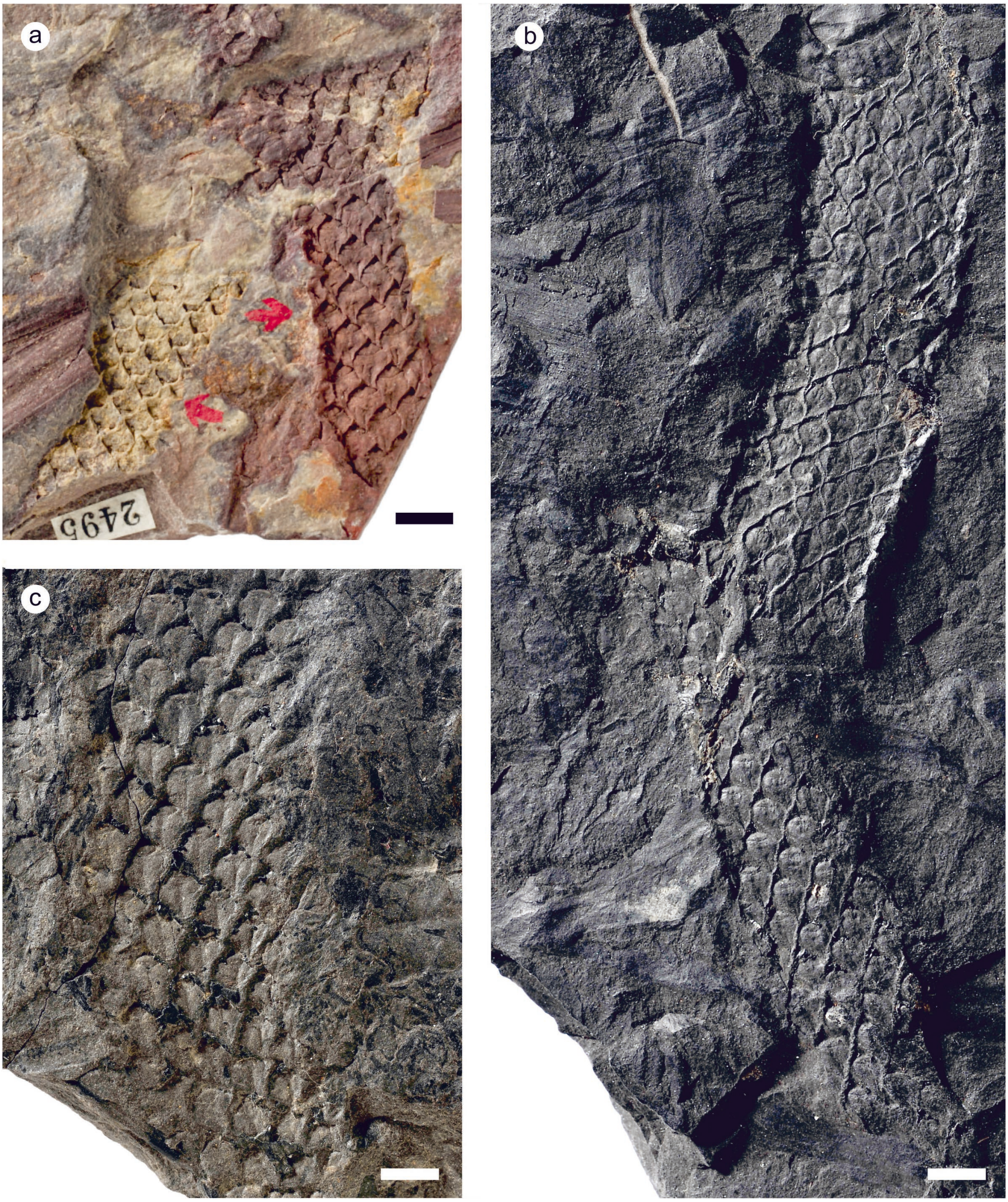
Occurrences. Mainly the upper Limestone Coal Formation, notably the Stripeside and Woodyett Pits, Denny, Stirlingshire; also from below the Orchard Limestone (Upper Limestone Formation).

Lepidodendron rhodianum Sternb., 1825
Text-fig. 4

1823 "Schuppenpflanze"; Rhode, p. 7, pl. 1, figs 1, 3, 4.
1825 *Lepidodendron rhodianum* Sternb., p. xi. (based on Rhode 1820: pl. 1, figs 1, 3)
1970 *Lepidodendron rhodianum* Sternb.; Thomas, p. 169, text-fig. 12.

Description. Stems with spirally-arranged, contiguous leaf cushions. Cushions more or less isodiametric, 3–4 mm in size, subrhomboidal to obovate, with an obtuse upper angle, an elongate, sinuous lower angle and rounded lateral angles. Rhomboidal leaf scar occurs in upper part of cushion, with lateral lines extending to upper margin of cushion and a keel below scar variable in length; infrafoliar parichnos clearly marked. Cushion surface smooth below scar, striate above the scar.

Remarks. Several specimens of relatively slender branches in the Kidston Collection recorded as *Lepidodendron rhodianum* Sternb. were mentioned but not figured by Crookall (1964). Cuticles from another specimen from the Upper Limestone Formation were described

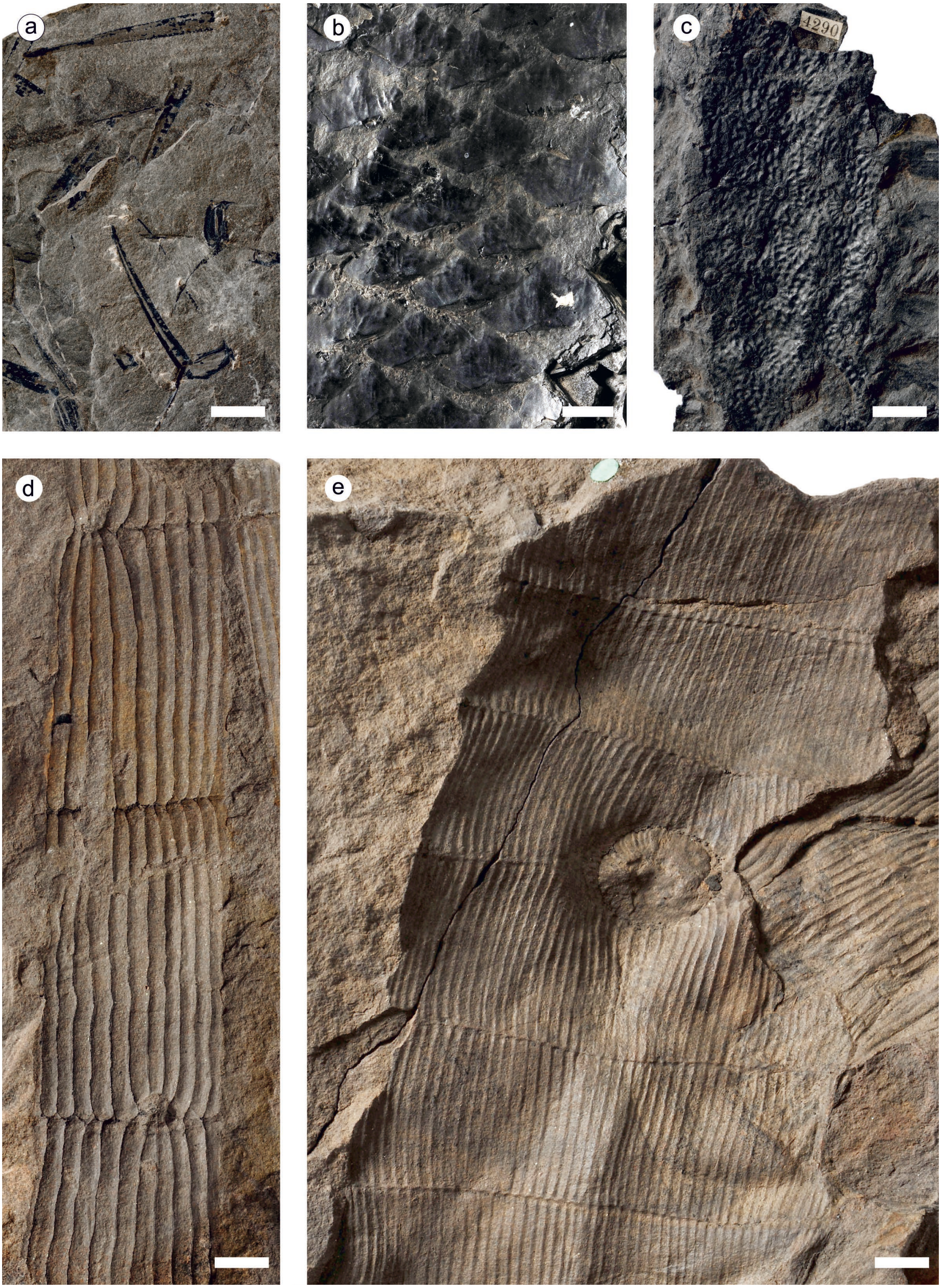


Text-fig. 4. ***Lepidodendron rhodianum*** **Sternb. a: Lochrim Burn, Corrie, Isle of Arran; Upper Limestone Formation; BGS Kidst.2495. b: Blaes, 20ft above Lower Ironstone, No. 6 Pit, Grange, Bo'ness, Linlithgowshire; Limestone Coal Formation; BGS Kidst.2494. c: New Braidbar Quarry, Giffnock, East Renfrewshire; below Orchard Limestone, Upper Limestone Formation; BGS Kidst.5361. All scale bars = 5 mm.**

by Thomas (1970). Relatively slender branches of *L. rhodianum* often occur in association with larger stems of *L. veltheimii* and it is possible that they represent parts of the same plant: smaller, more isodiametric cushions occur in the upper parts of the plant, larger, more elongate cushions in the upper part.

This species epithet is often given as *rhodeanum*, but in the protologue it is spelled *rhodianum* and so this is used here.

O c c u r r e n c e s . Known only from the Johnstone Shell Bed (Limestone Coal Formation) and below the Orchard Limestone (Upper Limestone Formation).



Text-fig. 5. a: ***Lepidostrobophyllum veltheimianum*** **(Geinitz) Strullu-Derrien, Cleal, Ducassou, A.R.T.Spencer, Stolle et Leshyk; New Braidbar Quarry, Giffnock, East Renfrewshire; below Orchard Limestone, Upper Limestone Formation; BGS Kidst.2625. b:** ***Lepidophloios grangeri*** **B.A.Thomas; Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire; Limestone Coal Formation; BGS Kidst.1828. c:** ***Stigmaria stellata*** **(Göpp.) Göpp.; above Steam Coal, Stripeside Pit, Herbertshire Colliery, Denny, Stirlingshire;**

Fossil-genus *Lepidophloios* Sternb., 1825

***Lepidophloios grangeri* B.A.Thomas, 1977**
Text-fig. 5b

1895 (?)*Lepidophloios macrolepidotus* Goldenb.; Kidston, p. 560. [see Remarks for details]
1964 *Lepidophloios laricinus* (Sternb.) Sternb.; Crookall, p. 310, pl. 74, fig. 6. [see Remarks for details]
1977 *Lepidophloios grangeri* B.A.Thomas, p. 286, pl. 36, figs 1–4.

Description. Stems with helically arranged leaf cushions. Cushions rhomboidal, laterally elongate, 10–12 mm tall, 22–25 mm wide, broader than long, with smooth surface and no keel. Ligule pit apertures immediately adjacent to upper angles of leaf scars. For details of cuticle see Thomas (1977).

Remarks. Only one specimen is known of this species. It was originally assigned to *L. macrolepidotus* and *L. laricinus* (see Synonymy), but differs from both species in the ligule being positioned much closer to the leaf scar and the stomatal density being higher (Thomas 1977). Another specimen of *Lepidophloios* shoot was described by Galtier and Scott (1986) from the basal Limestone Coal Formation, but in a different mode of preservation, and so was not assigned to Thomas's species.

Occurrence. Craw Coal (Limestone Coal Formation), No. 4 Mine, Grange, Boness, Linlithgowshire.

Fossil-genus *Sublepidophloios* Sterzel, 1907

***Sublepidophloios ventricosus* Hopping, 1956**

1956 *Sublepidophloios ventricosus* Hopping, p. 3, figs 1–3.
2013 *Sublepidophloios ventricosus* Hopping; Thomas et al., p. 317, figs 4A–B, 5, 6.

