Botany Letters

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tabg21

Insights into palaeobotany

Christine Strullu-Derrien, Thomas Servais & Paul Kenrick

To cite this article: Christine Strullu-Derrien, Thomas Servais & Paul Kenrick (2023) Insights into palaeobotany, Botany Letters, 170:2, 157-164, DOI: 10.1080/23818107.2023.2200293

To link to this article: https://doi.org/10.1080/23818107.2023.2200293

Published online: 11 Apr 2023.

Submit your article to this journal

Article views: 176

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=tabg21

BOTANY LETTERS
2023, VOL. 170, NO. 2, 157–164
https://doi.org/10.1080/23818107.2023.2200293

Taylor & Francis
Taylor & Francis Group

Check for updates

Insights into palaeobotany

Christine Strullu-Derrien [a,b], Thomas Servais [c] and Paul Kenrick [b]

[a]Institut Systématique Évolution Biodiversité, Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, Paris, France; [b]Science Group, The Natural History Museum, London, UK; [c]Unité Evo-Eco-Paléo – UMR 8198 CNRS/Université de Lille, Sciences et Technologies, Villeneuve d'Ascq, France

ARTICLE HISTORY Received 30 March 2023; Accepted 30 March 2023

Palaeobotany is the science devoted to the study of fossil plants and their evolution. Prior to the 17th century, fossils were collected as curiosities and seen as freaks of nature (*lusus naturae*), but during the 18th century natural historians gradually began to understand them as the remains of formerly living organisms (Andrews 1980). The foundation of the scientific discipline was established in the early 19th century by the Frenchman Adolphe Brongniart (1801–1876), the Czech Kaspar Maria von Sternberg (1761–1837), and the German Ernst Friedrich von Schlotheim (1764–1832), who are considered to be the "fathers" of modern Palaeobotany. They were among the first to apply the binomial system to fossil plants and to write systematic treatise with detailed descriptions and illustrations (Andrews 1980; Torrens 2005). The invention of thin sections and their application to permineralized fossils in 1831 was a major early technical breakthrough (Andrews 1980), enabling microscopy and the description of anatomical features, which greatly improved our knowledge of the relationships and biology of extinct plants. Advances like these led to our understanding of the plants that gave rise to the economically important coals of the Carboniferous Period. It was also soon realised that the geographic distributions of fossil plants conveyed information about Earth history. Fossil plants were central to the formulation of the concept of Gondwana (Suess 1885) and to the recognition of climate change through geological time (Heer 1861).

Palynology, on the other hand, is the science devoted to palynomorphs, a general term for entities found in palynological preparations, including pollen and spores, but also cysts or other organisms or parts of organisms. Pollen grains have been described since the 17th century (e.g. Grew 1682). Palaeopalynology was established during the 19th century, with works such as that of Reinsch (1884) who published micrographs of fossil pollen and spores from Russian coal measure. During the 20th century, palaeopalynology became extremely useful for biostratigraphy (i.e. placing rock units in stratigraphic order based on the fossils they contain), not only for the coal industry, but also for petroleum exploration (e.g. Potonie 1934; Schopf 1957).

During the first half of the 20th century the fossil record continued to inform on plant evolution through the discovery of key extinct groups that bridged major living clades, notably the pteridosperms (Oliver and Scott 1904), the early land plants of the Rhynie chert (Kidston and Lang 1921), and the progymnosperms (Beck 1960). One landmark synthesis was the ambitious *Traité de Paléobotanique*, which was edited by Édouard Boureau (1913–1999) and published in four volumes (Boureau 1964–1975). Other innovations included the further development of pollen analysis as a tool for the study of vegetation change during the Quaternary Period (Faegri and Iversen 1950).

Today, palaeobotany and palaeopalynology continue to play important roles in developing our understanding of the evolution of plants and floras, climate change, and biostratigraphy. They are developing as interdisciplinary fields. Research areas such as geochemistry, molecular developmental biology, microbiology, biomechanics, and phylogenetics are transforming our approaches to, and perceptions of, the analysis of fossil plants and ancient ecosystems (Taylor et al. 2009). Likewise, advances in imaging methods including electron and confocal microscopy and more recently high-resolution X-ray computed tomography are opening new ways of looking at plant fossils. Issue 169 (4) and the first part of issue 170 (2) present a selection of articles showing the dynamism of Palaeobotany today. These contributions are summarized below.

The early records of land plant colonization

Evidence from the calibrated plant tree of life and from fossil spores indicates that the earliest plants (embryophytes) evolved on land during the early

CONTACT Christine Strullu-Derrien c.strullu-derrien@nhm.ac.uk Institut de Systématique Évolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, UA, CP39, 57 rue Cuvier, Paris 75 005, France

