FOSSIL IMPRINT • vol. 80 • 2024 • no. 1 • pp. 125–134

NATIONAL MUSEUM

ANISOPTERIS SHUTEANA SP. NOV., A FERTILE ADPRESSION FOSSIL FROM THE MISSISSIPPIAN (LOWER CARBONIFEROUS) OF TEILIA QUARRY, NORTH WALES, UK

PETA ANGELA HAYES[1,*], HUGH LANCE PEARSON[2]

[1] Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom; e-mail: p.hayes@nhm.ac.uk.
[2] "Applecraft", Abbey Road, Leiston, IP16 4RE, United Kingdom.
*corresponding author

Hayes, P. A., Pearson, H. L. (2024): *Anisopteris shuteana* sp. nov., a fertile adpression fossil from the Mississippian (lower Carboniferous) of Teilia Quarry, North Wales, UK. – Fossil Imprint, 80(1): 125–134. Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

Abstract: *Anisopteris shuteana* Hayes et H.L.Pearson sp. nov., a rare fertile adpression fossil, is described from the Mississippian of Teilia Quarry, Gwaenysgor, North Wales, UK. The new species is based on material from the Margaret Benson Collection and named in honour of Cedric H. Shute who curated the Palaeobotany Collections at the Natural History Museum, London. The account arises from an unpublished typescript by Benson, who considered the specimen to be a fern fructification. *A. shuteana* is of particular importance because only two fertile fronds of *Anisopteris* have previously been described. Detailed comparisons are drawn between these two species, *Anisopteris fertilis* (J.Walton) Hirmer, 1940 and *Anisopteris lindseaeformis* (Bunbury) Hirmer, 1940 and *A. shuteana*, which is assigned to the Lyginopteridales.

Key words: *Anisopteris*, adpression, fertile, Teilia, Visean, Mississippian, lower Carboniferous, frond, sporangia, Wales, Euramerica

Received: July 31, 2024 | Accepted: October 10, 2024 | Issued: November 18, 2024

Introduction

Professor Margaret Jane Benson FLS (1859–1936), head of the Department of Botany at Royal Holloway College (1893–1922), conducted pioneering research including important work on the early evolution of seed plants (Fraser and Cleal 2007). She focused her palaeobotanical work on Carboniferous plants and published several papers based on her collection of permineralized material (Benson 1904, 1908a, b, c, 1911, 1912, 1918, 1922, 1933, 1935b). In her honour, Scott (1908) established the name *Bensonites* for a Carboniferous megasporangium from Burntisland, Scotland, and Pigg (1983) named a species of the genus Benson had instituted for permineralized sigillarian cones after her (*Mazocarpon bensoniae* Pigg, 1983; spelling amended here in accordance with Art.60.8.(b) of the ICN, Turland et al. 2018). After her retirement, Benson began working on adpression fossils and studied the Carboniferous flora of Teilia Quarry (Benson 1935a, c).

In July 1967, Cedric Shute dealt with the transfer of the large Benson Collection of plant fossil thin sections, plus accompanying catalogues, from Royal Holloway College, University of London, Egham, Surrey, UK, to the British Museum (Natural History) (BM(NH), now the Natural History Museum, London) at South Kensington, with the acquisition recorded in March 1968. However, a collection of Benson's plant fossil material had already been presented to the BM(NH) by her executors following her death in 1936. During our ongoing research on the Benson Collection, our focus has been drawn to Teilia Quarry specimens associated with an unpublished Benson typescript within this collection.

Cleal and Thomas (1995) summarized previous work on the Teilia Quarry flora, all published in the late nineteenth and early twentieth century. The flora includes species of *Lepidodendron*, *Archaeocalamites*, *Rhodeopteridium*, *Rhacopteris*, and several genera now included within the Lyginopteridales, along with material of unconfirmed affinities, described by Kidston (1890) and Walton (1926, 1931). Teilia Quarry is a site of outstanding palaeobotanical significance, especially for foliage assigned to *Rhacopteris* which has been one of the most common plant fossils collected and shows unusually high diversity (Cleal and Thomas 1995). However, this quarry that was formerly worked for making hydraulic cement had been disused for many years by the end of the nineteenth century (Morton 1886). It is largely degraded, with beds obscured by fallen rocks and reduced exposure hampering new collecting (Morton 1886, Warren et al. 1984). Existing museum collections are therefore of great importance as a source of information on this flora which is unique in North Wales.

Text-fig. 1. ***Anisopteris shuteana*** **Hayes et H.L.Pearson sp. nov., holotype, NHMUK V 25790, Benson collection, Teilia Formation, Teilia Quarry, North Wales, held in the collections of the Natural History Museum, London. a: Holotype part, V 25790a. b: Counterpart, V 25790b. Scale bar = 10 mm (a, b).**

Material and methods

The studied material was collected in August 1933 by Margaret Benson at Teilia Quarry, Gwaenysgor, Flintshire, North Wales, UK, [SJ 0793 8137]. Here the interbedded calcareous mudstones and dark grey, tabular-bedded, argillaceous limestones are within the Teilia Formation of the Craven Group (Morton 1886, Waters et al. 2009). The rock weathers to light brown (Morton 1886). Based on the bivalve and cephalopod fauna (P1c ammonoid zone), Warren et al. (1984) assigned the formation to the Brigantian substage of the Visean, Middle Mississippian (lower Carboniferous), making the flora about 330 million years old. During this period, the UK was under an equatorial climate (Juerges et al. 2015) and the allochthonous flora preserved within these marine beds probably grew on emergent land on the edge of the Wales-Brabant High (Kidston 1890, Waters et al. 2009).