Description. Stem fragment preserved in ironstone showing straight, vertically-elongated leaf-cushions 50 mm long, 15 mm wide. Central part of leaf-cushions bulge outwards by ca.10 mm and overlap lower part of cushion by ca. 2 mm. Leaf scars 2.5 mm long, 5 mm wide, with three foliar prints, and a ligule pit which is a little above the middle of the upper cushion surface.

Remarks. Only one specimen of this species is known, but it clearly shows the characteristic leaf-cushions of this fossil-genus that are intermediate between typical *Lepidodendron* and *Lepidophloios*. For a detailed account of this specimen see Thomas et al. (2013).

Occurrence. Possil Ironstone (Limestone Coal Formation), Robroyston Colliery, Lanarkshire.

Fossil-genus *Lepidostrobophyllum* Hirmer, 1927

***Lepidostrobophyllum veltheimianum* (Geinitz) Strullu-Derrien, Cleal, Ducassou, A.R.T.Spencer, Stolle et Leshyk, 2021**
Text-fig. 5a

1854 *Lepidophyllum veltheimianum* Geinitz, p. 52, pl. 4, figs 6–9.
1952 *Lepidocarpon waltonii* Chaloner, p. 572, pl. 21, figs 1–7.
1966 *Lepidocarpon waltonii* Chaloner; Crookall, p. 526, pl. 103, fig. 2.
1985 *Lepidostrobophyllum veltheimianum* (Geinitz) Stepanek et Vogellehner, nom. inval., p. 86.
2021 *Lepidostrobophyllum veltheimianum* (Geinitz) Strullu-Derrien, Cleal, Ducassou, A.R.T.Spencer, Stolle et Leshyk, p. 7, fig. 3H.

Description. Lanceolate sporophylls gradually tapering to an acute apex, up to 35 mm long, 4 mm wide; pedicel 8–13 mm long. Each sporophyll has a single megaspore up to 6.7 mm long, 2 mm wide, often accompanied by three much smaller abortive megaspores.

Remarks. These sporophylls were originally described as *Lepidocarpon waltonii*, but their slender, acute blades are closely comparable with the specimens from Maine-et-Loire described by Strullu-Derrien et al. (2021: fig. 3H) as *Lepidostrobophyllum veltheimianum*, the latter name having precedence. In both southern Scotland and Maine-et-Loire these sporophylls are often found associated with stems of *Lepidodendron veltheimii*, and are likely to have been produced by the same plant species.

This combination was first used by Stepanek and Vogellehner (1985), who referred to two of the syntypes figured by Geinitz (1854: pl. 4, figs 7, 8) as characterising the species. However, as they did not make a full reference to the basionym and, being published after 1953, this new combination by Stepanek and Vogellehner was not validly published (ICN, Art. 41). The first use of the combination that included a direct and full reference to the Geintiz basionym was by Strullu-Derrien et al. (2021), so the correct designation for the species is as given here.

Occurrences. Mainly from the coal-bearing interval above the Black Metals Band (Limestone Coal Formation); also from below the Orchard Limestone (Upper Limestone Formation).

Fossil-genus *Stigmaria* Brongn., 1822

***Stigmaria stellata* (Göpp.) Göpp. in Bronn 1848**
Text-fig. 5c

1841 *Stigmaria ficoides* var. *stellata* Göpp., p. 19, pl. 10, fig. 12.
1848 *Stigmaria stellata* (Göpp.) Göpp. in Bronn, p. 1201.
1966 *Stigmaria stellata* (Göpp.) Göpp.; Crookall, p. 558, pl. 104, fig. 5.

Description. Casts and compressions of axes up to 70 mm wide, surfaces covered with circular to oval scars 2–5 mm in size; scars have a slightly raised rim and a prominent raised vascular cicatrix. Each scar surrounded by 2–3 mm long radiating ridges giving a stellate-appearance.

Remarks. This distinctive fossil-species only seems to occur in lower Carboniferous macrofloras and can be

Limestone Coal Formation; BGS Kidst.4290. d: *Mesocalamites haueri* (Stur) Hirmer; left bank of stream, lower side of old stone bridge, Bilston Burn, near Polton, Midlothian; Bed underlying No. 6 Limestone, Upper Limestone Formation; BGS Kidst.4426. e: *Mesocalamites taitianus* (Kidst. et Jongm.) Hirmer; left bank of stream, lower side of old stone bridge, Bilston Burn, near Polton, Midlothian; Bed underlying No. 6 Limestone, Upper Limestone Formation; BGS Kidst.4428. All scale bars = 10 mm.

distinguished from the more widespread *Stigmaria ficoides* (Sternb.) Brongn. by the stallate surface markings on the axes between the root scars. Crookall (1966) suggested that they were the rhizophores of *Lepidodendron veltheimii* Sternb. (see also Jennings 1973). At one locality in the Limestone Coal Formation (Stripeside Pit, Herbertshire Colliery), Crookall (1966) also reported specimens of *Stigmaria ficoides* in association with *S. stellata*. However, these Stripeside Pit specimens are merely poorly preserved examples of *S. stellata*.

Occurrences. Limestone Coal Formation, between the Johnstone Shell Bed and the coal-bearing interval above the Black Metals Band; also, from below the Orchard Limestone (Upper Limestone Formation).

Family Sigillariaceae Unger in Endlicher 1842

Fossil-genus *Sigillaria* Brongn., 1822

Remarks. See Cleal and Thomas (2018) for an analysis of the taxonomic nomenclature of this fossil-genus.

***Sigillaria youngiana* Kidst., 1894**

1894a *Sigillaria youngiana* Kidst., p. 261, pl. 6, fig. 2.
1966 *Sigillaria youngiana* Kidst.; Crookall, p. 372, pl. 83, fig. 10.

Description. Stem with undulating 3–6 mm wide ribs. Leaf scars 2.5 mm long, 3 mm wide, occurring a short distance higher than the widest parts of ribs where they cover ca. ¾ of rib width; scar with emarginate upper margin, rounded lower margin, and prominent, downwards-projecting lateral angles; lateral lines extend downwards from lateral angles for 4–8 mm. A central (vascular) cicatrix and two lateral (parichnos) cicatrices occur just above the middle of the scar; no evidence of infrafoliar parichnos. Ligule pit occurs just above leaf scar and from which there is a plume of 2–5 short radiating lines.

Remarks. Only one specimen of this species has been reported, which we have not been able to see directly, but which is well-illustrated by Crookall (1966). The phyllotaxy of the stem is not completely typical of *Sigillaria* and Koehne (1904) compared it with *Lepidodendron volkmannianum* Sternb., although the leaf scars of the latter tend to be much larger.

Occurrence. Possil Ironstone (Limestone Coal Formation), Robroyston Colliery, Lanarkshire.

Order Calamitales Eichw., 1854
Family Calamitaceae Unger in Fürnrohr 1840

Fossil-genus *Mesocalamites* Hirmer, 1927

Remarks. Crookall (1969) assigned these stem fossils to *Calamites* sect. *Mesocalamites*, but to simplify the nomenclature *Mesocalamites* is taken here to be a fossil-genus in its own right. Although *Mesocalamites* is morphologically intermediate between *Archaeocalamites* Stur and *Calamites* Sternb., it is placed in the Calamitaceae based on its association elsewhere with calamitacean foliage and strobili (e.g., Strullu-Derrien et al. 2021). However, no foliage or strobili have been reported from the lower Clackmannan Group.

***Mesocalamites haueri* (Stur) Hirmer, 1927**
Text-fig. 5d

1877 *Calamites haueri* Stur, p. 195, pl. 2, fig. 7, pl. 5, figs 2, 3.
1927 *Mesocalamites haueri* (Stur) Hirmer, p. 382.
1969 *Calamites haueri* Stur; Crookall, p. 626, pl. 113, fig. 3, pl. 114, figs, 1–3, pl. 115, pl. 116, fig. 1.
1969 *Calamites roemeri* Göpp.; Crookall, p. 622, p. 122, fig. 4.
1969 *Calamites approximatiformis* Stur; Crookall, p. 629, pl. 118, fig. 2.

Description. Stems with coarse longitudinal ribs up to 4 mm wide, distally rounded with prominent circular tubercle. Nodes spaced up to 20 mm apart, with internodes sometimes wider than long, in others they may be more than twice as long as wide; at nodes, the ribs may pass straight through or be slightly offset. Occasional isolated oval branch scars sometimes occur immediately above node.

Remarks. This fossil-species represents the coarse-ribbed mesocalamitid stems found in these floras. They bear a superficial resemblance to *Calamites suckowii* Brongn., which is widespread in the Westphalian macrofloras of Euramerica but the latter has ribs that are more consistently offset at the nodes. Jongmans (1911) queried the significance of this differences, but overlooked the occurrence of occasional branch scars in *M. haueri* of a type rarely if ever seen in *C. suckowii*.

The specimens figured by Crookall as *Calamites roemeri* and *Calamites approximatiformis* have the coarse ribs with large distal tubercles similar to *M. haueri*. Crookall differentiated *C. roermeri* and *C. approximatiformis* mainly in them having more circular branch scars. However, neither of his specimens of these species show this feature and the justification for distinguishing them taxonomically seems weak.

Occurrences. Only in Upper Limestone Formation, notably below Castlecary Limestone, Bilston Burn, Midlothian.

***Mesocalamites taitianus* (Kidst. et Jongm.) Hirmer, 1927**
Text-fig. 5e

1915 *Calamites taitianus* Kidst. et Jongm., pl. 147, fig. 5, pl. 148, fig. 1, pl. 149, figs 1–5.
1917 *Calamites taitianus* Kidst. et Jongm.; Kidston and Jongmans, p. 195.
1927 *Mesocalamites taitianus* (Kidst. et Jongm.) Hirmer, p. 382.
1969 *Calamites taitianus* Kidst. et Jongm.; Crookall, p. 625, pl. 112, figs 1–3, pl. 113, figs 1, 2.
1969 *Calamites cistiformis* Stur; Crookall, p. 623, pl. 111, figs 1, 2.
1969 *Calamites ramifer* Stur; Crookall, p. 627, pl. 116, figs 2–4, pl. 117, fig. 1.
1969 *Archaeocalamites radiatus* (Brongn.) Stur; Crookall, p. 611, pl. 110, figs 2, 3 (non figs 1, 4).

Description. Stems with more-or-less straight longitudinal ribs, 1–2 mm wide, with rounded end and small indistinct distal tubercle. Weakly marked nodes at intervals of up to 70 mm, with ribs mostly passing directly over them but occasionally offset. Branch scars 7–22 mm in size, circular to transversely oval, widely distributed along stem, with no more than two at each node. Ribs tend to be deflected around scars.

R e m a r k s . This is one of the best-documented *Mesocalamites* species based on the material from the Bilston Burn site in Midlothian, and differs from *M. haueri* in having much finer longitudinal ribbing and occasional prominent branch scars. Very similar stems found in close association with *M. taitianus* were described by Crookall (1969) as *Calamites cistiformis* and *Calamites ramifer*, without giving any reason for separating them taxonomically other than the latter two have smaller and more widely-spaced branch scars. Since the branch scars distribution in *M. taitianus* is very variable, this is not a reliable character. Since the epithets *cistiformis* and *ramifer* were published before that of *M. taitianus* (Stur 1877) one of the former names might take precedence but, until the types of the former have been more fully documented, the latter name has been retained here.

The specimens figured by Crookall (1969) as *Archaeocalamites radiatus* from the Limestone Coal Formation are very similar to *M. taitianus* except that the ribs appear to cross the nodes more consistently. Given that this is also a variable character in *M. taitianus*, the latter name has been used for these specimens.

O c c u r r e n c e s . Ther Limestone Coal Formation, between the Johnstone Shell Bed and the coal-bearing interval above the Black Metals Band, and the Upper Limestone Formation, mainly from below Castlecary Limestone at Bilston Burn.

Order Sphenophyllales Wettst., 1903
Family Sphenophyllaceae Warm., 1891

Fossil-genus *Sphenophyllum* Brongn., 1828

***Sphenophyllum tenerrimum* Ettingsh. ex Helmhacker, 1874 emend. by Stur (1877)**
Text-fig. 6a

1874 *Sphenophyllum tenerrimum* Ettingsh. ex Helmhacker, p. 50, pl. 3, figs 5–16.
1877 *Sphenophyllum tenerrimum* Ettingsh. ex Helmhacker; Stur, p. 108, pl. 7, figs 1–14. (?Ettingshausen's types)
1969 *Sphenophyllum tenerrimum* Ettingsh. ex Helmhacker; Crookall, p. 602, pl. 108, fig. 6.