© 2023 Société botanique de France

Published online 11 Apr 2023

Paleozoic, probably sometime between ~500 and 480 million years ago (Morris et al. 2018; Puttick et al. 2018; Strother and Foster 2021). The nature of these first land plants is an enduring mystery as they have never been seen in their entirety. The oldest land plant fossils date back to the Silurian. However, there is now abundant evidence from the palynological record that land plants were already widespread beforehand. The earliest evidence comes from dispersed cryptospores, in which the most common configurations are permanent tetrads, dyads or hilate monads. The oldest of these assemblages are from the Middle Ordovician (Rubinstein et al. 2010). These cryptospores dominated assemblages for 60 million years (Edwards et al. 2022). Later, miospores (i.e. spores with trilete marks that are dispersed as single grains) provide evidence for rhyniophytoid land plants as they have been recovered from the sporangia of *Cooksonia pertoni* Lang in the late Silurian (Edwards and Kenrick 2015), although the first record of dispersed spores of this type comes from the Late Ordovician (Steemans et al. 2009). The two genera *Virgatasporites* and *Attritasporites*, described in the 1960′s from the Early Ordovician of Algeria, are morphologically close to miospores and therefore pose a dilemma, because these microfossils are recorded before the first appearance of the oldest land plant-derived spores. Several authors considered the two genera to be spore-like microfossils, whereas other authors classified them as acritarchs (i.e. organic-walled microfossils of unknown biological affinity). Navidi-Izad et al. (2022) revised the taxonomy, biostratigraphy and palaeobiogeography of the two genera. They concluded that they should be temporarily classified as *incertae sedis* (i.e. as acritarchs) until their true biological affinity is better understood.

Because of the nature of the early rock record, it is not until the Devonian that fossil evidence of land plants becomes truly abundant (Kenrick et al. 2012). During this period, the fossils document the initial diversification of many of the major groups of plants and the evolution of their fundamental organs and tissue systems, including roots (Kenrick and Strullu-Derrien 2014), leaves (Boyce and Knoll 2002), seeds (Prestianni et al. 2013; Meade et al. 2021), and wood (Strullu-Derrien 2010; Hoffman and Tomescu 2013; Strullu-Derrien et al. 2014; Pfeiler et al. 2021). French Lower Devonian floras are rare (Bureau 1913; Ducassou et al. 2009; Strullu-Derrien et al. 2010, 2014), especially compared to certain other Western European countries. Capel et al. (2022) reassessed a Lower Devonian assemblage collected in the 1930s in the Rebreuve quarry (Pas-de-Calais, northern France). The palaeoflora consists of 10 taxa, and the assemblage is typical of Emsian floras from Laurussia. It bears striking resemblance with coeval Belgian assemblages.

The Carboniferous biomes

The Carboniferous Period contains two major subdivisions: the Mississippian (358.9 to 323.2 Ma) and the Pennsylvanian (323.2 to 298.9 Ma). Compared to the coal-swamps that extended over large areas of palaeotropical Euramerica during the late Carboniferous and early Permian, the earliest evolution of the coal swamp biome in the latest Mississippian is less well understood. Palaeobotanical remains of that age are well preserved in the Pays-de-Loire region of north-western France and were documented in detail notably by Bureau (1913) and more recently by Strullu-Derrien et al. (2021). Most of this evidence was derived from coal mines that are no longer accessible. An interesting new macroflora has been recently discovered *in situ* at the “Coteaux du Pont Barré”, in the Southern Armorican Massif, France. This macroflora studied by Strullu-Derrien et al. (2023) differs in composition from those reported from the coal mines, especially in the total absence of lycopsids and *Calymmotheca* pteridosperms, and instead having abundant medullosan foliage (*Neuralethopteris*). These new data demonstrate floristic variation in the coal swamps at a landscape level.

Arborescent lycopods were among the most abundant plants of the Paleozoic coal swamps of the late Mississippian – early Permian. Thomas and Cleal (2022) re-examined the known species of arborescent lycopod leafy shoots from the Pennsylvanian and provide a key to identify them. Sometimes leafy shoots can be directly related to known species of stems that are defined on the surface features of leaf cushions as in *Lepidodendron, Lepidophloios* and *Ulodendron*, or directly on the stem surface as in *Bothrodendron*. Insight was also provided on the determinate growth pattern of these plants.

The isoetalean flora

The Mississippian is characterized by global cooling and the development of steeper latitudinal variation in the climate of the Earth. Whereas the tropical floras of the palaeoequatorial regions are relatively well known, higher latitude floras are still poorly understood. Argentina at that time occupied a latitude of about 60°S, which proves to be interesting in the context of its Mississippian vegetation. Prestianni et al. (2022) described a new isoetalean lycopsid, *Porongodendron minitensis*, from the Agua de Lucho Formation. This plant is shown to be of low stature and with features that are interpreted as representing specific adaptations to the harsher tundra conditions prevailing in these southern latitudes during the Mississippian.

Isoetes (Isoetaceae, Lycophytes) is the closest living relative of the isoetalean lycopsids that originated during the Paleozoic (Larsén et al. 2022). Although it is doubtful that any Paleozoic or Mesozoic fossil can confidently be attributed to the crown group (Wikström et al. 2023), *Isoetes beestonii* from the earliest Triassic shales of the Sydney and Bowen Basins of Australia is the most ancient species attributed to the genus (Retallack 1997). Palynology recently offered Nowak et al. (2023) the opportunity to reinvestigate four species of lycophytes from the early Middle Triassic of the Kühwiesenkopf/Monte Prà della Vacca section in the Dolomites (northern Italy). *In situ* spores of the lycophytes were studied with a focus on their variability. Microspores and a single megaspore from *Lycopia dezanchei* (order and family indet.) and possible poorly preserved microspores from *L. bechstaedtii* were described for the first time. The microspores from a paratype of *Isoetites brandneri* proved to be highly variable and unusual. Both micro- and megaspores from a specimen previously assigned to *I. brandneri* indicate that it is a biologically distinct species.