The material is preserved as adpressions (a term introduced by Shute and Cleal (1987)), including both part and counterpart (Text-fig. 1). The part of the holotype is in two pieces that have been reattached using adhesive in the past. The plant fossils from this site have not revealed evidence of cuticles (Cleal and Thomas 1995). Specimens have been photographed using cross-polarized light to increase contrast (Crabb 2001), which is a technique Cedric Shute was very keen to develop for palaeobotanical material at the Natural History Museum, London (Shute and Cleal 1987). High resolution imaging was carried out using the FEI Quanta 650 FEG scanning electron microscope at low pressure in secondary electron mode.

Benson's typescript provides an unpublished binomial and its diagnosis for a previously undescribed species of what she regarded as a specimen of *Rhacopteris*. In the Appendix here, quoted paragraphs are taken from Benson's typescript and the literature cited by Benson is incorporated within the main list of references. The only alteration is the replacement of Benson's chosen, unpublished epithet with "*Rhacopteris* sp. A nov.". Except for editing to use lower case for specific epithets and italicization according to Turland et al. (2018), there has been no taxonomic updating applied to the quoted text, so names are maintained according to Benson's views at that time.

The specimens and typescript are held at the Natural History Museum, London (NHMUK).

Systematic palaeobotany

Class Lyginopteridopsida Novák, 1961 emend. by Anderson et al. (2007)
Order Lyginopteridales Corsin, 1960

Genus *Anisopteris* (Ob.-Brink) Hirmer in Hirmer and Guthörl 1940

Type. *Cyclopteris inaequilatera* Göpp., 1859 ≡ *Anisopteris inaequilatera* (Göpp.) Hirmer in Hirmer and Guthörl (1940: 50) designated by Boureau and Doubinger (1975).

Remarks. Oberste-Brink (1914) originally established the name *Anisopteris* as a Section of the genus *Rhacopteris* Schimp., 1869. Oberste-Brink (1914) noted that *Anisopteris* was only known from the "Culm" (Mississippian), whilst the other Section, *Eurhacopteris*, was only known from the Pennsylvanian (although following Turland et al. (2018) the Section name *Eurhacopteris* is not valid as it included the type of the genus *Rhacopteris* and its epithet does not repeat the generic name unaltered). Due to the stratigraphic grouping, Walton (1926) believed that the division was biased and that it should not be adopted. However, Hirmer (1940) emended the diagnosis and elevated the name *Anisopteris* to full generic rank, asserting that the division was not merely stratigraphic, with the Lower Carboniferous species *Rhacopteris transitionis* excluded from *Anisopteris*. It was also reported that fertile fronds are unknown in *Rhacopteris*, while *Anisopteris* includes fertile material (Oberste-Brink 1914, Hirmer 1940). A type species for *Anisopteris* was only designated later when Boureau and Doubinger (1975) selected *Anisopteris inaequilatera* (Göpp.) Hirmer, 1940. *Anisopteris* is not a nomenclatural synonym of *Rhacopteris* Schimp., 1869 as these two generic names are heterotypic (with *Rhacopteris elegans* (Ettingsh.) Schimp., 1869 given as the type species of *Rhacopteris*; Kidston 1890). The taxa are considered morphologically distinct, with *Anisopteris* pinnules defined as strikingly asymmetrical, with no trace of a central vein (Oberste-Brink 1914, Boureau and Doubinger 1975).

***Anisopteris shuteana* Hayes et H.L.Pearson sp. nov.**
Text-figs 1–3

Holotype. V 25790, Palaeobotany Collections, NHMUK.

Plant Fossil Name Registry Number. PFN003401 (for the new species).

Etymology. This species is named in honour of Cedric H. Shute, former Curator of Palaeobotany at the Natural History Museum, London.

Type locality. Teilia Quarry, Gwaenysgor, Flintshire, North Wales, United Kingdom [SJ 0793 8137].

