Anatomically preserved "strobili" and leaves from the Permian of China (Dorsalistachyaceae, fam. nov.) broaden knowledge of Noeggerathiales and constrain their possible taxonomic affinities[1]

Shi-Jun Wang[2], Richard M. Bateman[3], Alan R. T. Spencer[4], Jun Wang[5], Longyi Shao[6], and Jason Hilton[7,8]

PREMISE OF THE STUDY: Noeggerathiales are an extinct group of heterosporous shrubs and trees that were widespread and diverse during the Pennsylvanian–Permian Epochs (323–252 Ma) but are of controversial taxonomic affinity. Groups proposed as close relatives include leptosporangiate ferns, sphenopsids, progymnosperms, or the extant eusporangiate fern *Tmesipteris*. Previously identified noeggerathialeans lacked anatomical preservation, limiting taxonomic comparisons to their external morphology and spore structure. We here document from the upper Permian of China the first anatomically preserved noeggerathialeans, which enhance the perceived distinctiveness of the group and better indicate its systematic affinity.

METHODS: We describe in detail the newly discovered, anatomically preserved heterosporous strobilus *Dorsalistachya quadrisegmentorum*, gen. et sp. nov., and redescribe its suspected foliar correlate, the pinnate leaf *Plagiozamites oblongifolius*.

KEY RESULTS: *Plagiozamites* possesses an omega (Ω)-shaped vascular trace and prominent cortical secretory cavities—a distinctive anatomical organization that is echoed in the newly discovered strobili. *Dorsalistachya* strobili bear highly dissected sporophylls alternately in two vertical rows, suggesting that they are homologs of leaf pinnae. If so, the "strobilus" is strictly a pseudostrobilus and consists of sporangium-bearing units that are one hierarchical level below true sporophylls. The "sporophylls" bear four microsporangia on the lower (abaxial) surface, occasionally interspersed with short longitudinal rows of megasporangia. A single functional megaspore develops within each winged megasporangium, suggesting adaptation for dispersal as a single unit.

CONCLUSIONS: *Dorsalistachya* presents a unique combination of reproductive features that amply justifies establishment of a new family, Dorsalistachyaceae. Noeggerathiales represent a distinct taxonomic Order of free-sporing plants that most resembles early-divergent eusporangiate ferns and the more derived among the extinct progymnosperms. By the early Permian, noeggerathialeans had attained levels of reproductive sophistication similar to the most derived among the Paleozoic sphenophytes and lycophytes, but their heterosporous life history may have contributed to their extinction during the Triassic climatic aridification.

KEY WORDS 3D reconstruction; *Dorsalistachya*; Dorsalistachyaceae; eusporangiate fern; heterospory; Noeggerathiales; paleobotany; Permian; phylogeny; progymnosperm; Xuanwei Formation

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Approximately half of the major groups of land-plants recognized today have left no close living relatives (e.g., Hilton and Bateman, 2006). However, gradually characterizing such groups until they can take their place in rigorous evolutionary studies requires painstaking paleobotanical research, building conceptual whole-plants from exceptionally preserved examples of their component organs (Bateman and Hilton, 2009). Our knowledge of land-plant phylogeny would remain rudimentary even today if paleobotanists had not recognized and circumscribed fossil groups that provide phylogenetic bridges between extant groups (e.g., Taylor et al., 2009): rhyniophytes linking bryophytes with lycophytes, progymnosperms linking ferns with seed-plants, and—within seed-plants—pteridosperms

linking several disparate groups of extant gymnosperms and the angiosperms. One major group that, until now, has evaded such confident phylogenetic placement is the Noeggerathiales sensu Němejc, 1931 (= Noeggerathiopsida sensu Boureau, 1964); a group for which we suggest the colloquial name 'bottle-brush ferns'.

Extending from the Mississippian to the Triassic, noeggerathialean fossils are a particularly important component of peat-forming plant communities in the Permian fossil floras of China (Wang et al., 2009, 2012). Recent research on in situ fossil forests has reconstructed members of the Noeggerathiales as fern-like trees that produced a dense crown of fern-/cycad-like leaves and elongate strobili of crowded sporophylls (Wang et al., 2009; Wang et al., 2012). Although these investigations provided important information on the growth architecture of members of the Noeggerathiales, the absence of anatomically preserved fossils precluded detailed comparison with other phylogenetically important plant groups. Consequently, noeggerathialeans have long been a 'phylogenetic football'; they have been linked with an extraordinarily wide range of major groups, including leptosporangiate ferns (Němejc, 1931), sphenopsids (Browne, 1933), progymnosperms (Beck, 1976, 1981; Meyen, 1987; Taylor et al., 2009), or ranked alongside these clades as a distinct group in its own right (Boureau, 1964); comparison has even been made with the primitive extant eusporangiate fern *Tmesipteris* Bernh. (Bierhorst, 1971).

Here, we document for the first time anatomically preserved noeggerathialean leaves, rachises, and strobili, whose spatial juxtaposition and anatomical similarity together suggest that they represent different parts of the same whole-plant species (Bateman and Hilton, 2009). The difficulty that we have experienced in placing taxonomically these morphologically disparate organs prompts a broader review of the classification and potential evolutionary significance of Noeggerathiales.