D e s c r i p t i o n . Ribbed stems with whorls of 9–12 leaves borne at about right-angles in proximal part of stem, but more obliquely in more distal positions. Leaves 3–10 mm long, deeply incised into 2–4 narrow-linear, splayed segments, the incisions usually extending about a half of the leaf length, each segment with a blunt apex. Occasionally the leaf segments divide for a second time. Leaf surface striate.

R e m a r k s . This is the most commonly-reported *Sphenophyllum* species found in lower Namurian macrofloras and is easily recognised by its whorls of deeply-incised leaves with splayed segments (e.g., Storch 1980, Havlena 1982, Terreaux de Felice et al. 2019). However, there are nomenclatural issues with the species epithet. According to Stur (1877) it was first used in manuscript but not published by Ettingshausen in 1853, and was mentioned by Stur (in Foetterle 1868: 50) in a species list but without description or illustration. The name *S. tenerrimum* was first validly used by Helmhacker (1874) who included a description and illustrated several specimens, although most of those specimens are now reported lost (Jongmans 1911). Nevertheless, Helmhacker made clear reference to Ettingshausen's specimens, which were later illustrated by Stur (1877), and so these can be legitimately taken as syntypes; Helmhaker's publication of the name was therefore valid.

An added complication is that Helmhacker (1873) had earlier referred to the specimens he figured in his 1874a paper as *Sphenophyllum binatum* Helmacker. However, this was a nomen nudum with no accompanying description or illustration, and so invalid.

This species is very similar to the upper Carboniferous *Sphenophyllum trichomatosum* Stur, but the leaves of the latter have segments with a more acute apex and the leaf surface tends to be smooth (non-striate) (Jongmans 1911).

O c c u r r e n c e . Ca. 10 m below Orchard Limestone, (Upper Limestone Formation), Robroyston Colliery, Lanarkshire.

Order Filicales Lindl., 1833 sensu Tryon (1952)
Family Tedeleaceae Eggert et T.N.Taylor, 1966

Fossil-genus *Pecopteris* (Brongn.) Sternb., 1825

R e m a r k s . This fossil-genus is being used in the sense of Cleal (2015) for fern fronds probably of the filicalean fern family Tedeleaceae, rather than marattialean fern remains as has historically happened (see also comments by Votočková Frojdová et al. 2020).

***Pecopteris aspera* Brongn., 1836**
Text-fig. 6c, d

1836 *Pecopteris aspera* Brongn., p. 339, pl. 120.
1901 *Pecopteris* (*Dactylotheca*) *aspera* f. *sturii* Sterzel, p. iii.
1923 *Dactylotheca sturii* (Sterzel) Kidston, p. 395, pl. 94, figs 4–6.
1939 *Dactylotheca sturii* (Sterzel) Kidston; Radforth, p. 747, pl. 1, figs 10–22.

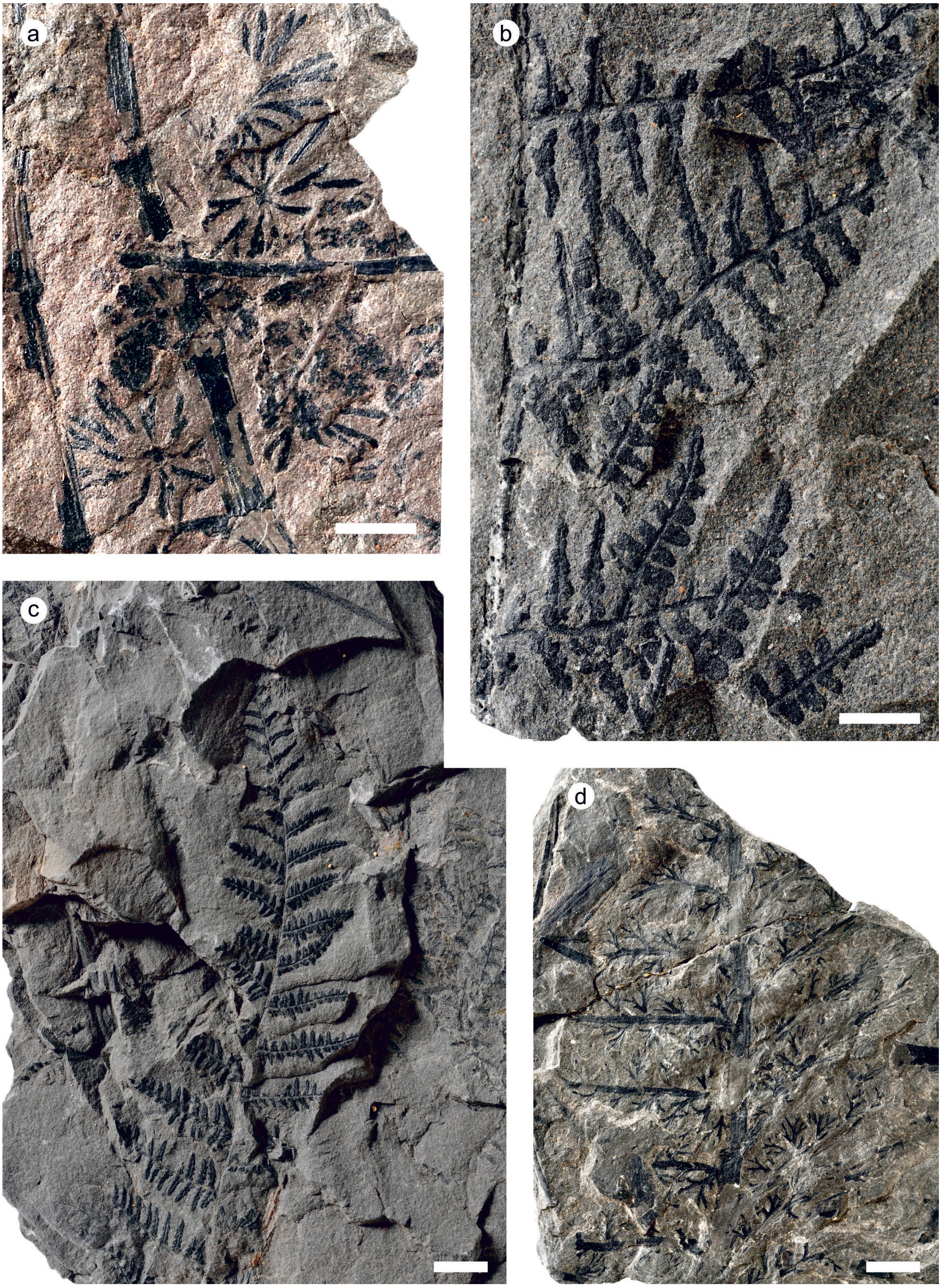
D e s c r i p t i o n . Fragments of pinnae with pinnules 2–5 mm long, 2–3 mm wide, inserted at near to right-angles. Pinnules rounded to linguaeform, broadly attached to rachis; midvein well-marked, extending for most of pinnule length, producing simple or occasionally one-formed, widely-spaced lateral veins. A few pinnules have up to 12 sporangia arranged in two rows, one on either side of midvein. Sporangia are single, oval with obtuse apex, ca. 0.5 mm long, with rudimentary apical annulus.

R e m a r k s . This species was recorded by Kidston (1924) as *Dactylotheca sturii* Sterzel but there is now general consensus that this species is indistinguishable from *P. aspera* (see Dalinval 1960). A detailed description (under the name *D. sturii*) of the reproductive structures was given by Radforth (1939) based on specimens from the same locality as those described by Kidston (1924).

O c c u r r e n c e . Upper Limestone Formation, Cuthill Shore, between Index and Orchard Limestones.

Fossil-genus *Artisophyton* Pfefferk., 1976

R e m a r k s . Corsin (1948) has shown these stems to have borne fronds now included in the family Tedeleaceae



Text-fig. 6. a: ***Sphenophyllum tenerrimum*** **Ettingsh. ex Helmhacker; Robroyston Colliery, 2.8 km SE of Bishopbriggs, Lanarkshire; ca. 10 m below Orchard Limestone, Upper Limestone Formation; BGS Kidst.156. b, c:** ***Pecopteris aspera*** **Brongn.; Cuthill Shore (near highwater mark) between Musselburgh and Prestonpans, Haddingtonshire; between Nos 4 and 5 Limestones, Upper Limestone Formation; BGS Kidst.5415 (b), BGS Kidst.4517 (c). d:** ***Zeilleria moravica*** **(Ettingsh.) Bureau; Thorneycroft No. 1 Borehole, 0.5 km NE of Cumbernauld Railway Station, Dumbartonshire; 389 m depth, Limestone Coal Formation; BGS Kidst.2420. Scale bars = 5 mm (a, b), 10 mm (c, d).**

(e.g., *Pecopteris penniformis* (Brongn.) Brongn., *Pecopteris plumosa* (Artis) Sternb.). They are similar to the marattialean stems *Megaphyton* Artis in having the leaf scars arranged in two longitudinal rows, one on either side of the main stem, but the scars tend to be squatter and more rectangular in shape. Two other fossil species from the Limestone Coal Formation were assigned by Crookall (1955) to *Megaphyton*: *Megaphyton circulare* Crookall and *Megaphyton obscurum* Crookall. However, both types are inadequate to circumscribe the taxon: that of *M. circulare* does not show details of the leaf trace, and that of *M. obscurum* has a vertically elongate branch scar atypical for these fern stems. Neither of these species will be dealt with further here.

Artisophyton chalmersii (Goodlet) comb. nov.

1957 *Megaphyton chalmersii* Goodlet, p. 158, pl. 6.

Basionym. *Megaphyton chalmersii* Goodlet, Geol. Mag., 94, p. 158, pl. 6.

Plant Fossil Names Registry Number. PFN003374 for new combination.

Description. Cast of stem 175 mm, long, 50 mm wide; two rows of crescent-shaped leaf scars 24 mm wide, 15 mm wide, distichously arranged on either side of stem, each scar with U-shaped leaf trace.

Remarks. This species was originally assigned to the marattialean fossil-genus *Megaphyton* (Goodlet 1957). However, there is no other evidence of marattialeans in the Limestone Coal Group, and the squatter, crescent-shaped leaf scars are more similar to those of the tedeleacean stems *Artisophyton* (e.g., Pfefferkorn 1976). Since fronds of the tedeleacean *Pecopteris aspera* are well documented from the Limestone Coal Group, an attribution of this species to *Artisophyton* seems more reasonable and so a new combination is proposed here.

Occurrence. Between Mynheer Coal and Pittencrieff Blackband Ironstone (Limestone Coal Formation), Elgin Colliery, Fife.

Family Urnatopteridaceae Doweld, 2001

Fossil-genus _Zeilleria_ Kidst., 1884

Remarks. The systematic position of *Zeilleria* ferns remains uncertain but are here assigned to the Urnatopteridaceae based on Brousmiche (1983).

Zeilleria moravica (Ettingsh.) Bureau, 1914
Text-fig. 6d

1865 *Trichomanes moravicum* Ettingsh., p. 77, pl. 6, fig. 4.
1914 *Zeilleria moravica* (Ettingsh.) Bureau, p. 276.
1924 *Zeilleria moravica* (Ettingsh.) Bureau; Kidston, p. 441, pl. 62, figs 3–5, pl. 108, fig. 4.

Description. Fragments of pinnae with alternate pinnules, 5–10 mm long. Pinnules deeply incised into up to six linear-acute, filiform segments; in larger pinnules the segments may be bifid. A single slender vein runs along each segment of pinnule.

Remarks. None of the Scottish specimens have yielded reproductive structures but Bureau (1914) reported pinnules of this species sometimes had "capsules" borne terminally on the lobes, which resemble *Zeilleria* sporangia.

Occurrences. Mainly in Upper Limestone Formation, between below the Orchard Limestone and the Calmy Limestone; also one record from the Limestone Coal Formation.

Order Lyginopteridales Corsin, 1960

Remarks. The taxonomy of the lyginopteridalean fronds is based on Cleal and Thomas (2023).