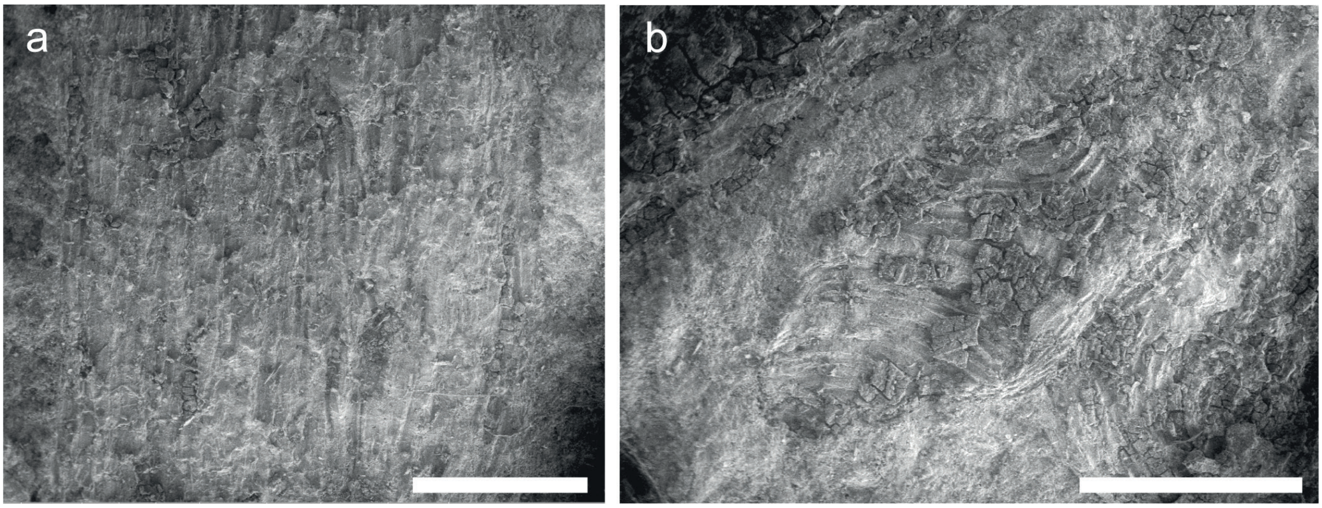
Type horizon. Teilia Formation, Craven Group.

Age. Brigantian, Visean, Middle Mississipian (lower Carboniferous).

Diagnosis. Rachis covered with longitudinal striations spaced approx. 0.1 mm apart. Primary rachis width approx. 2.5 mm, narrowing slightly to 2 mm after the first dichotomy. Angle of divergence of first dichotomy narrow acute; angle of divergence of subsequent repeated dichotomies wide acute to obtuse. Ultimate rachises up to 0.6 mm wide. Clusters of pedicellate sporangia attached terminally on ultimate rachises. Sporangia narrow ovate in outline, each sporangium roughly symmetrical and approx. 2.1 mm in length and 0.8 mm in width.

Description. The specimen is a fertile portion of a plant, with the maximum dimensions of this fragmentary specimen approx. 6 cm in length and 3 cm in width (Text-fig. 1a, b). There is no attachment to a sterile section of frond bearing pinnules. The rachis appears slightly flexuous. The primary rachis is approx. 2.5 mm wide, narrowing slightly to 2 mm after the first dichotomy, which is approx. 2 cm above the base of the fossil, with ultimate rachises of up to 0.6 mm wide. The rachis is covered with longitudinal striations spaced approx. 0.1 mm apart (Text-fig. 2a, 3a). The first dichotomy preserved in this specimen is narrow acute (42°). The rachis then dichotomizes at least two more times at an angle of divergence of 70–110° (mean 94°) (Text-fig. 2b). The irregularity of the branching preserved in this adpression fossil is suggestive of a three-dimensional branching axis rather than a two-dimensional frond. The sporangia are attached to the ultimate rachises in clusters of at least four, but the state of preservation does not allow them to be counted precisely (Text-fig. 2b). The majority of the pedicellate sporangia observed appear pendent (Text-fig. 2c, d). The pedicel appears to be approx. 0.5 mm long and 0.1 mm wide (Text-fig. 2d). The sporangia are narrow ovate in outline, with an average length:width ratio of approx. 2.5:1 (Text-fig. 2b, c, d). Each sporangium appears roughly symmetrical. As a result of the clustering and overlapping of the sporangia precise measurement of each sporangium is difficult. The sporangia appear to range in size from 2.0 to 2.7 mm long (mean 2.1 mm) and 0.7 to 1.0 mm wide (mean

Text-fig. 2. ***Anisopteris shuteana*** **Hayes et H.L.Pearson sp. nov., holotype, V 25790, Benson collection, Teilia Formation, Teilia Quarry, North Wales. a: Detail of longitudinal striations covering rachis, V 25790a. b: Dichotomizing of rachis and clusters of sporangia, V 25790a. c: Detail of sporangium within cluster, V 25790a. d: Detail of sporangia within cluster, V 25790b. Scale bar = 5 mm (b), 1 mm (a, c, d).**



Text-fig. 3. *Anisopteris shuteana* Hayes et H.L.Pearson sp. nov., holotype, V 25790a, Benson collection, Teilia Formation, Teilia Quarry, North Wales. Variable pressure scanning electron microscope secondary electron images, at 70 Pa, 5.00 kV. a: Detail of longitudinal striations covering rachis. b: Detail of fine striations covering surface of sporangium illustrated in Text-fig. 2c. Scale bar = 1 mm (a, b).

0.8 mm) (Text-fig. 2b, c, d). The surfaces of the sporangia are covered with fine striations (Text-fig. 3b).

Additional material. V 25777. Specimens that appear similar to these fertile organs have been found in association with sterile fronds, but organic connection has not been observed (Text-fig. 4a, b).

