

COMMENTARY

Great moments in plant evolution

Gregory J. Retallack^{a,1} 

Just as dinosaurs can be regarded as protobirds (1) and synapsids as protomammals (2), understanding the evolution of plants depends on extinct fossil groups, such as those linking spore and seed plants. A profound paleobotanical surprise in 1904 was discovery of pteridosperms, commonly called seed ferns, because of their unexpected combination of seeds and fern-like leaves (3). Another paleobotanical surprise in 1960 was discovery of progymnosperms, spore plants with woody anatomy comparable to modern conifer trees (4, 5). Now, Wang et al. (6) in PNAS report a Chinese Permian (298 Ma) fossil plant, *Paratinga wuhaia*. These permineralized fossils convincingly expand the progymnosperm clade to include the enigmatic Noeggerthiales, variously regarded as leptosporangiate or eusporangiate ferns, sphenopsids, cycads, or possible progymnosperms (7).

The insight comes from permineralized fossils, sometimes mistakenly called petrified, or, literally, turned to stone. In contrast to petrified limb casts, permineralized plants retain original cell walls infiltrated by colloidal silica, revealing details of histology and reproduction in thin sections and acetate peels. *Paratinga* bore numerous (perhaps as many as 200) spore-bearing pseudostrobili within a fertile zone of a single, unbranched trunk of modest size (2 m), crowned with long (50 cm) pinnate leaves. Most noeggerthialean fossils are plant impressions without internal anatomical detail, but permineralized spores and eustele with pycnoxylic secondary xylem now mark *Paratinga* as a progymnosperm. *P. wuhaia* also had spores of two different sizes, roughly 35 and 800 μm in diameter (6). Such heterospory is found in other progymnosperms, such as *Archaeopteris*, as an evolutionary transition from progymnosperms to seed ferns (8).

Middle Devonian progymnosperms such as *Archaeopteris* (Fig. 1) are among the oldest known trees. Along with cladoxyl tree ferns such as *Wattieza*, increased stature and depth of tree rooting during the Devonian played a role in global cooling toward the Permian–Carboniferous Ice Age (9). Noeggerthiales were also trees, appearing during the

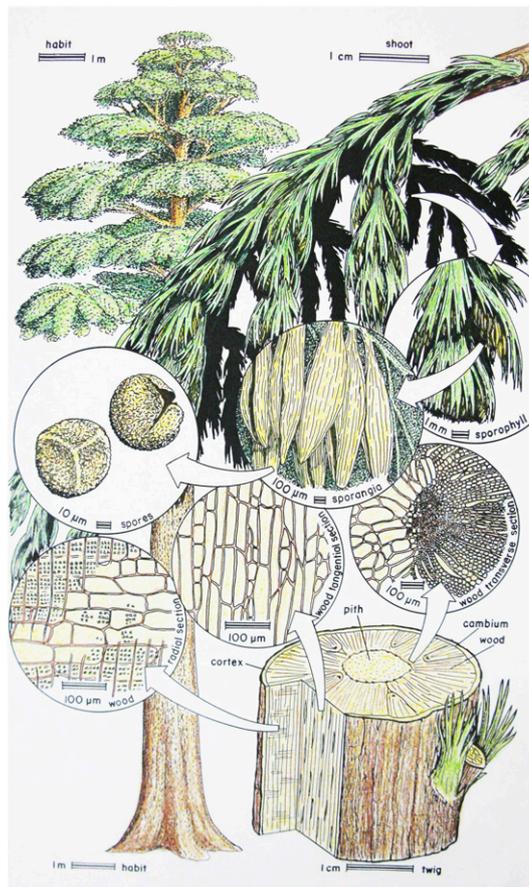


Fig. 1. Classical concept of progymnosperms exemplified by *Archaeopteris macilenta* (leaves and sporangia), *Callixylon zalesskyi* (permineralized wood), and *Geminospora lemurata* (spores) from the Late Devonian (Frasnian, 366 Ma) lower Walton Formation, near Sidney, New York (4), is similar to a conifer (5), in contrast with the palm-like, newly reconstructed progymnosperm *P. wuhaia* from the Permian of China (6). Reprinted with permission from ref. 21.

early Carboniferous and persisting at least to the end of the Permian (6). Noeggerthiales may have survived (7) the extensive Late Permian mass extinction of plants in China

^aDepartment of Earth Sciences, University of Oregon, Eugene, OR 97403

Author contributions: G.J.R. designed research, performed research, and wrote the paper.

The author declares no competing interest.

Published under the [PNAS license](https://www.pnas.org/licenses/pnas-license).

See companion article, "Ancient noeggerthialean reveals the seed plant sister group diversified alongside the primary seed plant radiation," [10.1073/pnas.2013442118](https://doi.org/10.1073/pnas.2013442118).

¹Email: greg@uoregon.edu.

Published March 26, 2021.

(10). A case has been made that progymnosperms are not extinct but live in the form of ophioglossaleans such as *Botrychium* (11), small herbaceous plants that have a very poor fossil record (12). Alternatively, Ophioglossales have been regarded as nested within true ferns (13).