Family Sphenopteridaceae Göpp., 1836

Fossil-genus _Sphenopteris_ (Brongn.) Sternb., 1825

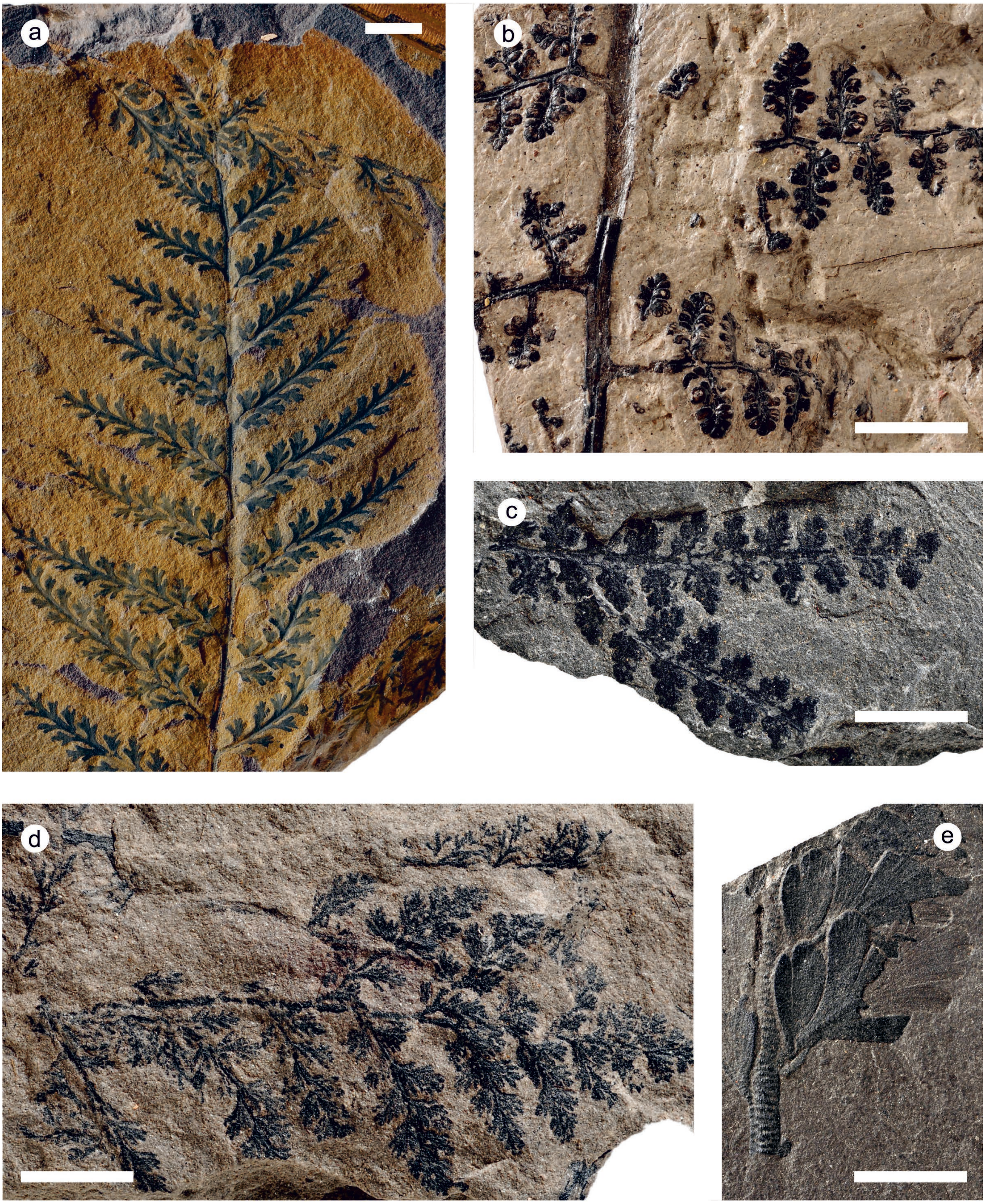
Remarks. *Sphenopteris* is characterised by a dichotomy of the primary rachis in the lower part of the frond, no pinnae being attached below the fork, and transverse markings on the surface of the rachises due to sclerotic bands in the cortex.

Sphenopteris elegans (Brongn.) Sternb., 1825
Text-fig. 7a

1820 *Filicites adiantoides* Schloth., nom. inval., p. 408, pl. 21, fig. 2.
1822 *Filicites* (*Sphenopteris*) *elegans* Brongn., p. 233, p. 2, fig. 2.
1825 *Sphenopteris elegans* (Brongn.) Sternb., p. xv.
1834 *Sphenopteris adiantoides* Schloth. ex Lindl. et Hutton, p. 91, fig. 115.
1877 *Diplothmema adiantoides* (Schloth. ex Lindl. et Hutton) Stur, p. 230.
1903 *Diplotheca stellata* Kidst. in Peach, p. 131.
1923 *Diplothmema adiantoides* (Schloth. ex Lindl. et Hutton) Stur; Kidston, p. 242, pl. 64, figs 1–4, pl. 65, pl. 66, figs 1–3, pl. 67, figs 4, 5.
1924 *Diplotheca stellata* Kidst.; Kidston, p. 462, pl. 104, figs 1, 2.
2023 *Sphenopteris elegans* (Brongn.) Sternb.; Cleal and Thomas, fig. 2.

Description. Fronds bone spirally on stem up to 40 mm wide. Petiole of frond bifurcates at wide angle to produce two asymmetrically-deltoid, primary pinna branches up to 0.2 m long; no pinnae attached below main frond bifurcation. Primary rachis branches bear once or twice pinnate secondary pinnae. All rachises have central longitudinal zone with transverse ridges. Pinnules alternate, cuneate to deltoid in shape, digitate with linear to cuneate lobes.

Remarks. This is the most abundant and distinctive pteridosperm species in the Serpukhovian floras of Scotland. It is the type species of the fossil-genus *Sphenopteris*. Sporangial clusters that may have been borne on *S. elegans* fronds were described by Kidston (in Peach 1903) as *Diplotheca stellata* Kidst., although that genus name is illegitimate (*Diplotheca* Kidst. was a later homonym of a name used for extant angiosperms). A large specimen of this species showing the frond architecture from the Upper Limestone Formation was figured by Cleal and Thomas (2023).



Text-fig. 7. a: *Sphenopteris elegans* (Brongn.) Sternb.; Cuthill Shore (near highwater mark) between Musselburgh and Prestonpans, Haddingtonshire; between Nos 4 and 5 Limestones, Upper Limestone Formation; BGS Kidst.3816. b: *Sphenopteris dicksonioides* (Göpp.) C.E.Weiss; No. 6 Pit, Grange, Bo'ness, Linlithgowshire; above Red Coal, Limestone Coal Formation; BGS Kidst.781. c: *Sphenopteris taitiana* Kidst.; Cuthill Shore between Musselburgh and Prestonpans, Haddingtonshire; between Nos 4 and 5 Limestones, Upper Limestone Formation; BGS Kidst.341. d: *Sphenopteris mira* Kidst.; New Braidbar Quarry, Giffnock, East Renfrewshire; below Orchard Limestone, Upper Limestone Formation; BGS Kidst.2416. e: *Sphenopteridium dissectum* (Göpp.) Schimp.; Swinless Glen, Dalry, Ayrshire; above Garibaldi Ironstone, Limestone Coal Formation; BGS Kidst.5320. All scale bars = 10 mm.

Occurrences. Abundant in between the Johnstone Shell Bed (lower Limestone Coal Formation) and the Lyoncross Cement Limestone (upper Upper Limestone Formation).

Sphenopteris dicksonioides (Göpp.) C.E.Weiss, 1881

Text-fig. 7b

1836 *Aspidites dicksonioides* Göpp., p. 361, pl. 28.
1881 *Sphenopteris dicksonioides* (Göpp.) C.E.Weiss, p. 11, pl. 11, figs 65, 66.
1923 *Sphenopteris dicksonioides* (Göpp.) C.E.Weiss; Kidston, p. 73, pl. 18, fig. 1.

Description. Small pinnate fragments, up to tripinnately divided. Antepenultimate rachises 2–3 mm wide, bearing alternate penultimate pinnae at near to right-angles. Penultimate rachises spaced at 17 mm intervals, ca. 1 mm wide, bearing alternate ultimate pinnae at near to right-angles. Ultimate pinnae with up to 12 pairs of small, petiolate, subtriangular pinnules up to 4 mm long and 2 mm wide, with vaulted limb; each pinnule has three to five rounded, deeply separated lobes. Veins not clearly visible.

Remarks. The type of the basionym of this species originated from the Serpukhovian of Upper Silesia. The only figured specimen from Scotland (Kidston 1923: pl. 18, fig. 1) is a small fragment, whose affinities must be regarded as uncertain. Some authors have placed this species in *Lyginopteris* Potonié auct. (i.e., *Calymmotheca* Stur) (e.g., Patteisky 1957, Purkyňová 1970). However, no reproductive structures are known, nor any of the diagnostic features such as anastomosed rachial surface markings, and so the species has been retained here in *Sphenopteris*.

Occurrences. Limestone Coal Formation, between the Johnstone Shake Bed and the coal-bearing interval above the Black Metals Band.

Sphenopteris taitiana Kidst., 1923

Text-fig. 7c

1923 *Sphenopteris taitiana* Kidst., p. 78, pl. 18, figs 4, 5.

Description. Bipinnate fragments with punctate ultimate rachises 2–3 mm wide. Subopposite ultimate pinnae attached at near to right-angles, spaced at 20–25 mm intervals, tapered along most of length. Pinnules deltoid with a well-developed petiole, up to 6 mm long and 4 mm wide; more distal pinnules are more or less entire, the most proximal pinnules have up to six lobes with the lobes sometimes themselves being shallowly lobed. Veins not clearly preserved.

Remarks. The types of this species originated from the Upper Limestone Formation. Kidston compared the species with *Sphenopteris linkii* (Göpp.) C.Presl, widely regarded as a later heterotypic synonym of *Sphenopteris fragilis* Brongn. *auct.* (*Calymmotheca divaricata* (Göpp.) Stur). However, Kidston's specimens show none of the characteristic features of *Calymmotheca* (e.g., rachises with anastomosed surface markings) and the species is here regarded as a true *Sphenopteris* with distinctive, small pinnules. The species has also been recorded from Upper Silesia (Patteisky 1929).

Occurrences. Rare in Upper Limestone Formation, in interval below Orchard Limestone.

Sphenopteris mira Kidst., 1923

Text-fig. 7d

1923 *Sphenopteris mira* Kidst., p. 138, pl. 30, fig. 2.

Description. A single specimen showing part of a bipinnate segment. Pinnules alternately attached to ultimate rachis; pinnules small, subrhomboidal, 3–5 mm long, each with 3–6 narrow linear segments. A single vein enters each pinnule segment.

Remarks. Only one specimen of this small-pinnuled species is known from Scotland (Kidston 1923: pl. 30, fig. 2) but it has also been described from the Serpukhovian of Upper Silesia (Purkyňová 1970). There are no distinctive features that allow it to be definitely placed in a particular fossil-genus and so provisionally it has been retained in its original fossil-genus.

Occurrence. Rare in Upper Limestone Formation, only reported from below the Orchard Limestone at New Braidbar Quarry, Renfrewshire.

Fossil-genus *Sphenopteridium* Schimp., 1874

Remarks. This fossil-genus consists of remains of fronds similar to *Sphenopteris* but where the main dichotomy occurs in the middle part of the frond resulting in pinnae being attached to the main rachis below the fork.