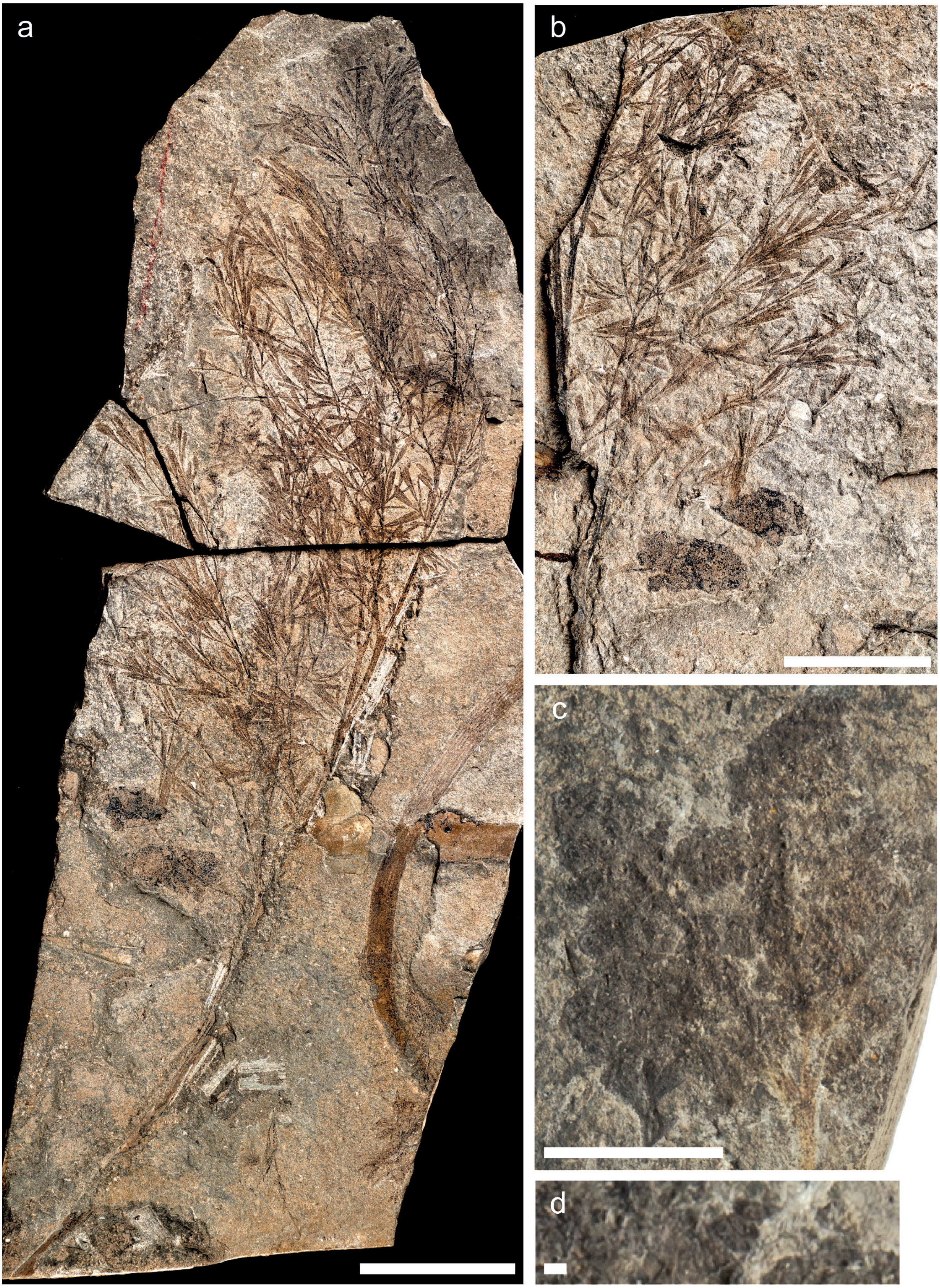
Discussion. The report of Benson's collecting recording the association of many specimens of *Rhacopteris* fronds, now assigned to *Anisopteris*, with this fertile material at Teilia Quarry supports the assignment of this species to *Anisopteris*, but no sterile fronds have been found in organic connection with this fertile specimen. This species is assigned to the genus *Anisopteris* on the basis of observed similarities with *Anisopteris fertilis* (J.Walton) Hirmer, 1940, a single specimen that was also collected from Teilia Quarry and originally described as *Rhacopteris fertilis* Walton, 1926 (Text-fig. 4c, d). Hirmer (1940) included *R. fertilis* within *Anisopteris* due to its similarity to the fertile frond section of *Anisopteris lindseaeformis* (Bunbury) Hirmer, 1940, the only species which includes both sterile and fertile material since Kidston (1923) synonymized *Rhacopteris paniculifera* Stur, 1875 with *Rhacopteris lindseaeformis* (Bunbury) Kidston in Patton (1884) and which Hirmer transferred to *Anisopteris* remarking on the asymmetry of the sterile pinnules. There are therefore two fertile species of *Anisopteris* available for comparison with *A. shuteana*.

Anisopteris shuteana is similar to *A. fertilis* in that both species possess a longitudinally striated, flexuous, dichotomizing rachis, that is approximately 2.5 mm wide. The two species are of a similar size, with the fertile part of the branching system from the first dichotomy to the termination of the ultimate rachises for both species approximately 4 cm in length. The sporangia for both species are borne in clusters and are similar in shape, with the sporangia of *A. fertilis* reported as ovoid, with a length:width ratio of over 2:1, comparable with the narrow ovate outline of the sporangia in *A. shuteana*. However, the sporangia of *A. fertilis* are sessile and asymmetrical, while the sporangia of *A. shuteana* are pedicellate, pendent, and symmetrical in form. Unfortunatelly the illustration of *A. lindseaeformis* (*R. paniculifera* Stur, 1875) is inadequate for detailed comparison. The new specimen cannot be placed in *A. lindseaeformis* because it differs in the nature of branching, with the branches of *A. lindseaeformis* shown to diverge at a narrow acute angle compared to the wide acute to obtuse dichotomizing of *A. shuteana*, and the different shape of the sporangia, as the sporangia of *A. lindseaeformis* are described as globular. These differences in the nature of branching and the attachment and shape of the sporangia means that it is not possible to place this new specimen in either *A. fertilis* or *A. lindseaeformis* and that it represents a new taxon.