Plant traits and interactions

Well-preserved material from the Carboniferous offers the possibility to date the appearance of significant functional traits, for example the occurrence of tyloses in wood (De Micco et al. 2016). These are protoplasmic swellings formed by a parenchyma cell projecting into the lumen of an adjacent conducting cell; they extend through a pit, and some eventually occlude the entire lumen of the conducting cell. Tyloses develop as part of a heartwood formation process or in response to embolism or pathogen infection. Decombeix et al. (2022) reported the oldest evidence of tyloses from the wood of ca 350 Ma progymnosperm *Dameria hueberi* from Australia. They provided details of different developmental stages in the formation of the tyloses, but the trigger for their development (fungal or not) was not resolved. Combined with previous reports the authors suggested that tyloses may have played important roles in the early evolution of arborescence.

Upper Triassic deposits bearing fossil plants are of unequal distribution on Earth. The Leigh Creek Coal Measures in South Australia yield exquisitely preserved plant fossils of a mid- to high-latitude Gondwanan flora. From this site, Unverfärth et al. (2022) provided a detailed cuticular analysis of the ginkgoalean leaf *Sphenobaiera insecta*. They also reported evidence of a particular type of herbivory damage along the leaf margin in the form of small semi-circular patches, each lined by a crescent-shaped, darkened reaction rim. The consistency of these features in size and position suggests that they represent arthropod feeding damage, which appears to have been primarily within the leaf mesophyll. These features are reminiscent of simple forms of marginal leaf mining evident in various other Permian and Triassic plant groups.

By the mid Cretaceous, forests diversified as angiosperms rose to ecological prominence. Insect damage on fossil plants provides direct evidence of the past ecological history between the two groups. Santos et al. (2022a) recorded plant – insect interactions from a lower Cenomanian palaeoforest in western France, the Puy-Puy Quarry of the Nouvelle-Aquitaine Region. The authors identified functional feeding groups and insect damage types preserved on the foliage and demonstrated preferential herbivory of angiosperms amid a forest composed of ferns, gymnosperms, and angiosperms. The most diverse interactions were mining and galling, indicating a mosaic of humid and xeric habitats for the Puy-Puy palaeoforest,

New groups of plants developed through time

During the Permian (298.9 to 251.9), Euramerica was characterized by a progressive trend towards drier climates (Hilton and Cleal 2007; Montanez et al. 2007). By the end of the Permian, evidence from the Val Gardena flora in the southern Alps and the Zechstein flora (England and Germany) shows that European plant assemblages were dominated by conifers with adaptations to an arid climate (Grauvogel-Stamm and Ash 2005). Many late Permian conifer remains are difficult to identify based on their morphology because leaf compressions of different taxa can look very similar. Kerp et al. (2022) studied conifers from Gera-Trebnitz, east Thuringia, Germany, and found that the two genera, *Ortiseia* and *Majonica*, so far only known from the Southern Alps, were well represented in the Zechstein Basin and that they had a much wider distribution than originally thought, not being restricted to coastal regions of the Palaeotethys. Xeromorphic features observed in the cuticles, such as strongly sunken stomata, stomatal pores covered by overarching papillae, and a high density of hairs, demonstrated the aridity of the climate.

For many decades, liverworts have been widely viewed as the earliest diverging land plant group (e.g. Kenrick and Crane 1997a, b). This hypothesis has been overturned by recent molecular analyses that resolve tracheophytes (vascular plants) and bryophytes (liverworts, hornworts and mosses) as sister clades (Morris et al. 2018; Puttick et al. 2018; Harris et al. 2020). The simple morphology of liverworts more probably reflects losses of traits rather than their primitive absence. The fossil record of bryophytes is meagre compared with the high number of living species. For example, it is notable that there are only 40 records from Jurassic deposits around the world (Tomescu et al. 2018). Santos et al. (2022b) described a new species of liverwort from the Upper Jurassic Lastres Formation in Asturias (NW Spain, Iberian Peninsula). This new species, found in life position, represents the oldest evidence of a bryophyte from the Mesozoic of the Iberian Peninsula. Palynological studies showed that some areas of the Lastres Formation preserved shallow freshwater pools in channel abandonment areas that provided habitats for the liverworts during the semiarid climatic conditions that prevailed at the time.

Bennettitales is an extinct group of seed plants with reproductive structures that are similar in some respects to both Gnetales and angiosperms, but systematic relationships among the three clades remain controversial (Rothwell et al. 2009). They were clearly present in Gondwana by the Middle Triassic and became one of the chief plant groups of lowland ecosystems across Gondwana from the Early Jurassic to mid-Cretaceous (Bomfleur et al. 2018). Upper Triassic plant macro-remains are extremely rare in an equatorial belt stretching across the North of Gondwana, from northern South America to Arabia. Based on impressions from ferruginous crusts, El Atfy et al. (2022) provided the first record of plant macro-remains belonging to the bennettitalean taxon *Zamites* aff. *persicus* from the Late Triassic Minjur Formation of Saudi-Arabia. This new finding at least tentatively supports palynological data that indicated similarities between the Late Triassic flora of the southern and northern parts of the Tethys.