Sphenopteridium dissectum (Göpp.) Schimp., 1874

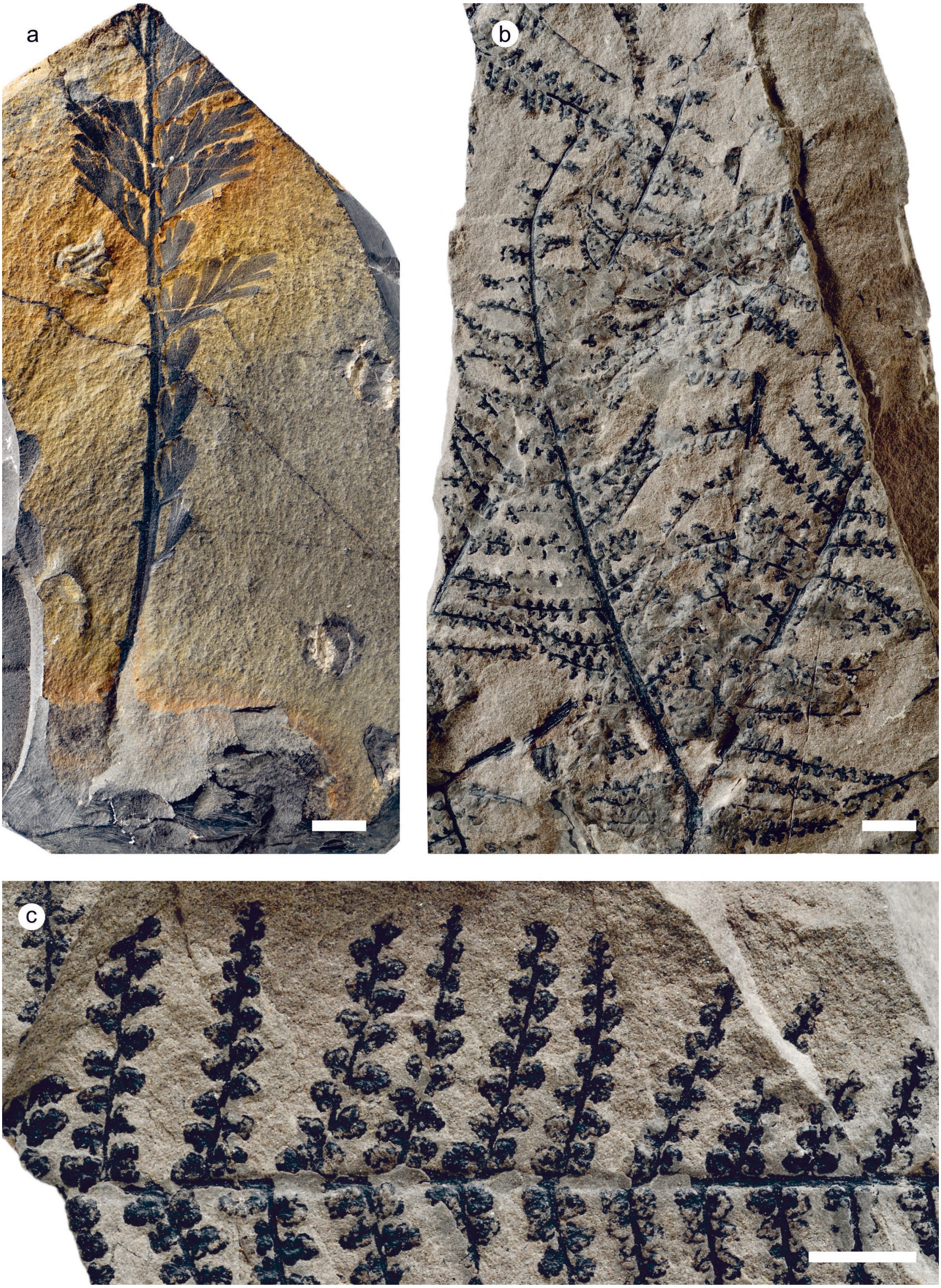
Text-fig. 7e

1852 *Cyclopteris dissecta* Göpp., p. 161, pl. 14, figs 3, 4.
1874 *Sphenopteridium dissectum* (Göpp.) Schimp., p. 488, pl. 107, fig. 12.
1923 *Sphenopteridium dissectum* (Göpp.) Schimp.; Kidston, p. 160, pl. 37, figs 1–4.

Description. Bipinnate fragments with clear transverse marks on the rachises. Ultimate pinnae up to 30 mm long, closely-spaced (often touching); pinnae have a pair of oblique, obovate pinnules in the proximal part, and a cuneate terminal pinnule comprising up to 7 segments with rounded apices. Pinnules thick-limbed with a rugous surface. Numerous fine, dichotomous, radiating veins.

Remarks. None of the Scottish specimens figured by Kidston (1923: pl. 37, figs 1–4) shows the diagnostic features of a *Sphenopteridium* frond. However, specimens of this species from Saalfeld (Ludwig 1869: pl. 22, fig. 3) and Upper Silesia (Stur 1875: pl. 5, fig. 8) show the characteristic dichotomy with pinnae attached below the fork (see comments by Kidston 1923). Clusters of *Calathiops*-like ovulate structures were found associated with these fronds at Swinless Glen and described and figured by Crookall (1976: pl. 171, figs 15, 16) as *Lagenostoma smithii* Kidst. ex Crookall.

Occurrences. Rare in Lower Limestone Formation, mainly from just above the Hurlet Limestine, and one record from the lower Limestone Coal Formation (Garibaldi Ironstone, Dalry).



Text-fig. 8. **a:** ***Rhacopteris transitionis*** **Stur; Limekilns, East Kilbride, Lanarkshire; Calderwood Limestone, Lower Limestone Group; BGS Kidst.5288. b, c:** ***Calymmotheca stangeri*** **Stur; pit sinking at Robroyston Colliery, 2.8 km SE of Bishopbriggs, Lanarkshire; ca. 10 m below Orchard Limestone, Upper Limestone Formation; BGS Kidst.5596 (b), BGS Kidst.5591 (c). Scale bars = 10 mm.**

Fossil-genus *Eusphenopteris* Simson-Schar., 1934

Eusphenopteris foliolata (Stur) van Amerom, 1975

Text-fig. 10d, e

1875 *Sphenopteris foliolata* Stur, p. 22, pl. 5, figs 3–6.
1923 *Sphenopteris foliolata* Stur; Kidston, p. 113, pl. 23, figs 1–4.
1975 *Eusphenopteris foliolata* (Stur) van Amerom, p. 76, pl. 43, figs 4–6.

Description. Bipinnate fragments. Alternate ultimate deltoid pinnae, widely spaced, each with 1–3 or more pairs of pinnules. Pinnules petiolate, subrotund to subreniform, up to 10 mm long. Fine veins radiate from petiole, dichotomising 4–6 times.

Remarks. The most detailed taxonomic analysis of this species was by van Amerom (1975), who regarded its position within *Eusphenopteris* as being uncertain. If accepted, however, this will be the earliest known species of this genus.

Occurrences. Rare in Upper Limestone Formation, most notably from below the sandstone on which Ardross Castle was built, Fifeshire.

Fossil-genus *Rhacopteris* Schimp., 1869

Remarks. Kidston (1923) recorded several other *Rhacopteris* species from the lower Clackmannan Group but in most cases, there were no accompanying illustrations or voucher specimens in his collection (*R. inaequilaterata* (Göpp.) Stur, *R. lindsaeformis* (Bunbury) Kidst., *R. petiolata* (Göpp.) Kidst.). The systematic position of *Rhacopteris* remains uncertain but based on the rachial anatomy Galtier et al. (1997) suggested possible lyginopteridealean affinities.

Rhacopteris transitionis Stur, 1875

Text-fig. 8a

1875 *Rhacopteris transitionis* Stur, p. 77, 86, pl. 8, figs 5–7.
1923 *Rhacopteris transitionis* Stur; Kidston, p. 219, pl. 50, fig. 1, pl. 53, fig. 1 (?pl. 51, fig. 4).

Description. Once-pinnate frond with stout, finely-striate rachis up to 5 mm wide. Petiolate pinnules touching or very close, attached to rachis at 70–80°. Pinnules ca. 15 mm long, 7 mm wide in middle of frond, becoming gradually smaller in more distal and proximal positions. Pinnule shape asymmetrically rhomboidal, shallowly divided into up to seven lobes. Fine veins radiate from base with a single vein entering each pinnule lobe.

Remarks. Although a rare species, Kidston (1923) documented some particularly well-preserved specimens from the Lower Limestone Formation. The systematic affinities of this species remain uncertain and Hübers et al. (2014) suggested that it might be an immature pteridosperm, by implication a lyginopteridalean. However, the very robust rachis and asymmetrical pinnules suggest that it is probably a *Rhacopteris*.

Occurrences. Rare in Lower Limestone Formation, notably from the Top Hosie Limestone (Limekilns), Lanarkshire; and a record from an ironstone above the Top Hosie Limestone (lower Limestone Coal Formation).

Family Lyginopteridaceae Potonié in Engler et al. 1902

Fossil-genus *Calymmotheca* Stur, 1877

Remarks. This fossil-genus was often named *Lyginopteris* Potonié (Potonié 1897). However, that name was predated by *Calymmotheca* Stur (Stur 1877; see Strullu-Derrien et al. 2021). Zeiller (1883) suggested that the spelling should be changed for linguistic reasons but the original spelling must be retained.

Calymmotheca stangeri Stur, 1877

Text-fig. 8b, c

1877 *Calymmotheca stangeri* Stur, p. 257, pls 8–9.
1924 *Calymmatotheca stangeri* Stur; Kidston, p. 465, pl. 105, figs 1–7, pl. 106, figs 1–9, pl. 107, figs 1–6.

Description. Spinose stems up to 30 mm wide bearing helically-arranged fronds; both stems and rachises with anastomosed surface patterning. Petiole / primary rachis of fronds dichotomous producing divergent, tri-to quadri-pinnate, lanceolate to ovate pinna-branches, with ultimate pinnae borne both below and above the dichotomy. Ultimate pinnae linear-lanceolate to lanceolate depending on position in frond, bearing alternately to oppositely arranged pinnules. Pinnules thick-limbed, quadrate-ovate to triangular-ovate, basally constricted, with entire margin or shallowly lobed. Veins thin, dichotomous, with several veins entering each pinnule lobe. Cupulate ovules borne on rachises lacking sterile pinnule.

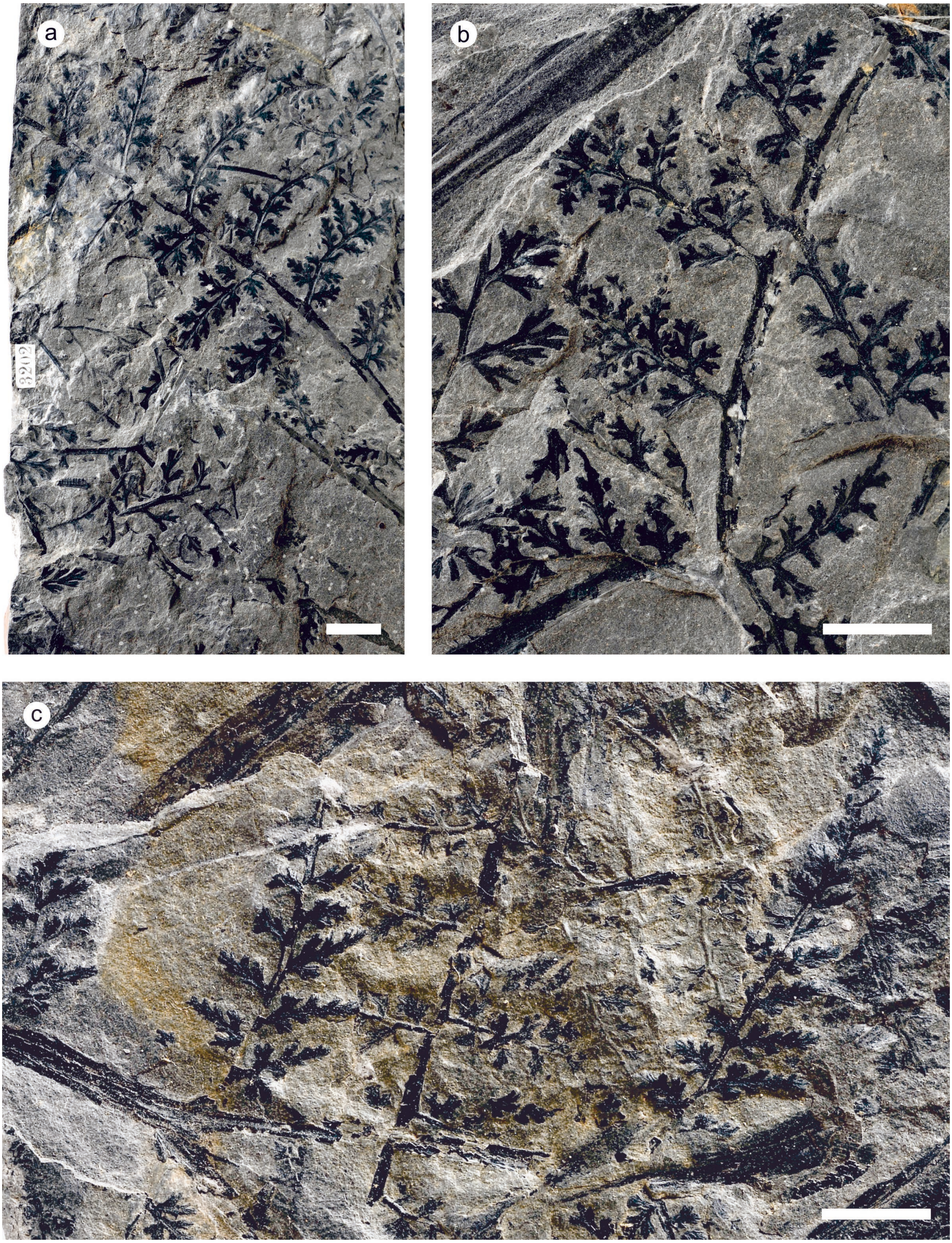
Remarks. This species is the type of the fossil-genus *Calymmotheca*. It is very similar to *Calymmotheca dubuissonis* (Brongn.) Stur as occurs abundantly in the Serpukhovian of Maine-et-Loire, France (Bureau 1914, Strullu-Derrien et al. 2021) but the latter has pinnules that are more oblique to the rachis, are more divided and have more acute lobes. It is not widespread in the Scottish Serpukhovian floras, although at least it was reported as very abundant in Braidbar Quarry and Robroyston Pit that allowed Kidston (1924) to prepare a detailed description.