There has been a long history of differing interpretations of the botanical affinities for *Anisopteris*. In her unpublished typescript, Benson agreed with Stur (1875) and Walton (1926) that the affinity of this type of frond is most likely with the ferns. Corsin (1960) classified *Anisopteris* under the Archaeopteridales, and Cleal and Thomas (1995) also remarked on the similarity of the fertile frond of *A. fertilis* (*Rhacopteris fertilis*) from Teilia Quarry to *Archaeopteris* fructifications and suggested that these may be representatives of progymnosperms. However, Galtier et al. (1998) analysed permineralized foliage material of *A. lindseaeformis* (*Rhacopteris lindseaeformis*) from the Visean of Scotland that revealed anatomical detail in addition to external morphology. They concluded that the sterile foliage of *A. lindseaeformis* showed *Lyginorachis*-type anatomy and suggested that the fronds represented the remains of arborescent seed ferns. *A. shuteana* is therefore included within the Lyginopteridales, but it has not been possible to assign this new species to a family.

Summary

Mississippian plant fossils are generally rare in Europe, with known floras occurring only in restricted areas (Hübers et al. 2014). Teilia Quarry provides a unique insight into the



Text-fig. 4. **a, b: Possible fertile material found in association with sterile frond but organic connection not observed, NHMUK V 25777, Benson collection, Teilia Formation, Teilia Quarry, North Wales; a – Part, V 25777a, in three pieces temporarily placed together for imaging; b – Counterpart, V 25777b, possible fertile organs to the right of rachis below pinnae. c, d: *Anisopteris fertilis* (J.Walton) Hirmer, 1940, holotype, MANCH LL.48, Walton collection, Teilia Formation, Teilia Quarry, North Wales, held in the**

Visean flora of North Wales, yielding an unusual diversity of *Anisopteris* foliage (Cleal and Thomas 1995). For many years exposure at this site has been much reduced, hampering any new collecting. Museum collections are therefore a crucial source of evidence. Here a new species based on materials from the Benson Collection is documented for the first time. *Anisopteris shuteana* sp. nov., a fertile adpression fossil, is of particular importance because previously only two fertile fronds of *Anisopteris* have been described, each represented by a single specimen. This new species has been assigned to the Lyginopteridales and makes new information available on rare reproductive organs to contribute to furthering the understanding of these plants.

Acknowledgments

We are grateful to Dr Chris Cleal for inviting us to submit this paper in commemoration of Cedric Shute. HP extends his thanks also to Prof. Margaret Collinson for encouraging him to become involved again in active palaeobotanical research on the Benson collection after a lengthy hiatus. We thank Dr Chris Cleal and Dr Milan Libertin for their helpful criticisms, Mr Roger Pinkney for his photographic help and advice, and Mr Nathaniel Hayes for assistance in reassembling a fragmented specimen. PH is very grateful to Jonathan Jackson of the NHM Photo Unit for photography under cross-polarized light, to Innes Clatworthy of the NHM Core Research Laboratories for support with scanning electron microscopy, and the staff of the NHM Library and Archives. We also acknowledge the Manchester Museum and the GB3D Type Fossils project for the images of the holotype of *Anisopteris fertilis* (J.Walton) Hirmer, 1940 and thank them for making images available under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported License, https://creativecommons.org/licenses/by-nc-sa/3.0/.

References

Anderson, J. M., Anderson, H. M., Cleal, C. J. (2007): Brief history of the gymnosperms: classification, biodiversity, phytogeography and ecology. – South African National Biodiversity Institute, Pretoria, x + 280 pp.

Benson, M. J. (1904): *Telangium scotti*, a new species of *Telangium* (*Calymmatotheca*) showing structure. – Annals of Botany, 18: 161–177. https://doi.org/10.1093/oxfordjournals.aob.a088950

Benson, M. J. (1908a): *Miadesmia membranacea*, Bertand; a new Palaeozoic lycopod with a seed-like structure. – Philosophical Transactions of the Royal Society of London,B, 199: 409–425. https://doi.org/10.1098/rstb.1908.0010

Benson, M. J. (1908b): On the contents of the pollen chamber of a specimen of *Lagenostoma ovoides*. – Botanical Gazette, 45: 409–412. https://doi.org/10.1086/329595

Benson, M. J. (1908c): The sporangiophore – a unit of structure in the Pteridophyta. – The New Phytologist, 7: 143–149. https://doi.org/10.1111/j.1469-8137.1908.tb06081.x

Benson, M. J. (1911): New observations on *Botryopteris antiqua*, Kidston. – Annals of Botany, 25: 1045–1057, pls 81–83.