Traditional and advanced imaging techniques for palaeobotany and palynology

Traditionally fossil plants and palynomorphs have been studied using standard light microscopy. Thanks to technological advances in the 1970s, electron microscopy became a new tool for these studies. T.N. Taylor (1938–2016) pioneered the use of scanning and transmission electron microscopy for the study of fossil spores and pollen (Taylor 1973). El Atfy et al. (2023) studied palynomorphs from the Paleocene (66–56 Ma) Konservat-Lagerstätte of Menat (Puy-de-Dôme, France). Using light microscopy and scanning electron microscopy, selected palynomorphs were analysed with the single grain technique. This preliminary study demonstrated the occurrence of diverse lineages comprising algae, plant spores and pollen; angiosperms were the most diverse group.

3D scanners are non-contact metrology (science of measurement) systems which utilize laser or structured light-based scanning technology. The first scanning technology appeared in the late 1960s. Due to their ability to measure complex geometrical features with precision and reliability, these scanners are now widely used in industry and also in research to reconstruct objects of large size. Using standard light microscopy and a 3D handheld laser scanner, Steart et al. (2023) document the overall habit and affinity of the most complete Mesozoic Era tree to be excavated in the UK. The fossil was found *in situ* in a palaeosol of the Upper Jurassic Purbeck Group of southern England (ca. 152–145 million years). Anatomical details reveal that the wood belongs to the fossil-genus *Agathoxylon*. This conifer tree was of modest size, not greatly exceeding 12 m in height. Its habit differed significantly from most modern arborescent conifers, and from known growth forms in the Cheirolepidiaceae, an important extinct group of Mesozoic conifers Figure 1.

Figure 1. Reconstruction of the Eocene flora from Anjou by V. O. Leshyk (with courtesy).

More recently, non-invasive X-ray imaging techniques have proved to be extremely useful tools to document fossil plants and palynomorphs in three dimensions. Among these techniques, X-ray computed tomography (CT) was originally developed in the 1980s as a medical diagnostic tool. Since then, the method has been extended to additional industrial and scientific applications. Because X-ray dose is not an issue for fossils, high-resolution X-ray computed tomography (HRXCT) can take advantage of a variety of optimizations such as higher energy x-rays, smaller detectors, and longer exposure times than is practical in conventional medical CT devices (DeVore et al. 2006). Selected fruits and seeds preserved as moulds and casts in sediments from the Eocene Anjou flora of Maine-et-Loire (Figure 1) have been re-examined with the aid of X-ray computed tomography by Strullu-Derrien et al. (2022). Virtual casts and surface renderings from micro-CT scanning data revealed external and internal morphological characters that were not visible using standard reflected light microscopy. Application of this methodology led to a revision of the fruit formerly treated as *Juglandicarya* (Juglandaceae) showing that its probable affinity is within Sapindaceae.

Perspectives

The collection of papers presented in these volumes provides an insight into some of the varied contemporary questions, methods, and approaches in palaeobotany. For half a billion years, the evolution of plants has shaped the development of life on Earth and also the geochemistry of land, ocean, and atmosphere. New plants continue to be discovered and new technologies allow us to study them in unprecedented ways increasing our knowledge of their evolutionary history. Plants and climate are intimately linked; investigating these links is also a booming area in Palaeobotany. Important steps still need to be taken, for example deciphering the origins of the angiosperms and increasing our knowledge on the interactions between plants and their fungal parasites, pathogens and symbionts (Krings et al. 2007; Strullu-Derrien et al. 2014).

Several key areas would benefit from further cross-disciplinary developments. First, the comparative investigation of modern relatives is informative and can be key to interpreting early fossils and the evolution of fundamental tissues and organ systems in plants [e.g. identification of transfer cells (Edwards et al. 2022), early evolution of roots (Hetherington et al. 2021)]. Second, establishing the sequence in which events occurred during plant evolution is important, hence the fossil record is crucial to improve time-tree calibrations (Morris et al. 2018), especially when the application of different molecular clock models results in greatly different tree calibrations (Coiro et al. 2019; Wikström et al. 2023). Fossils also provide insights into the diversity of depauperate modern groups like gymnosperms (Hilton and Bateman 2006; Friis et al. 2007, 2009; Dilcher et al. 2021) and are likely eventually to shed light on the origins of angiosperms (Herendeen et al. 2017; Shi et al. 2021). Third, improving our knowledge of the extinct plant groups allied to modern bryophytes, lycopods, and ferns will help inform our developing understanding of the how the plant genome works (Donoghue et al. 2021; Harris et al. 2020; Bowman 2022).

With this initiative, we would like to invite palaeobotanist colleagues to continue publishing their results in Botany Letters and to encourage botanists to engage in collaboration with palaeobotanists.

Acknowledgments

CS-D and guest editors TS and PK thank the editors-in chief of Botany Letters for their support in developing a collection devoted to Paleobotany. A total of 11 articles were published in issue 169 (4) and 4 articles are published in this issue 170 (2). We thank all our colleagues for their contributions and all of the reviewers. CS-D acknowledges Victor Leshyk for his permission to use the reconstruction of the Eocene landscape.