The palm-like reconstruction of *Paratingia*, following Corner's plant-architectural model (14), contrasts with conifer-like reconstruction of the first described Devonian progymnosperms (Fig. 1), revealing an unexpected diversity of progymnosperm biology and ecology. Parasol-like, unbranched trunks and massive reproductive zones characterize pioneer tropical trees, such as *Cecropia* (15). *Paratingia* may have been similar because, like other Noeggerathiales (16), it was found within a weakly developed, thin (66 cm) soil (Vitrand) of fresh volcanic ash in a humid lowland peat swamp at tropical paleolatitudes. *Archaeopteris*, on the other hand, was rooted in subhumid to semiarid, well-drained quartzofeldspathic soils (Vertisols and Alfisols) of fluvial levees and floodplains (9). Similar architectural divergence is seen in angiosperm *Quercus* trees versus *Cocos* palms (14), cycadeoid *Williamsonia* versus *Monanthesia* (17), pteridosperm *Glossopteris* versus *Medullosa* (18), and lycopsid *Diaphorodendron* versus *Pleuromeia* (17). Palm-like architecture is created by unusually large terminal meristems that are frost-sensitive, unlike small terminal and lateral meristems of copiously

branched plants (19). Thus, palms are restricted now to subtropical latitudes, within 30° of the equator and the 15 °C isotherm of mean annual temperature (20), and the same was likely for other monocaul fossils, including *P. wuhaia*.

The slow pace of paleobotanical discovery starting with pteridosperms in 1904 (3), progymnosperms in 1960 (4), and now progymnosperm affinities for Noeggerathiales (6) is due to the need for minor miracles of discovery, preparation, and restoration. Permineralized fossils need to be discovered, then their cellular preservation must be proven by cutting the hard rock with diamond saws and preparing thin sections, or making acetate peels. In the present study (6), peels were prepared from slabs etched with hydrofluoric acid, a dangerous material that many paleobotanists refuse to use. Then, there is the problem of making a whole-plant restoration by establishing which of the various parts of the plant jumble, often named using separate organ genera (18), belonged to the same species. This can be inferred from anatomical peculiarities of the various permineralized organs (3) but most effectively by attachment of various organs (4), as in the present case (6). Whole-plant reconstruction of *P. wuhaia* is thus a rare and important step for understanding the evolution of early trees.

- 1 R. L. Nudds, G. J. Dyke, Forelimb posture in dinosaurs and the evolution of the avian flapping flight-stroke. *Evolution* **63**, 994–1002 (2009).
- 2 D. R. Prothero, *The Princeton Field Guide to Prehistoric Mammals* (Princeton University Press, Princeton, NJ, 2016).
- 3 F. W. Oliver, D. H. Scott, On the structure of the Palaeozoic seed, *Lagenostoma lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. *Proc. R. Soc. Lond.* **73**, 4–5 (1904).
- 4 C. B. Beck, The identity of *Archaeopteris* and *Callixylon*. *Brittonia* **12**, 351–368 (1960).
- 5 H. Keng, The phylloclade of *Phyllocladus* and its possible bearing on the branch systems of progymnosperms. *Ann. Bot.* **38**, 757–764 (1974).
- 6 J. Wang *et al.*, Ancient noeggerathialean reveals the seed plant sister group diversified alongside the primary seed plant radiation. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2013442118 (2021).
- 7 S. J. Wang *et al.*, Anatomically preserved “strobili” and leaves from the Permian of China (Dorsalistachyaceae, fam. nov.) broaden knowledge of Noeggerathiales and constrain their possible taxonomic affinities. *Am. J. Bot.* **104**, 127–149 (2017).
- 8 T. L. Phillips, H. N. Andrews, P. G. Gensel, Two heterosporous species of *Archaeopteris* from the Upper Devonian of West Virginia. *Palaeontographica Abt. B Paläophytol.* **139**, 47–71 (1972).
- 9 G. J. Retallack, C. Huang, Ecology and evolution of Devonian trees in New York, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **299**, 110–128 (2011).
- 10 J. Yu *et al.*, Vegetation changeover across the Permian–Triassic boundary in Southwest China: Extinction, survival, recovery and palaeoclimate: A critical review. *Earth Sci. Rev.* **149**, 203–224 (2015).
- 11 M. Kato, The phylogenetic relationship of Ophioglossaceae. *Taxon* **37**, 381–386 (1988).
- 12 G. W. Rothwell, S. A. Stockey, Fossil Ophioglossales in the Paleocene of Western North America. *Am. J. Bot.* **76**, 637–644 (1989).
- 13 G. W. Rothwell, Fossils and ferns in the resolution of land plant phylogeny. *Bot. Rev.* **65**, 188–218 (1999).
- 14 F. Hallé, R. A. Oldeman, P. B. Tomlinson, *Tropical Trees and Forests: An Architectural Analysis* (Springer, Berlin, 2012).
- 15 A. F. S. L. Lok, K. Tan, K. Y. Chong, T. P. L. Nghiem, H. T. W. Tan, The distribution and ecology of *Cecropia* species (Urticaceae) in Singapore. *Nat. Singap.* **3**, 199–209 (2010).
- 16 H. W. Pfefferkorn, J. Wang, Paleocology of Noeggerathiales, an enigmatic, extinct plant group of Carboniferous and Permian times. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **448**, 141–150 (2016).
- 17 T. N. Taylor, E. L. Taylor, M. Krings, *Paleobotany: The Biology and Evolution of Fossil Plants* (Elsevier, Amsterdam, 2009).
- 18 G. J. Retallack, D. L. Dilcher, Reconstructions of selected seed ferns. *Ann. Mo. Bot. Gard.* **75**, 1010–1057 (1988).
- 19 J. D. Mauseth, Giant shoot apical meristems in cacti have ordinary leaf primordia but altered phyllotaxy and shoot diameter. *Ann. Bot.* **94**, 145–153 (2004).
- 20 A. Sakai, W. Larcher, *Frost Survival of Plants* (Springer, Berlin, 1987).
- 21 G. J. Retallack, *Soils of the Past* (Wiley, Chichester, UK, 3rd Ed., 2019).