Benson, M. J. (1912): *Cordaites felicis*, sp. nov., a cordaitean leaf from the lower Coal Measures of England. – Annals of Botany, 26: 201–207. https://doi.org/10.1093/oxfordjournals.aob.a089385

Benson, M. J. (1918): *Mazocarpon* or the structural *Sigillariostrobus*. – Annals of Botany, 32: 569–589. https://doi.org/10.1093/oxfordjournals.aob.a089693

Benson, M. J. (1922): *Heterotheca grievii* the microsporange of *Heterangium grievii*. – Botanical Gazette, 74: 121–142. https://doi.org/10.1086/333069

Benson, M. J. (1933): The roots and habit of *Heterangium grievii*. – Annals of Botany, 47: 313–315. https://doi.org/10.1093/oxfordjournals.aob.a090386

Benson, M. J. (1935a): The fructification, *Calathiops bernhardti*, n. sp. – Annals of Botany, 49: 155–160. https://doi.org/10.1093/oxfordjournals.aob.a090493

Benson, M. J. (1935b): The new evidence of isospory in Palaeozoic seed plants. – The New Phytologist, 34: 92–96. https://doi.org/10.1111/j.1469-8137.1935.tb06831.x

Benson, M. J. (1935c): The ovular apparatus of *Sphenopteridium affine* and *bifidum* and of *Diplopteridium* (*Sphenopteridium*) *teilianum* (Walton). – The New Phytologist, 34: 232–244. https://doi.org/10.1111/j.1469-8137.1935.tb06843.x

Boureau, E., Doubinger, J. (1975): Traité de Paléobotanique IV (2) Pteridophylla (première partie). – Masson et Cie, Paris, 768 pp.

Cleal, C. J., Thomas, B. A. (1995): Palaeozoic palaeobotany of Great Britain (Geological Conservation Review Series No. 9). – Joint Nature Conservation Committee, Peterborough, 295 pp.

Corsin, P. (1960): Classification des ptéridophytes et des ptéridospermophytes du Carbonifère. – Bulletin de la Société Géologique de France, Sér. 7, 2(5): 566–572. https://doi.org/10.2113/gssgfbull.S7-II.5.566

Crabb, P. (2001): The use of polarised light in photography of macrofossils. – Palaeontology, 44: 659–664. https://doi.org/10.1111/1475-4983.00196

Fraser, H. E., Cleal, C. J. (2007): The contribution of British women to Carboniferous palaeobotany during the first half of the 20th century. – In: Burek, C. V., Higgs, B. (eds), The role of women in the history of geology. – Geological Society, London, Special Publications, 281: 51–82. https://doi.org/10.1144/SP281.4

Galtier, J., Meyer-Berthaud, B., Brown, R. (1998): The anatomy and seed plant affinities of *Rhacopteris* and *Spathulopteris* foliage from the Dinantian (lower Carbo-

collections of the Manchester Museum. Images courtesy of the Manchester Museum and the GB3D Type Fossils project, CC BY-NC-SA 3.0; c – General view; d – Detail of structures described by Walton (1926) as sporangia. Scale bar = 50 mm (a), 20 mm (b, c), 1 mm (d).

niferous) of Scotland. – Transactions of the Royal Society of Edinburgh, Earth Sciences, 88: 197–208. https://doi.org/10.1017/S0263593300006945

Göppert, H. R. (1859): Über die fossile Flora der silurischen, der devonischen und unteren Kohlenformation oder des sogenannten Übergangsgebirges. – s. n., s. l., 182 pp. [reprint (= Separatdruck) from "Novorum Actorum Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum / Verhandlungen der kaiserlichen Leopoldinisch-Carolinischen deutschen Akademie der Naturforscher", Bd. 27, published in 1860, with pagination [425]–606] https://www.digitale-sammlungen.de/de/view/bsb10226017?page=,1

Hirmer, M. (1940): 2. Rhacopteris Schimper. – In: Hirmer, M., Guthörl, P. (eds), Die Karbon-flora des Saargebietes. Abteilung 3: Echte filicales und verwandte. – Palaeontographica, Supplement 9: 1–60.

Hübers, M., Bomfleur, B., Krings, M., Pott, C., Kerp, H. (2014): A reappraisal of Mississippian (Tournaisian and Visean) adpression floras from central and northwestern Europe. – Zitteliana, A, 54: 39–52.

Juerges, A., Hollis, C. E., Marshall, J., Crowley, S. (2015): The control of basin evolution on patterns of sedimentation and diagenesis: an example from the Mississippian Great Orme, North Wales. – Journal of the Geological Society, 173: 438–456. https://doi.org/10.1144/jgs2014-149

Kidston, R. (1890): On some fossil plants from Teilia Quarry, Gwaenysgor, near Prestatyn, Flintshire. – Transactions of the Royal Society of Edinburgh, 35: 419–428. https://doi.org/10.1017/S0080456800017713

Kidston, R. (1923): Fossil plants of the Carboniferous rocks of Great Britain. – Memoirs of the Geological Survey of Great Britain, 2: 199–274, pl. XLVIII–LXVIII.

Morton, G. H. (1886): The Carboniferous Limestone and Cefn-y-Fedw Sandstone of Flintshire. – Proceedings of the Liverpool Geological Society, 5: 169–197.