The co-editors apologize to Prof. Hans Kerp for the mistake concerning the cover illustration of the issue 169 (4) that was taken from Kerp et al. and not from Bomfleur et al.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Christine Strullu-Derrien http://orcid.org/0000-0003-1131-9546
Thomas Servais http://orcid.org/0000-0002-4089-7874
Paul Kenrick http://orcid.org/0000-0002-3626-5460

References

Andrews, HN. 1980. The fossil hunters: in search of ancient plants. Ithaca and London: Cornell University Press.

Beck, CB. 1960. Connection between *Archaeopteris* and *Callixylon*. Science. 131(3412):1524–1525. doi:10.1126/science.131.3412.1524.

Bomfleur, B, P Blomenkemper, H Kerp, S McLoughlin. 2018. Polar regions of the Mesozoic–Paleogene greenhouse world as refugia for relict plant groups. In M Krings, C Harper, N Cúneo, and G Rothwell, editors. Transformative Palaeobotany. Amsterdam: Academic Press; p. 593–611. doi:10.1016/B978-0-12-813012-4.00024-3.

Boureau, É. 1964-1975. Traité de paléobotanique. Vols. 1-4. Paris: Masson et Cie.

Bowman, JL. 2022. The origin of a land flora. Nature Plants. 8(12):1352–1369. doi:10.1038/s41477-022-01283-y.

Boyce, CK, AH Knoll. 2002. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. Paleobiology. 28(1):70–100. doi:10.1666/0094-8373(2002)028<0070:EODPAT>2.0.CO;2.

Bureau, É. 1913. Bassin Houiller de la Basse Loire. Fascicule II. Description des Flores Fossiles. Paris: Imprimerie Nationale (Études des Gîtes Minéraux de la France) – 1914. Atlas published 1913, Text published 1914.

Capel, E, C Prestianni, B Cascales-Miñana. 2022. Revisiting the Rebreuve plant assemblage from the Lower Devonian of Artois, northern France. Bot Lett. 169(4):540–556. doi:10.1080/23818107.2022.2101516.

Coiro, M, JA Doyle, J Hilton. 2019. How deep is the conflict between molecular and fossil evidence on the age of angiosperms? New Phytol. 223(1):83–99. doi:10.1111/nph.15708.

Decombeix, A-L, CJ Harper, J Galtier, B Meyer-Berthaud, M Krings. 2022. Tyloses in fossil plants: new data from a Mississippian tree, with a review of previous records. Bot Lett. 169(4):510–526. doi:10.1080/23818107.2022.2099461.

De Micco, V, A Balzano, EA Wheeler, P Baas. 2016. Tyloses and gums: a review of structure, function and occurrence of vessel occlusions. Iawa J. 37(2):186–205. doi:10.1163/22941932-20160130.

DeVore, ML, P Kenrick, KB Pigg, RA Ketcham. 2006. Utility of high resolution X-ray computed tomography (HRXCT) for paleobotanical studies: an example using London Clay fruits and seeds. Amer J Bot. 93 (12):1848–1851. doi:10.3732/ajb.93.12.1848.

Dilcher, D, J Hilton, HW Pfefferkorn, S Wang, Y Zhang, J Bek, J Pšenička, LJ Seyfullah, D Dilcher. 2021. Ancient noeggerathialean reveals the seed plant sister group diversified alongside the primary seed plant radiation. Proc Natl Acad Sci U S A. 118(11):e2013442118. doi:10.1073/pnas.2013442118.

Donoghue, PCJ, CJ Harrison, J Paps, H Schneider. 2021. The evolutionary emergence of land plants. Curr Biol. 31 (19):R1281–1298. doi:10.1016/j.cub.2021.07.038.

Ducassou, C, C Strullu-Derrien, M Ballevre, MP Dabard, P Gerrienne, H Lardeux, C Robin. 2009. Age and depositional environment of the Sainte-Anne Sandstone Formation (Armorican Massif, France): the oldest (Emsian/Eifelian) evidence for mountain erosion in the Variscan belt. Bull Soc Geol Fr. 180(6):529–544. doi:10.2113/gssgfbull.180.6.529.

Edwards, D, P Kenrick. 2015. The early evolution of land plants, from fossils to genomics: a commentary on Lang (1937) 'On the plant-remains from the Downtonian of England and Wales'. Philos Trans R Soc Lond B Biol Sci. 370(1666):20140343. doi:10.1098/rstb.2014.0343.

Edwards, D, JL Morris, L Axe, JG Duckett, S Pressel, P Kenrick. 2022. Piecing together the eophytes – a new group of ancient plants containing cryptospores. New Phytol. 233(3):1440–1455. doi:10.1111/nph.17703.

Edwards, D, JL Morris, L Axe, WA Taylor, JG Duckett, P Kenrick, S Pressel. 2022. Earliest record of transfer cells in Lower Devonian plants. New Phytol. 233 (3):1456–1465. doi:10.1111/nph.17704.