Occurrences. Below Orchard Limestone, Upper Limestone Formation, from New Braidbar Quarry and Robroyston Colliery.

Calymmotheca divaricata (Göpp.) Stur, 1877

Text-fig. 9

1836 *Cheilanthites divaricatus* Göpp., p. 238, pl. 12, figs 1, 2.
1836 *Gleichenites linkii* Göpp., p. 182, pl. 2, fig. 1.
1875 *Sphenopteris falkenhainii* Stur, p. 26, pl. 6, fig. 1.
1877 *Calymmotheca divaricata* (Göpp.) Stur, p. 165, pl. 13, figs 1–3.
1923 *Sphenopteris falkenhainii* Stur; Kidston, p. 79, pl. 19, fig. 1.
1923 *Sphenopteris fragilis* Kidst. (non Schlotheim), p. 86, pl. 17, figs 1–5.
1923 *Schuetzia bennieana* Kidst.; Kidston, pl. 107, fig. 8.
1924 *Schuetzia* cf. *bennieana* Kidst.; Kidston, pl. 107, figs 9–13.



Text-fig. 9. ***Calymmotheca divaricata*** **(Göpp.) Stur. a: Wimbledon Pit, Machrihanish, Campbeltown, Mull of Kintyre; shale above Main Coal, Limestone Coal Formation; BGS Kidst.3202. b, c: Machrihanish Water, 290 m west of Wimbledon Pit, Campbeltown, Mull of Kintyre; Limestone Coal Formation; BGS Kidst.3210 (b), BGS Kidst.4488 (c). Scale bars = 10 mm.**

D e s c r i p t i o n . Bifurcate fronds attached to stems up to 15 mm wide with elongate-anastomosed surface markings. Primary rachis ca. 3 mm wide, bifurcating at 35° about 40 mm away from the attachment to the stem to form bipinnate to tripinnate primary rachis branches. Gently-tapered ultimate pinnae attached at 70–90°, oppositely or suboppositely arranged, spaced up to 15 mm apart. Pinnules up to 5 mm long and 3 mm wide, alternately to suboppositely arranged, and somewhat obliquely (70–80°) attached to rachis by a broad but short petiole; pinnule shape deltoid to subrhomboidal. The most proximal pinnules are deeply incised with five to seven cuneate lobes, with each lobe sometimes being further shallowly divided; more distal pinnules are less divided and at the ends of the ultimate pinnae they become simple or bifid.

R e m a r k s . This fossil-species is widespread in the upper Visean and Serpukhovian of Europe (Mosseichik 2010). Historically it has often been referred to as "*Sphenopteris fragilis* Schloth.". That name was not validly published as Schlotheim's (1820) work pre-dated the starting point for palaeobotanical nomenclature but was subsequently validated by Brongniart (1828). As pointed out by Strullu-Derrien et al. (2021), however, the type of that name (Schlotheim 1804: pl. 10, fig. 17) is difficult to interpret and the earliest legitimate name with a type that can definitely be assigned to this species is *Cheilanthites divaricatus* the basionym of *Calymmotheca divaricata*.

Kidston (1923: pl. 17, figs 1–5) figured specimens of this species from the Upper Limestone Formation as *S. fragilis* Brongn. He also (Kidston 1923: pl. 19, fig. 1) figured a specimen with somewhat less divided pinnules as *Sphenopteris falkenhainii* Stur (Stur 1875) but Patteisky (1957) regarded this species as being merely a variety of *C. divaricata* and the distinction is not recognised here.

Clusters of sporangia associated with *C. divaricata* fronds were described by Kidston (1924) as *Schuetzia* cf. *bennieana* but Walton (1931) showed this generic attribution to be incorrect; they are almost certainly the pollen organs of *C. divaricata*.

O c c u r r e n c e s . Widespread through the Limestone Coal Formation from the coal-bearing interval above the Black Metals Band, and through the Upper Limestone Formation to just below the Castlecary Limestone.

Calymmotheca distans (Sternb.) Strullu-Derrien, Cleal, Ducassou, A.R.T.Spencer, Stolle et Leshyk, 2021

1820 *Filicites bermudensiformis* Schloth., nom. inval., p. 409, pl. 21, fig. 2.
1825 *Sphenopteris distans* Sternb., p. xvi.
1832 *Filicites bermudensiformis* Schloth., nom. illeg., pp. 7, 10, pl. 10, fig. 18 left b, pl. 21, fig. 2.
1913 *Diplothmema bermudensiforme* (Schloth.) Gothan, nom. illeg. p. 73, pl. 15, fig. 5.
1923 *Diplothmema bermudensiforme* (Schloth.) Gothan; Kidston, p. 250, pl. 61, fig. 3, pl. 67, fig. 3.
2021 *Calymmotheca distans* (Sternb.) Strullu-Derrien, Cleal, Ducassou, A.R.T.Spencer, Stolle et Leshyk, p. 15.

D e s c r i p t i o n . Pinnate fragments, with rachises with anastomosed surface markings. Ultimate pinnae oblong-lanceolate, with alternating, widely spaced, obliquely-attached pinnules; pinnules deltoid, up to ca. 8 mm long, 4–5 mm wide, with 3–5 lobes separated by shallow sinus; pinnule lobes oblong-rounded and in larger pinnules spread out in fan.

R e m a r k s . This species has often been assigned the epithet *bermudensiforme* / *bermudensiformis* but as pointed out by Strullu-Derrien et al. (2021) this name is invalid and the correct name is *C. distans*. The species is widely distributed in the upper Visean and lower Serpukhovian of Euramerica and was documented from the Clackmannan Group by Kidston (1923), although the specimens can no longer be located in his collection. Like the previous species the anastomosed surface markings on the rachises clearly point to it belonging to *Calymmotheca*, but differs from the more widespread *C. divaricata* by the less incised pinnules.

O c c u r r e n c e s . Rare in Lower Limestone and Upper Limestone Formations, but absent from Limestone Coal Formation.

Fossil-genus _Spathulopteris_ Kidst., 1923

Spathulopteris clavigera (Kidst.) J.Walton, 1931
Text-fig. 10a

1923 *Sphenopteris clavigera* Kidst., p. 142, pl. 32, fig. 2.
1931 *Spathulopteris clavigera* (Kidst.) J.Walton, p. 361, pl. 24, fig.19.

D e s c r i p t i o n . Relatively stout rachis, 6 mm wide, with smooth surface; narrow-deltoid penultimate pinnae alternate, bearing 2–4 pairs of small, clavate pinnules with up to 3 lobes in basal part of pinnae, entire in distal part; pinnule limb thick, showing little of the venation.

R e m a r k s . This fossil-species was based on a specimen from the Lower Limestone Group. Kidston (1923) was uncertain as to the frond architecture and so placed it in the generalised fossil-genus *Sphenopteris*. However, Walton (1931) showed that it was otherwise indistinguishable from *Spathulopteris*.

O c c u r r e n c e . Only reported from above the Top Hosie Limestone (Lower Limestone Formation), East Kilbride.

Fossil-genus _Archaeopteridium_ Kidst., 1923

R e m a r k s . This fossil-genus has been reviewed by Rowe (1992), who pointed out that it differs from both *Sphenopteris* and *Sphenopteridium* in the absence of transverse markings on the rachis caused by cortical sclerotic plates. However, its distinction from *Spathulopteris* is less clear-cut. Kidston (1923) noted that the main difference is that *Archaeopteridium* pinnules tend to be decurrent and more broadly attached to the rachis, and have a more lobed margin, but whether these differences are sufficient to merit a generic separation is unclear. Nevertheless, for the time being *Archaeopteridium* has been kept as a separate fossil-genus.

Archaeopteridium tschermakii (Stur) Kidst., 1923
Text-fig. 10b, c

1875 *Archaeopteris tschermakii* Stur, p. 57, pl. 12, fig. 1, pl. 16, fig. 1.

Text-fig. 10. a: *Spathulopteris clavigera* (Kidst.) J.Walton; East Kilbride, Lanarkshire; Calderwood Limestone, Lower Limestone Formation; BGS Kidst.792. b, c: *Archaeopteridium tschermakii* (Stur) Kidst.; East Kilbride, Lanarkshire; Calderwood Limestone, Lower Limestone Formation; BGS Kidst.791 (b), BGS Kidst.792 (c). d, e: *Eusphenopteris foliolata* (Stur) van Amerom; Ardross Castle, Fifeshire; sandstone below castle, Upper Limestone Formation; BGS Kidst.2838 (d), BGS Kidst.2841 (e). Scale bars = 10 mm.

1894a *Plumatopteris elegans* KIDST., p. 258, pl. 5, fig. 1.
1923 *Archaeopteridium tschermakii* (STUR) KIDST., p. 182, pl. 40, fig. 3, pl. 41, figs 1, 2, pl. 43, fig. 6.
1923 *Plumatopteris elegans* KIDST.; Kidston, p. 185, pl. 41, figs 3, 4, pl. 43, figs 4, 5.

Description. Bipinnate frond fragments with longitudinally striate rachises. Ultimate pinnae with up to 9 alternately attached pinnules. Pinnules oblong, spathulate to obovate. Distal pinnules with entire margin, and broadly and decurrently attached to rachis; more proximal pinnules tend to become somewhat lobed and basally constricted, but never petiolate. Several radiating veins enter the pinnule at its base; in larger pinnules, an incipient midvein may develop.

Remarks. This is a rare but widespread species in upper Visean and Serpukhovian floras. The types of *P. elegans* were described by Kidston (1923) in close association with *A. tschermakii* and were only differentiated by adjacent pinnules being more fused along the rachis; they undoubtedly represent variation within *A. tschermakii* (see also comments by Rowe 1992: 883).

Occurrences. Several occurrences in the Lower Limestone Formation, and from ironstone bands below the Black Metals Band (Limestone Coal Formation).

Discussion

Vegetation trends

There is little evidence as to how these fossils were collected but it seems likely that they were the result of non-systematic sampling. Consequently, most of the localities recorded in this study yielded very few species (Tab. 2): about three-quarters of the localities have only one species and another 10 % only two species. Just one locality (New Braidbar Quarry) yielded more than five species. These proportions are more or less the same for the Lower Limestone, Limestone Coal and Upper Limestone Formations. This makes it difficult to draw conclusions concerning the changes that were taking place in the vegetation and habitats through the lower Clackmannan Group. Nevertheless, four general macrofloral phases (zones) can be identified (Text-fig. 11):

1. The Lower Limestone Formation and lower Limestone Coal Formation (up to the Johnstone Shell Bed) have only a few, low diversity macrofloras dominated by pteridosperms (such as *Archaeopteridium*, *Rhacopteris*, *Spathulopteris*, *Sphenopteridium*). These compare with the upper Visean allochthonous macrofloras found in shallow marine deposits such as at Glencartholm in southern Scotland (Kidston 1905) and Teilia Quarry in north Wales (Kidston 1890, Walton 1928, 1931). This interval has few coal deposits except in Fife (Forsyth and Chisholm 1977, Fielding et al. 1988), suggesting the coal swamp biome had not yet fully developed in southern Scotland at this time.

2. The Limestone Coal Formation above the Johnston Shell Bed is characterised by diverse macrofloras belonging to the *Calymmotheca stangeri* Zone of Wagner (1984) and Opluštil et al. (2022a), and including arborescent lycopsids (*Lepidodendron*), equisetopsids (*Mesocalamites*) and pteridosperms (*Sphenopteris*, *Calymmotheca*). They are mostly allochthonous macrofloras but there are also some autochthonous remains of arborescent lycopsid swamps, such as in the Victoria Park Fossil Grove in Glasgow (Gastaldo 1986, Webster and Allison 2022). Also seen here are the first significant coal seams indicating the coal swamp biome had started to become fully developed.