Novák, F. A. (1961): Vyšší rostliny. Tracheophyta [Higher plants. Trachaeophyta]. Nakladatelství Československé akademie věd, Praha, 941 pp. (in Czech)

Oberste-Brink, K. (1914): Beiträge zur kenntnis der farne und farnähnlichen gewächse des Culms von Europa. – Jahrbuch der Königlich Preussischen Geologischen Landesanstalt zu Berlin, 35: 63–153.

Patton, A. (1884): Geological observations in the parish of East Kilbride, Lanarkshire. – Transactions of the Geological Society of Glasgow, 7: 309–333. https://doi.org/10.1144/transglas.7.2.309

Pigg, K. B. (1983): The morphology and reproductive biology of the sigillarian cone *Mazocarpon*. – Botanical Gazette, 144: 600–613. https://doi.org/10.1086/337417

Schimper, W. P. (1869): Traité de Paléontologie Végétale, ou la Flore de Monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. Tome Premier. J. B. Baillière et Fils, Paris, Hyppolyte Baillière, Londres, C. Bailly-Baillière, Madrid, 738 pp. https://doi.org/10.5962/bhl.title.60570

Scott, R. (1908): On *Bensonites fusiformis*, sp. nov., a fossil associated with *Stauropteris burntislandica*, P. Bertrand, and on the sporangia of the latter. – Annals of Botany, 22: 683–687, pl. XXXIV. https://doi.org/10.1093/oxfordjournals.aob.a089194

Shute, C. H., Cleal, C. J. (1987): Palaeobotany in museums. – The Geological Curator, 4: 553–559. https://doi.org/10.55468/GC865

Stur, D. (1875): Die Culm-Flora des mährisch-schlesichen Dachschiefers. – Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt, 8(1): 1–106, 17 pls.

Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J., Smith, G. F. (2018): International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017 (Regnum Vegetabile, no. 159). – Koeltz Botanical Books, Glashütten, xxxviii + 254 pp. https://doi.org/10.12705/Code.2018

Walton, J. (1926): Contributions to the knowledge of lower Carboniferous plants. I. On the genus *Rhacopteris*, Schimper. II. On the morphology of *Sphenopteris teiliana*, Kidston, and its bearing on the position of the fructification on the frond of some lower Carboniferous plants. – Philosophical Transactions of the Royal Society of London, B, 215: 201–224. https://doi.org/10.1098/rstb.1927.0004

Walton, J. (1931): On the fossil-flora of the Black Limestones in Teilia Quarry, Gwaenysgor, near Prestatyn, Flintshire, with special reference to *Diplopteridium teilianum* Kidston sp. (gen. nov.) and some other fern-like fronds. – Philosophical Transactions of the Royal Society of London, B, 219: 347–379. https://doi.org/10.1098/rstb.1931.0007

Warren, P. T., Price, D., Nutt, M. J. C., Smith, E. G. (1984): Geology of the country around Rhyl and Denbigh (Memoir for 1:50 000 geological sheets 95 and 107 and parts of sheets 94 and 106. England and Wales). – Memoir of the British Geological Survey, sheets 95 and 107, 217 pp.

Waters, C. N., Waters, R. A., Barclay, W. J., Davies, J. R. (2009): A lithostratigraphical framework for the Carboniferous successions of southern Great Britain (onshore). – British Geological Survey Research Report, RR/09/01. British Geological Survey, Keyworth, 184 pp.

Appendix

Benson's typescript

This Appendix contains a transcript of an unpublished typescript by Margaret Benson that accompanies the specimens held at the Natural History Museum, London.

Explanatory Comments

The literature within the typescript is within square brackets as in Benson's typescript, but she used numbers (instead of name and year) and the numbers related to a longer list of references, most of which were not included in the typescript so this list was not added to the Appendix.

Plates associated with Benson's unpublished typescript were not finished. Some of the features referred to in the typescript are illustrated in the figures here as follows:
Plate figs 1, 2 – see Text-fig. 1a, b.
Fig. 4 – see Text-fig. 4d.
Figs 8, 9 – see Text-fig. 4a, b.

Text of Benson's typescript

Rhacopteris sp. A nov., a new specimen of a Lower Carboniferous fern fructification.

M. Benson

The new specimen was found in August, 1933, during an excavation at the Teilia Quarry, Flintsh., N. Wales. It is the first specimen of a fertile frond of *Rhacopteris* found in British rocks, the only other being recorded by Stur from the Culm, Silesia [Stur 1875]. No photograph of the latter has been published and I have been unable to secure the loan of it from the Vienna Geol. Surv. Museum, but it has been described by its discoverer and figured both by him and in various text-books. Photographs are given of the new specimen on (Plate figs 1 & 2). A drawing from the counterpart is given in Text fig. 1 as the specimen does not admit of the adequate photographing of the sporangia v. T. fig. 1A. The specimen is somewhat immature as the ultimate branch rachids are circinately curved.

The main rachis and arms of the first dichotomy are 2 mm across whereas those of Stur's specimen are 3.5 and 3 respectively. One third of the length on the stone is barren and unbranched, then occur at intervals repeated dichotomies showing a wide angle of divergence and some suggestion of alternation of planes of division. In these latter respects the new species differs from Stur's. In Text fig.1 the sporangia can be seen to be unilocular, rounded in form and about 1mm x .9mm in length and breadth. These symmetric ovate sporangia are borne at the apex of the ultimate ramifications of the rachis.