El Atfy, H, SS Aba Alkhayl, D Uhl. 2022. *Zamites* (Bennettitales) from the Minjur Formation (Norian) of Saudi Arabia – a unique record from the Late Triassic palaeotropics of Gondwana. Bot Lett. 169(4):588–597. doi:10.1080/23818107.2022.2088614.

El Atfy, H, KN Paudayal, D Uhl. 2023. A combined LM and SEM study of selected palynomorphs from the palaeoflora of the Paleocene Konservat-Lagerstätte Menat (Puy-de-Dôme, France), Bot. Lett. 170(2):208–228. doi:10.1080/23818107.2022.2113559.

Faegri, K, J Iversen. 1950. Textbook of modern pollen analysis. Copenhagen: Einar Munksgaard.

Friis, EM, PR Crane, KR Pedersen, S Bengtson, PCJ Donoghue, GW Grimm, M Stampanoni. 2007. Phase-contrast x-ray microtomography links Cretaceous seeds with Gnetales and Bennettitales. Nature. 450 (7169):549–552. doi:10.1038/nature06278.

Friis, EM, KR Pedersen, PR Crane. 2009. Early Cretaceous mesofossils from Portugal and eastern North America related to the Bennettitales-Erdtmanithecales-Gnetales group. Am J Bot. 96(1):252–283. doi:10.3732/ajb.0800113.

Grauvogel-Stamm, L, SR Ash. 2005. Recovery of the Triassic land flora from the end-Permian life crisis. C R Palevol. 4 (6–7):593–608. doi:10.1016/j.crpv.2005.07.002.

Grew, N. 1682. The Anatomy of plants, with an idea of a philosophical history of plants, and several other lectures, read before the Royal Society. London: W. Rawlins.

Harris, BJ, JW Clark, D Schrempf, GJ Szöllősi, PCJ Donoghue, AM Hetherington, TA Williams. 2020. Divergent evolutionary trajectories of bryophytes and tracheophytes from a complex common ancestor of land plants. Nat Ecol Evol. 6(11):1634–1643. doi:10.1038/s41559-022-01885-x.

Harris, BJ, CJ Harrison, AM Hetherington, TA Williams. 2020. Phylogenomic evidence for the monophyly of bryophytes and the reductive evolution of stomata. Curr Biol. 30(11):2001–2012.e. doi:10.1016/j.cub.2020.03.048.

Heer, O. 1861. Recherches sur le Climat et la Végétation du Pays Tertiaire. Paris: Genève.

Herendeen, PS, EM Friis, KR Pedersen, PR Crane. 2017. Palaeobotanical redux: revisiting the age of the angiosperms. Nature Plants. 3(3):17015. doi:10.1038/nplants.2017.15.

Hetherington, AJ, SL Bridson, A Lee Jones, H Hass, H Kerp, L Dolan. 2021. An evidence-based 3D reconstruction of *Asteroxylon mackiei*, the most complex plant preserved from the Rhynie chert. eLife. 10:e69447. doi:10.7554/eLife.69447.

Hilton, J, RM Bateman. 2006. Pteridosperms are the backbone of seed-plant phylogeny. J Torrey Bot Soc. 133 (1):119–168. doi:10.3159/1095-5674(2006)133[119:PATBOS]2.0.CO;2.

Hilton, J, CJ Cleal. 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. Earth Sci Rev. 85(3–4):85–116. doi:10.1016/j.earscirev.2007.07.003.

Hoffman, LA, MF Tomescu. 2013. An early origin of secondary growth: *Franhueberia gerriennei* gen. et sp. nov. from the Lower Devonian of Gaspé (Quebec, Canada). Am J Bot. 100(4):754–763. doi:10.3732/ajb.1300024.

Kenrick, P, PR Crane. 1997a. The origin and early diversification of land plants: a cladistic study. Washington & London: Smithsonian Institution Press.

Kenrick, P, C Strullu-Derrien. 2014. The origin and early evolution of roots. Plant Physiol. 166(2):570–580. doi:10.1104/pp.114.244517.

Kenrick, P, CH Wellman, H Schneider, GD Edgecombe. 2012. A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. Phil Trans R Soc B. 367(1588):519–536. doi:10.1098/rstb.2011.0271.

Kerp, H, H Bödige, B Bomfleur, JW Schneider. 2022. First records of the conifers *Majonica* and *Ortiseia* from the

German Zechstein (Upper Permian) of east Thuringia and west Saxony, Germany. Bot Lett. 169(4):423–441. doi:10.1080/23818107.2022.2122555.

Kidston, R, WH Lang. 1921. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part IV. Restorations of the vascular cryptogams, and discussion on their bearing on the general morphology of the pteridophyta and the origin of the organization of land-plants. Trans R Soc Edinb. 52:831–854.

Krings, M, TN Taylor, H Hass, H Kerp, N Doltzer, EJ Hermsen. 2007. Fungal endophytes in a 400-million-yr-old land plant: infection pathways, spatial distribution, and host responses. New Phytol. 174(3):648–657. doi:10.1111/j.1469-8137.2007.02008.x.

Larsén, E, N Wikström, A Khodabandeh, C Rydin. 2022. Phylogeny of Merlin's grass (Isoetaceae): revealing an "Amborella syndrome" and the importance of geographic distribution for understanding current and historical diversity. BMC Ecol Evo. 22(1):32. doi:10.1186/s12862-022-01988-w.