3. The Upper Limestone Formation up to the Orchard Limestone yielded similar *C. stangeri* Zone macrofloras, but also including *Sphenophyllum tenerrimum*, the fern *Pecopteris aspera* and pteridosperms *Sphenopteris mira* and *Calymmotheca stangeri*.

4. The Upper Limestone Formation macrofloras above the Orchard Limestone are much less diverse. The interval is regarded as Arnsbergian in age based on goniatite biostratigraphy (Ramsbottom 1977) and so would be expected to yield *Calymmotheca larischii* Biozone macrofloras (e.g., Jirásek et al. 2018). However, none of the diagnostic species have been found, possibly due to the low diversity of the macrofloras.

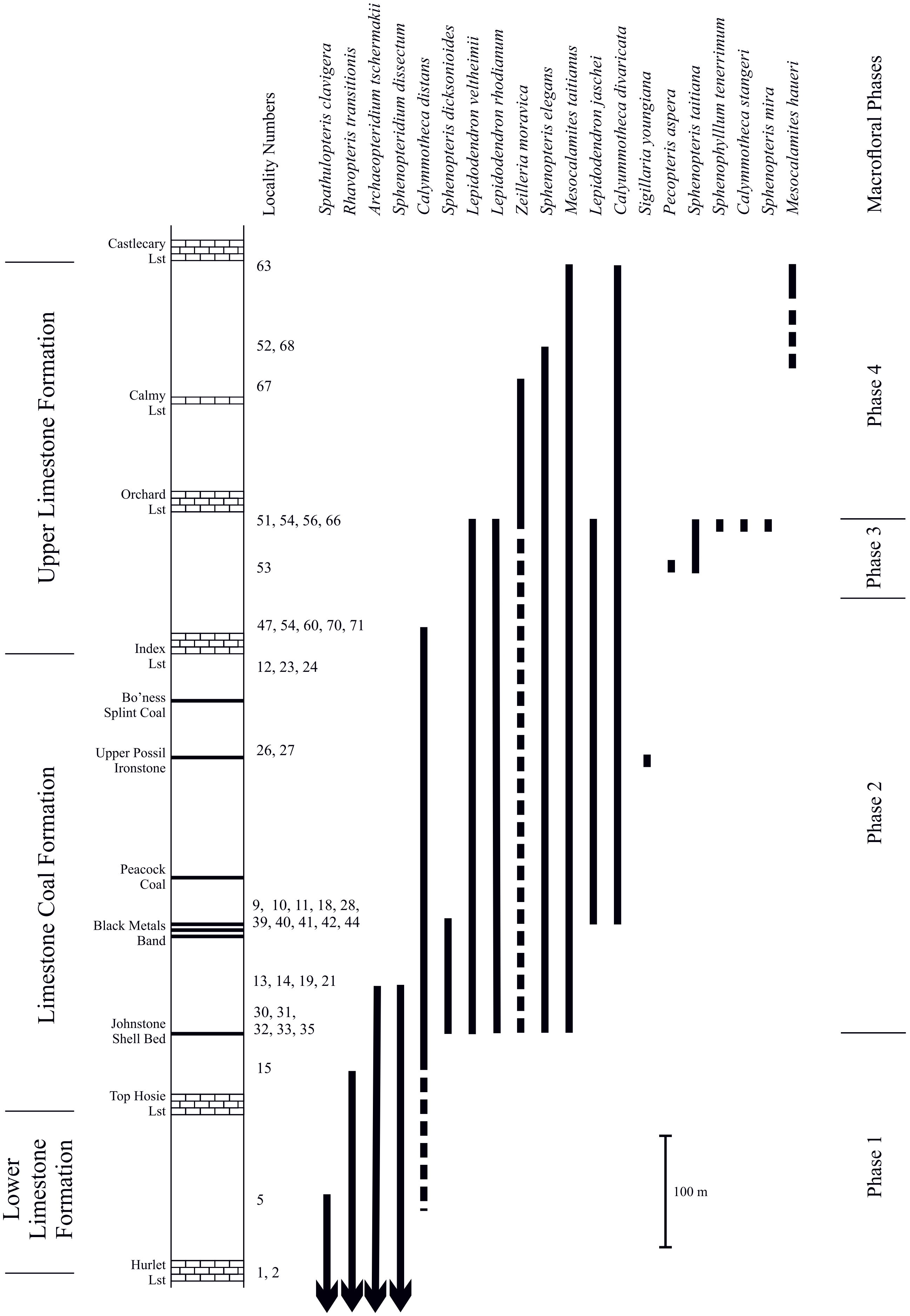
The upper boundary of the Clackmannan Group is marked by a major stratigraphical and palaeobotanical hiatus (Kidston 1894b, Crookall 1939); there is also a clear break in the vertebrate fossil record (Smithson 1985). The overlying Kinderscoutian – Marsdenian Passage Group comprises paralic, fluvio-deltaic deposits with few coals or macrofloras (Neves et al. 1965, Read 1981, 1989), suggesting the coal swamp biome had disappeared from southern Scotland at that time.

Comparison with Upper Silesia

Upper Silesia has a similar-aged paralic sequence that has been correlated in detail with the lower Clackmannan Group based on goniatite biostratigraphy (Jirásek et al. 2018) and has revealed a similar pattern of vegetation change (Purkyňová 1970, Zdanowski and Żakowa 1995). The Kyjovice Shale (upper Hradec-Kyjovice Formation) is a predominantly marine sequence with relatively low diversity macrofloras (designated Zone NA_1 by Purkyňová 1970). This has been dated as earliest Namurian (Pendleian – low E_1) based on goniatite biostratigraphy (Klomínský 1994) and so correlates with the Lower Limestone Formation and lower Limestone Coal Formation.

Table 2. Number of localities yielding different species diversities.

Formation	1 Species	2 Species	3 Species	4 Species	>4 Species
Upper Limestone Formation	19	2	1	1	2
Limestone Coal Formation	28	5	4	0	1
Lower Limestone Formation	7	0	1	0	0
Total	54	7	6	1	3



Text-fig. 11. Stratigraphical ranges of the most significant plant fossil-species through the Lower Clackmannan Group, showing the four informal zones discussed in the text.

The overlying Ostrava Formation sees a marked increase in macrofloral diversity and the appearance of economically significant coal deposits (Hýlová et al. 2013, 2016). The base of the formation has been correlated with the Black Metals Band in southern Scotland (Jirásek et al. 2018) where similar changes in facies and macrofloras occur. The lower Ostrava Formation (Petřkovice and Hrušov Members) macrofloras were designated Floral Zone NA_2 by Purkyňová (1970) and are very similar to those found in the coal-bearing part of the Limestone Coal Formation. The increasingly terrestrial conditions indicated by the Ostrava Formation (and by implication the Limestone Coal Formation) have been interpreted as a response to the northwards migration of the Variscan Front (Hartley and Otava 2001). However, the synchronous habitat and vegetation changes in these widely separated areas suggest they were more likely a response to more pervasive factors such as eustatic sea-level changes. The Lower Limestone Formation already shows evidence of eustatic fluctuations probably caused by the onset of the first main glacial phase (C1) of the late Palaeozoic Ice Age (Fielding and Frank 2015). As this glacial phase increased in intensity through Pendleian times, areas of continental shelf in palaeotropical Euramerica would have been exposed on which the coal swamp biome could develop, as seen in the Ostrava and Limestone Coal Formations.

A marked flora change occurs at the Enna Marine Zone in the middle Ostrava Formation (between the Hrušov and Jaklovec Members) and has been interpreted as a response to global warming and a significant rise in sea-levels (Gastaldo et al. 2009a, b). The Enna Marine Zone correlates with the Orchard Limestone in the Upper Limestone Formation (Jirásek et al. 2018) where the marked reduction in macrofloral diversity may also be reflecting this climatic change. The upper Ostrava Formation sees a return of coal-bearing deposits and diverse macrofloras (Zone NA_3 of Purkyňová 1970), but this is not seen in the upper Upper Limestone Formation where marine conditions predominate. The climatic warming indicated by the upper Ostrava and Upper Limestone Formations can be correlated with the end of the C1 Glacial Phase of (Fielding et al. 2023), which has been dated as ca. 325 Ma, just before the end of the Serpukhovian.

Above the Ostrava Formation is a stratigraphical and palaeobotanical hiatus referred to as the "Florensprung" (Gothan 1913). Above this break is the Kinderscoutian – Marsdenian Karviná Formation consisting of purely continental, predominantly fluvial deposits with some lacustrine bands (Kumpera 1990, Dopita and Kumpera 1993, Kędzior et al. 2007, Opluštil et al. 2022b), comparable to the Passage Group in southern Scotland. The Karviná Formation has a few thick coal deposits but no significant macrofloras.

Comparison with Maine-et-Loire

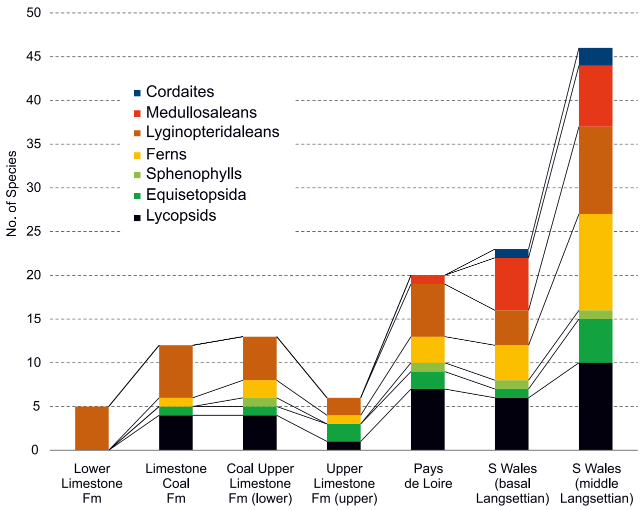
Similar coal swamp vegetation preserved in the lower Clackmannan Group and Ostrava Formation has also been reported from northwest France, in the Maine-et-Loire (Bureau 1914, Strullu-Derrien et al. 2021, 2023). There is no radiometric or faunal dating for these Maine-et-Loire deposits but the macrofloras belong to the *Calymmotheca stangeri* Zone, similar to those of the Limestone Coal and Ostrava Formations. These French macrofloras have similar diversities to those of southern Scotland and Upper Silesia, and are almost indistinguishable in terms of the more abundant species; where there are differences, it involves relatively rare taxa, such as *Cardioneuropteris antecedens* (Stur) Strullu-Derrien et al., *Bothrodendron wiikianum* (Heer) Kidst., *Calymmotheca tridactylites* (Brongn.) Stur and *Zeilleria antiquum* (Bureau) Cleal et al. in the French floras, and *Sigillaria youngiana*, *Sphenopteris taitiana*, *Sphenopteris mira*, *Eusphenopteris foliolata* and *Adiantites tenuifolius* in the Scottish flora. The Maine-et-Loire deposits have been interpreted as being formed in an intramontane basin (Barthet 2005) and so might be expected to have quite different vegetation from the paralic southern Scotland and Upper Silesia basins. However, the elevation of the Maine-et-Loire depositional basin during the Serpukhovian is uncertain, and the effect on the vegetation of this physiographic difference seems to have been less marked than with the Moscovian / late Westphalian intramontane basins (e.g., Gothan 1915, 1925, 1929, 1954, Cleal and Cascales-Miñana 2019).

Comparison with other areas

General reviews of Serpukhovian floras (e.g., Mosseichik 2010, 2022) have shown that *Calymmotheca stangeri* Zone macrofloras occur elsewhere in tropical Euramerica north of the Central Pangaea (Variscan – Appalachian) mountains such as the Mauch Chunk Group in Pennsylvanian, USA (Blake et al. 2002), the lower Chokier Formation in Belgium (Stockmans and Willière 1953), Lower Silesia and Lublin in Poland (Zdanowski and Żakowa 1995), Dobrudzha in Bulgaria (Kulaksuzov and Tenchov 1973) and Zonguldak in northern Turkey (Jongmans 1955). However, these macrofloras are in need of taxonomic revisions before detailed comparisons are possible.