Stur's description of his own specimen is as follows:-
"The sporangia are small and about 1mm in diameter and are quite round. They do not exhibit such regular order as in the case of *Botrychium* but give quite the same impression as the sporangia of *Botrychium lunaria*. The rachis above the insertion of the first pinnule is 1/3rd the length of the sporangiferous part."

Stur called his specimen *R. paniculifera*, but as it was found attached to the frond now called *R. lindseaeformis* Bunbury sp., Kidston suggested it should be called by that name. Unfortunately the new specimen is not attached to a frond. It was however associated with many specimens of *R. circularis*, Walton sp. one of the commonest plants at the Teilia Quarry so that it is very probably the fructification of that species. There occur, however, fronds of *R. petiolata*, *flabellata* and *machaneki*, also, so that I am compelled to give it a non-committal name and have much pleasure in calling it after XXX who has been most helpful in my work XXX.

Rhacopteris sp. A nov.

Diagnosis:- A fructification of *Rhacopteris* Schimper closely similar but smaller than that of Stur's specimen of *R. paniculifera*. The sporangia in optical transverse section are circular, but are ovate in form. They have smooth walls and measure 1mm in length and .9mm in width. They are inserted terminally on the delicate, ultimate rachids wh. arise by repeated dichotomies at intervals on the main branches of the frond.

Locality:- Teilia Quarry, Flintsh., N. Wales.

Horizon:- Black Limestone of the Calc. Sandst. Series, Lower Carboniferous.

The description given has been the more detailed as *Rhacopteris* has been found difficult to distinguish from Pteridosperms. On securing this new specimen I compared it with a specimen which had been described as a fructification of *Rhacopteris* under the name of *R. fertilis* by Walton [1926]. This specimen was so admirably figured that I was able at once to distinguish it as a fertile pinna of a Pteridosperm. The sporangia were pyriform, obliquely striated and sessile on the length of the rachis. (Fig. 4). They thus exactly correspond with those of *Heterotheca grievii* which I have described from structural material as the pollen sac of *Heterangium grievii* except that they are slightly smaller. They measure about 2mm in length and .75mm in width. With Prof. Walton's permission I now transfer this specimen to the form-genus *Heterotheca* as *H. fertilis* (v. Text fig. 3).

This is not the occasion for a full description of this specimen as I hope later to give a comparative account of the pollen sacs of Pteridosperms as far as our present knowledge permits but as a further confirmation of the identity of *H. fertilis* it may be useful to refer to a discovery made in the field at the time *R*. sp. A nov. was secured.

A magnificent specimen, in two counterparts, of a frond of *Adiantites machaneki* was found to be closely associated with 2 black fan-shaped masses (Figs. 8 & 9) directed towards the main fork of the frond. They were overarched by delicate rachids bearing pinnules of the frond. These masses on examination have proved to resemble very closely the masses attached to the flexuous rachis of *H. fertilis*. Actually the whole surface in both cases is one mass of the striae of *Heterotheca* type of sporange and the white arrow (Fig. 3) shows a typical *Heterotheca* which may be compared with one of the sections of *H. grievii* in Fig. 7.

This at once suggested the mode of insertion of the *H. fertilis* specimen to a Pteridosperm frond (v. Text fig. 4) and it was found that the flexuous rachis with attachment area (T. fig. 3B) was of a length suited to connect up the masses in the *Ad. machaneki* specimen to the main fork of the frond.

Supplementary evidence is available in the exactly similar parallel lines shown on the rachids of the large frond to those on the *H. fertilis* rachid. Moreover it is worthy of note that some pinnules of another common species of *Adiantites*, e.g. *A. antiqua* are to be seen adhering to the specimen of *H. fertilis*, just as those of *Ad. machaneki* are found abutting on the masses associated with the large frond of the latter species. Thus it may well be that *H. fertilis* is the detached male pinna of an *Ad. antiqua* frond, and the large Pteridospermic frond, one foot four inches in height was a primitive stamen. If so, it was organized exactly on the same plan as the ovuliferous fronds of several other Lower Carboniferous Pteridosperms already known to science, such as *Diplopteridium teilianum* and *Sphenopteridium affine* and *bifidum*.

To return in conclusion to *Rhacopteris*, if we consider the new evidence as to sporangia, and habit as shown in Kilpatrick's specimen of stem bearing leaves figured by Walton [1926] we may fairly safely accept Stur's view of the affinity of the genus with the Ophioglosseae. In my opinion the little meadow plant, *Botrychium lunaria*, is the vascular plant of the present age which has retained its character less changed than any other represented in the Lower Carboniferous Rocks.

Summary.
This paper records the discovery of a new species of the fructification of *Rhacopteris*, *R*. sp. A nov. in the limestone of the Calc. Sandst. Series, of Teilia Quarry, N. Wales. It is compared with the specimen recorded by Stur from the Culm of Silesia, *R. paniculifera*.

R. sp. A nov. is found to differ radically from a specimen hitherto included in the genus. This in turn, being identified with *Heterotheca* has enabled the author to demonstrate how the pollen sacs of *Adiantites* were borne on the male frond.

Acknowledgements.
I am glad to acknowledge my indebtedness to F. Morton, Esq. J.P., the owner of the Teilia Quarry, for permission to carry out the excavation which yielded the various specimens described in this paper. Also to Prof. J. Walton for kindly presenting photographs for the purposes of this work.