Meade, LE, ARG Plackett, J Hilton. 2021. Reconstructing development of the earliest seed integuments raises a new hypothesis for the evolution of ancestral seed-bearing structures. New Phytol. 229(3):1782–1794. doi:10.1111/nph.16792.

Montañez, IP, NJ Tabor, D Niemeier, , WA DiMichele, DF Tracy, CR Fielding, JL Isbell, LP Birgenheier, MC Rygel. 2007. CO2 forced climate and vegetation instability during Late Paleozoic deglaciation. Science. 315(5808):87–91. doi:10.1126/science.1134207.

Morris, JL, MN Puttick, JW Clark, D Edwards, P Kenrick, S Pressel, CH Wellman, Z Yang, H Schneider, PCJ Donoghue. 2018. The timescale of early land plant evolution. Proc Natl Acad Sci U S A. 115(10):E2274–2283. doi:10.1073/pnas.1719588115.

Navidi-Izad, N, H Benachour, DM Kroeck, P Steemans, T Servais. 2022. *Virgatasporites* and *Attritasporites*: the oldest land plant derived spores, cryptospores or acritarchs? Bot Lett. 169(4):495–509. doi:10.1080/23818107.2022.2113560.

Nowak, H, E Kustatscher, G Roghi, JHA Van Konijnenburg-van Cittert. 2023. *In situ* spores of lycophytes from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora in northern Italy. Bot Lett. 170(2):194–207. doi:10.1080/23818107.2022.2113561.

Oliver, FW, DH Scott. 1904. On the structure of the Palaeozoic seed *Lagenostoma lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. Philos Trans R Soc Lond. B197:193–247.

Pfeiler, KC, AMF Tomescu, L Seyfullah. 2021. An Early Devonian actinostelic euphyllophyte with secondary growth from the Emsian of Gaspé (Canada) and the importance of tracheid wall thickening patterns in early euphyllophyte systematics. Pap Palaeontol. 7 (2):1081–1095. doi:10.1002/spp2.1335.

Potonie, R. 1934. I. Zur Morphologie der fossilen Pollen und Sporen. Arbeiten des Instituts Palaobotanik Petrographie Brennsteine. 4:5–24.

Prestianni, C, J Hilton, W Cressler. 2013. Were All Devonian Seeds Cupulate? A Reinvestigation of *Pseudosporogonites hallei*, Xenotheca bertrandii, andAglosperma spp. Int J Plant Sci. 174(5):832–851. doi:10.1086/670235.

Prestianni, C, JJ Rustán, D Balseiro, NE Vaccari. 2022. *Porongodendron minitensis* gen. nov. sp. nov. a new lycopsid from the Mississippian of Argentina with adaptations to tundra-like conditions. Bot Lett. 169 (4):527–539. doi:10.1080/23818107.2022.2101515.

Puttick, MN, JL Morris, TA Williams, CJ Cox, D Edwards, P Kenrick, S Pressel, CH Wellman, H Schneider, D Pisani, et al. 2018. The Interrelationships of land plants and the nature of the ancestral embryophyte. Curr Biol. 28(5):733–745.e2. doi:10.1016/j.cub.2018.01.063.

Reinsch, P. 1884. Micro-Palaeophytologia formationis carboniferae. Krische: Erlangen.

Retallack, GJ. 1997. Earliest Triassic origin of Isoetes and quillwort evolutionary radiation. J Paleontol. 71 (3):500–521. doi:10.1017/S0022336000039524.

Rothwell, GW, WL Crepet, RA Stockey. 2009. Is the anthophyte hypothesis alive and well? New evidence from the reproductive structures of Bennettitales. Am J Bot. 96 (1):296–322. doi:10.3732/ajb.0800209.

Rubinstein, CV, P Gerrienne, GS de la Puente, RA Astini, P Steemans. 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). New Phytol. 188(2):365–369. doi:10.1111/j.1469-8137.2010.03433.x.

Santos, AA, LM Sender, L Piñuela, JC García-Ramos, JB Diez. 2022b. First evidence of Ricciaceae in the Jurassic of the Iberian Peninsula (Asturias, NW Spain): Ricciopsis asturicus sp. nov. 169(4):557–567. doi:10.1080/23818107.2022.2124452

Santos, AA, L Xiao, CC Labandeira, D Néraudeau, É Dépré, J-D Moreau, V Perrichot, T Wappler. 2022a. Plant–insect interactions from the mid-Cretaceous at Puy-Puy (Aquitaine Basin, western France) indicates preferential herbivory for angiosperms amid a forest of ferns, gymnosperms, and angiosperms. Bot Lett. 169(4):568–587. 2092772. doi:10.1080/23818107.2022.2092772.

Schopf, JM. 1957. Spores and related plant microfossils – PaleozoicSpores and related plant microfossils – PaleozoicIn H LaddeditorPaleoecology: geological Society of America MemoirVol. 67(2), pp. 703–707.

Shi, G, F Herrera, PS Herendeen, EG Clark, PR Crane. 2021. Mesozoic cupules and the origin of the angiosperm second integument. Nature. 594(7862):223–226. doi:10.1038/s41586-021-03598-w.