Later developments

Coal swamps returned to the lowland, paralic areas of palaeotropical Euramerica at the start of Westphalian times



Text-fig. 12. Changes in species richness through the Lower Clackmannan Group (data in this paper), the Pays de la Loire (data from Strullu-Derrien et al. 2021) and the lower Westphalian of South Wales (data from Cleal 2007).

(late Bashkirian, ca. 316–317 Ma; Waters and Condon 2012). This is coincident with the onset of the C3 Glacial Phase of Fielding et al. (2023). Initially the vegetation of the returning coal swamps was similar to that of the Serpukhovian swamps except for the presence of cordaitaleans and more diverse medullosaleans (Text-fig. 12). As sea-levels continued to fall, however, the coal swamp vegetation further diversified among all plant groups present, resulting in the classic coal measures macrofloras found extensively in the upper Bashkirian and Moscovian of palaeotropical Euramerica (e.g., Cleal 2005, 2007, Uhl and Cleal 2010, Molina-Solís et al. 2024).

Conclusions

The Limestone Coal Formation and Upper Limestone Coal Formation of southern Scotland yield evidence of early coal swamps – a wetland biome dominated by arborescent lycopsids and equisetopsids, ferns and lyginopteridalean pteridosperms. The interval correlates with the Ostrava Formation in Upper Silesia and the coal-bearing sequence in Maine-et-Loire. These early coal swamp sequences span much of the Pendleian and Arnsbergian Substages of the Heerlen Regional Chronostratigraphy (Wagner and Winkler Prins 2016), and the Serpukhovian Stage in the IUGS Global Chronostratigraphy (Davydov et al. 2010), and so coincide with the first (C1) glacial phase of the Late Palaeozoic Ice Age. It has been suggested that the start of the Late Palaeozoic Ice Age was partly caused by the development of the coal swamp biome reducing levels of atmospheric CO_2 (e.g., Berner 2004, Feulner 2017) but this seems unlikely. Even though there were also Serpukhovian coal swamps in Kazakhstan (e.g., Goganova et al. 2002), estimated to have covered ca. 150×10^3 km^2 (based on Litinovitch et al. 1979, Cleal and Thomas 2005) they would have been insufficient to lower atmospheric CO_2 levels to cause major global cooling. More likely, it was the drop in global sea levels at the start of the Late Palaeozoic Ice Age, triggered by factors such as enhanced weathering of newly-developing orogenic areas such as the Central Pangaea Mountains (e.g., Eyles 1993, Veevers 2009, Goddéris et al. 2017), that provided newly-exposed areas of continental shelf on which the swamps could develop; it was the start of the Late Palaeozoic Ice Age that caused the coal swamps to develop, not the other way around.

Acknowledgements

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Appendix

Localities List

The following is a list of all of the localities from which specimens used in this study were collected. The locality numbers relate to Table 1. Where possible, the stratigraphical position of the localities has been determined from various resources, notably Macgregor (1931) and McLean (2018). Digital latitude and longitude given in square bracket where known.

Lower Limestone Formation

1. Shale overlying thin limestone (?Hurlet Limestone), Corrie Burn waterfall, Arran. [55.628008, –5.166685]
2. Hurlet Limestone, Paduff Burn, Kilbirnie, 0.7 km upstream from Largs Road, Ayrshire [55.758322, –4.709303]
3. Black shale below 4 ft Crinoidal Limestone, 0.4 km west of Rosyth Farm, Fifeshire. [56.030221, –3.45287]
4. Shale over white limestone, St Monans, Fifeshire. [56.207047, –2.751551]
5. Calderwood (Top Hosie) Limestone, East Kilbride, Lanarkshire. [55.771613, –4134369]
   Unknown horizon, Auchentibber, 1.5 km south of High Blantyre, Lanarkshire. [55.769956, –4.115449]
7. Braidwood Burn, lower side of avenue bridge near Braidwood House, Lanarkshire. [55.712704, –3.843183]
8. Unknown horizon, Talla Water Tunnel, Whitefield, near Macbie Hill Railway Station, Peebleshire. [55.763668, –3.317296]

Limestone Coal Formation

9. Shale above Main Coal, Wimbledon Pit, Machrihanish, Campbeltown, Mull of Kintyre. [55.424246, –5.716569]
10. Shale interleaved with sandstone, 290 m west of Wimbledon Pit, Machrihanish, Campbeltown, Mull of Kintyre. [55.4241105, –5.710275]
11. Shale below lower Coal, Bed of Burn, Tirfergus Glen, Machrihanish, Campbeltown, Mull of Kintyre. [55.402645, –5.698821]
12. Below Index Limestone, Lugton Water, Ayrshire. [55.676474, –4.618738]
13. Lower ironstone beds above Garibaldi Ironstone, Swinlees Glen, Dalry, Ayrshire. [55.737241, –4.717981]
14. Between the Clayband and Blackband ironstones, Swinlees Glen, Dalry, Ayrshire. [55.737241, –4.717981]
15. Ironstone beds between Top Hosie Limestone and Johnstone Shell Bed, Pitcon Burn, Kilbirnie, 0.2 km downstream from Gowkhouse Burn, Ayrshire. [55.743644, –4.718524]
16. Spoil tip at Netherwellwood Colliery, Muirkirk, Ayrshire. [55.502589, –4.122238]
17. 389 m depth, Thorneycroft No. 1 Borehole, 0.5 km NE of Cumbernauld Railway Station, Dumbartonshire. [55.945708, –3.971283]
18. 44 m below Lochgelly Splint Coal, Balfour Borehole, Markinch, Fifeshire. [56.193803, –3078039]
19. Between Mynheer Coal and Pittencrieff Blackband Ironstone, Wallsend Pit, Elgin Colliery, near Dunfermline, Fifeshire. [56.082818, –3.483920]
20. Unknown level, borehole near Drunaird, northwest of Leven, Fifeshire. [56.218807, –3.033512]
21. Jewel Coal, Northfield Pit, Prestonpans, Haddingtonshire. [55.958086, –2.986628]
22. Unknown horizon, Mineral Railway cutting, near Bankton Pit, Prestonpans, Haddingtonshire. [55.947996, –2.2958144]
23. 4 m below Index Limestone, River Avon, Kingslade Castle, Lanarkshire. [56.014849, –3.592009]
24. 22 m below Index Limestone, Netherton Borehole, southwest of Westcraig railway station, Lanarkshire. [55.869938, –3.756632]
25. 110 m below Index Limestone, Bedlay, near Chryston, Lanarkshire. [55.905603, –4.092777]
26. Possil Ironstone, Keppock Hill, near Glasgow, Lanarkshire. [55.876904, –4.247487]
27. Possil Ironstone, Robroyston Colliery, 2.8 km SE of Bishopbriggs, Lanarkshire. [55.886094, –4.195300]
28. 36 m above Main Coal, Burnlip Borehole, 3 km north of Coatbridge, Lanarkshire. [55.887080, –4.025980]
29. Depth 237 m, No. 3 Killermount Borehole, Garscube, Lanarkshire. [55.905628, –4.305580]
30. Above Red Coal, No. 6 Pit, Grange, Bo'ness, Linlithgowshire. [56.006498, –3.601495]
31. Shale above Ironstone, No. 6 Pit, Grange, Bo'ness, Linlithgowshire. [56.006498, –3.601495]
32. Shale below No. 6 Coal, No. 6 Pit, Grange, Bo'ness, Linlithgowshire. [56.006498, –3.601495]
33. Easter Main Coal, Bo'ness, Linlithgowshire. [56.012383, –3.603402]
34. Brown Ironstone, Bo'ness, Linlithgowshire. [56.012383, –3.603402]
35. Blaes, 20ft above Lower Ironstone, No. 6 Pit, Grange, Bo'ness, Linlithgowshire. [56.006498, –3.601495]
36. Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire. [unknown]
37. Unknown horizon, Cowden, near Dalkeith, Midlothian. [55.892585, –3.040246]
38. Unknown horizon, Burghlee Pit, Loanhead, Midlothian. [55.872393, –3.156059]
39. Above Steam Coal, Woodyett Pit, Herbertshire Colliery, Denny, Stirlingshire. [56.021561, –3.922193]
40. Above Steam Coal, Stripeside Pit, Herbertshire Colliery, Denny, Stirlingshire. [56.021561, –3.922193]
41. Shale above Blackband Ironstone, Woodyett Pit, Denny, Stirlingshire. [56.021561, –3.922193]
42. Knightswood Gas Coal, borehole at University of Glasgow, Stirlingshire. [55.872763, –4.292357]
43. Auchengleich Colliery, Chryston, near Glasgow, Stirlingshire. [55.915142, –4.101964]
44. Knott Coal (Edge Coal Group), No 1 Pit, Polmaise Colliery, Fallin, Stirlingshire. [56.100401, –4.131750]

45. Todholes, 400 yds above bridge on Denny Road, Bannocknurn Stirlingshire. [56.048901, –4.131750 ?]
46. Raploch Quarry, Stirlingshire. [56.125635, –3.954526]

Upper Limestone Formation

47. Above Highfield (Index) Limestone, near Monkredding, Cunningham, Ayrshire. [55.670980, –4.663867]
48. Base of sandstone, Glencyran, north of Cumbernauld Railway Station, Dumbartonshire. [55.944986, –3.969523]
49. Unknown horizon in Midstrathmore Borehole, Thornton, Fifeshire. [56.166085, –3.160587]
50. Shale below sandstone on which Ardross Castle was built, Fifeshire. [56.196250, –2.793674]
51. Orchard Limestone, 188.7 m (103 fathoms, 1 ft) from surface, No. 3 Bore, Lands of Milton, Springburn, Glasgow. [55.885019, –4.182881]
52. Above Lyoncross Cement Limestone, Depth 64 m, No. 3 Bore, Lands of Milton, Springburn, Glasgow. [55.885019, –4.182881]
53. Between the Index (No. 4) and Orchard (no. 5) Limestones, Cuthill Shore, between Musselburgh and Prestonpans, Haddingtonshire. [55.953357, –3.009140]
54. Above Index Limestone, shore between Links Pit (Prestonpans) and Cockenzie Harbour, Haddingtonshire. [55.968400, –2.969035]
55. Above Index Limestone, shore east of Port Seton Harbour, Haddingtonshire. [55.973170, –2.947370]
56. 10 m below Orchard Limestone, Robroyston Colliery, 2.8 km SE of Bishopbriggs, Lanarkshire. [55.886094, –4.195300]
57. Depth 139 m, Croftfoot Borehole, Glenboig, Lanarkshire. [55.893420, –4.059256]
58. Unknown horizon, bore at Muirend Farm, Glenboig, Lanarkshire. [55.916639, –4.032613]
59. Unknown horizon, Haggmuir Borehole, north of Coatbridge, Lanarkshire. [55.895629, –4016009]
60. Shale in sandstone above Index Limestone, Maidenpark Quarry, Kinneil, Linlithgowshire. [56.009512, –3.617104]
61. Shale above Index (No. 4) Limestone, Gore Water, Gorebridge, Midlothian. [55.840875, –3.059064]
62. Beds between Calmy and Castlecary Limestones, Bilston Burn, near Polton, Midlothian. [55.871471, –3.1455210]
63. Bed underlying Castlecary Limestone, left bank of stream, lower side of old stone bridge, Bilston Burn, near Polton, Midlothian. [55.871471, –3.1455210]
64. Unknown horizon, Levenhall shore, west of stream at Ravenshaugh Bridge, Midlothian. [55.949503, –3.013343]
65. South bank of River South Esk, 90 metres downstream from bridge, 0.4 km west of Arniston, Midlothian. [55.821356, –3.085690]
66. Immediately below Orchard Limestone, New Braidbar Quarry, Giffnock, Renfrewshire. [55.057647, –4.283149]
67. Depth 24 m above Calmy Limestone, Rosehill Borehole, Plean, Stirlingshire. [56.057647, –3.833781]
68. Depth 20 m from Lyoncross Cement (between Orchard and Calmy Limestones), Rosehill Borehole, Plean, Stirlingshire. [56.057647, –3.833781]
69. Depth 340 m, Rosehill Borehole, Plean, Stirlingshire. [56.057647, –3.833781]
70. Carnock No. 3 Borehole, 0.4 km south of Carnock House, 3.2 km west of Airth, Stirlingshire. [56.046632, –3.866844]
71. No. 1 Borehole, near top of Bishopbriggs Sandstone, just above Index Limstone,1.2 km NE of Cumbernauld railway station, Stirlingshire. [55.945420, –3.971333]