Steart, D, J Needham, C Strullu-Derrien, M Philippe, J Krieger, L Stevens, ART Spencer, PA Hayes, P Kenrick. 2023. New evidence of the architecture and affinity of fossil trees from the Jurassic Purbeck Forest of southern England. Bot Lett. 170(2):165–182. doi:10.1080/23818107.2023.2197973.

Steemans, P, A Le Hérissé, J Melvin, MA Miller, F Paris, J Verniers, CH Wellman. 2009. Origin and radiation of the earliest vascular land plants. Science. 324(5925):353. doi:10.1126/science.1169659.

Strother, PK, C Foster. 2021. A fossil record of land plant origins from charophyte algae. Science. 373(6556):792–796. doi:10.1126/science.abj2927.

Strullu-Derrien, C 2010. Recherches sur la colonisation du milieu terrestre par les plantes au cours du Dévonien inférieur et sur les interactions plantes/microorganismes durant les périodes Dévonien-Carbonifère. PhD Thesis, University of Angers (France) and University of Liège (Belgium).

Strullu-Derrien, C, M Ballèvre, ART Spencer, E Guillou, J-P Gislard, H Lardeux, CJ Cleal. 2023. The Carboniferous (Serpukhovian) macroflora from the "Coteaux du Pont Barré", Beaulieu- sur-Layon (Maine-et-Loire), South of the Armorican Massif, France. Bot Lett. 170(2):183–193. doi:10.1080/23818107.2023.2183899.

Strullu-Derrien, C, CJ Cleal, C Ducassou, ART Spencer, E Stolle, VO Leshyk. 2021. A rare Late Mississippian flora from Northwestern Europe (Maine-et-Loire Coalfield, Pays de la Loire, France). Rev Palaeobot Palynol. 285:104359. doi:10.1016/j.revpalbo.2020.104359.

Strullu-Derrien, C, C Ducassou, M Ballèvre, MP Dabard, P Gerrienne, H Lardeux, A Le Hérissé, C Robin, P Steemans, and DG Strullu. 2010. The early land plants from the Armorican Massif: sedimentological and palynological considerations on age and environment. Geol Mag. 147(6):830–843. doi:10.1017/S001675681000004X.

Strullu-Derrien, C, P Kenrick, S Pressel, JG Duckett, JP Rioult, , and DG Strullu. 2014. Fungal associations in *Horneophyton ligneri* from the Rhynie Chert (c. 407 million year old) closely resemble those in extant lower land plants: novel insights into ancestral plant–fungus symbioses. New Phytol. 203(3):964–979. doi:10.1111/nph.12805.

Strullu-Derrien, C, P Kenrick, P Tafforeau, H Cochard, JL Bonnemain, A Le Herisse, H Lardeux, E Badel. 2014. The earliest wood and its hydraulic properties documented in c 407-million-year-old fossils using synchrotron microtomography. Bot J Linn Soc. 175(3):423–437. doi:10.1111/boj.12175.

Strullu-Derrien, C, ART Spencer, P Kenrick, WS Judd, D De Franceschi, SR Manchester. 2022. Revisions to the Eocene carpoflora of Anjou, western France, with new data from X-ray tomography. Bot Lett. 169(4):454–465. doi:10.1080/23818107.2022.2101518.

Suess, E. 1885. Das Antlitz der Erde. Vol. 1. Leipzig, Germany: G. Freytag.

Taylor, TN. 1973. Combined transmission and scanning electron microscopy of *in situ* Paleozoic spores. Palaeontology. 16:765–776.

Taylor, TN, EL Taylor, M Krings. 2009. The Biology and Evolution of Fossil Plants. 2nd ed. Amsterdam: Academic Press.

Thomas, BA, CJ Cleal. 2022. A reassessment of the leafy shoots of Pennsylvanian-age arborescent lycopods. Bot Lett. 169(4):466–494. doi:10.1080/23818107.2022.2101517.

Tomescu, AM, B Bomfleur, AC Bippus, A Savoretti. 2018. Why are bryophytes so rare in the fossil record? A spotlight on taphonomy and fossil preservation. In M Krings, C Harper, N Cúneo G Rothwell, editors. Transformative Paleobotany. London: Academic Press; pp. 375–416.

Torrens, HS. 2005. The Moravian minister Rev. Henry Steinhauer (1782–1818); his work on fossil plants, their first 'scientific'description and the planned Mineral Botany. Geol Soc Lond Spec Publ. 241(1):13–28. doi:10.1144/GSL.SP.2003.207.01.03.

Unverfärth, J, S McLoughlin, M Möllmann, B Bomfleur. 2022a. *Sphenobaiera insecta* from the Upper Triassic of South Australia, with a clarification of the genus *Sphenobaiera* (fossil Ginkgophyta) and its delimitation from similar foliage genera. Bot Lett. 169(4):442–453. doi:10.1080/23818107.2022.2076259.

Wikström, N, E Larsén, A Khodabandeh, C Rydin. 2023. No phylogenomic support for a Cenozoic origin of the "living fossil" *Isoetes*. Am J Bot. 110(1):e16108. doi:10.1002/ajb2.16108.