MATERIALS AND METHODS

Geological context—The plant fossils described here were found in Guizhou Province, southwestern China (Wang et al., 2011; Fig. 1), occurring within the Xuanwei Formation, which extends through western Guizhou and eastern Yunnan provinces. These deposits date to the Wuchiapingian to Changhsingian stages of the Lopingian Epoch (late Permian Period), ca 260–252 Ma (Seyfullah et al., 2010; Neregato et al., 2016). They consist of gray sandstones, gray siltstones, dark gray mudstones, and abundant coal seams, with some pebbly conglomerates in the lower part of the sequence (Wang et al., 2011). The formation represents a series of depositional environments that formed along the eastern side of the Kangdian Oldland landmass, and includes terrestrial, fluvial, peat-forming mire, and deltaic facies with periodic marginal marine influences, as well as pebble-conglomerate tuffaceous horizons that contain anatomically preserved plants (Seyfullah et al., 2010; Wang et al., 2011; Neregato et al., 2016). The origin of the tuffaceous sediments is unknown, as they have only been found ex situ, but it is most likely related to the later phases of the volcanism that emplaced the underlying Emeishan Basalt (Bond et al., 2010).

Exceptionally preserved noeggerathialean cones plus several isolated rachises were collected at Huopu coal mine (25°39′31″N 104°25′04″E; Fig. 1). They are here compared with leaves of *Plagiozamites oblongifolius* Halle (Guo et al., 1990) that were obtained from nearby compression/impression floras within the same formation. This particular leaf-species was first described as a cycad,
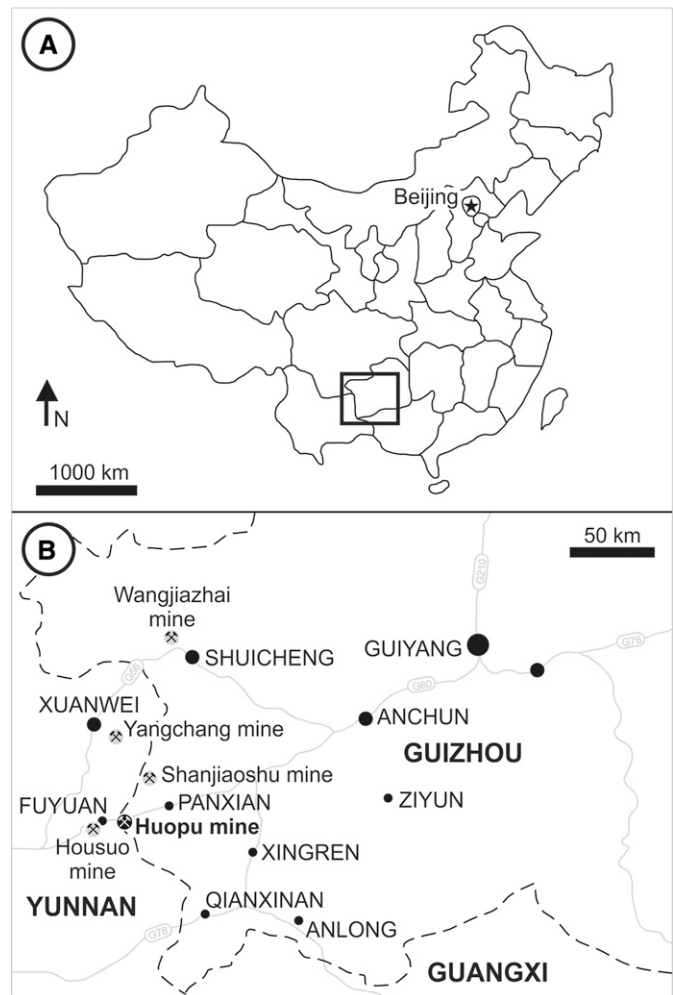

FIGURE 1 Location of Huopu coal mine. (A) Outline map of China showing provincial boundaries; boxed area enlarged in (B). (B) The location of Huopu coal mine in Guizhou Province indicated by a white hammer-and-pick symbols in a black circle. Major towns are shown as filled circles, provincial boundaries as dashed lines, major roads as solid gray lines, and other major coal mines by black hammer-and-pick symbols in gray circles. Map modified after Wang et al. (2006).

even though the leaf-genus *Plagiozamites* is more commonly interpreted as being of noeggerathialean affinity (Wang, 2008).

Plant organs preserved as two-dimensional compression–impression fossils are abundant in the Xuanwei Formation (Zhao et al., 1980), but anatomical preservation is rare. Such preservation was facilitated by dissolution and redeposition of calcium carbonate within tuffaceous sediments; permineralization occurred rapidly after deposition, thus limiting plant decay (Neregato et al., 2016).

Specimens—The present specimens were preserved in a large block of volcaniclastic tuff (numbered as HP2007-1). The block was first cut perpendicular to bedding into six parallel slabs to provide ten cut surfaces (labeled A, B/Top, B/Bot, C/Top, C/Bot, D/Top, D/Bot, E/Top, E/Bot, and F); these exposed several plant fossils, including the noeggerathialean strobili.

The most complete strobilus extends for 115 mm from slab B to slab F, and is well preserved but apically and distally incomplete.

Numbered HP2007-1-A, it is here designated as the holotype of a new species, which also serves as the type of a new genus and family. The block also contains two partially preserved strobili, one revealed in transverse section (HP2007-1-B) and the other in oblique section (HP2007-1-C). In addition, the block contains an isolated strobilar axis that is exposed in a longitudinal section (HP2007-1-D) but bears only basal portions of the sporophylls. The cut surfaces also expose isolated microsporangia and megasporangia of the present species, plus isolated vascular bundles of vegetative rachises (numbered HP2007-1-E, F, and G, respectively).

Information on the morphology and anatomy of the new strobilus species was gathered primarily from slab E of HP2007-1-A (holotype). Serial acetate peeling (e.g., Galtier and Phillips, 1999) of the upper surface (numbered as HP2007-1 E/Top) of slab E yielded 41 transverse sections, revealing the arrangement and orientation of the sporophylls on the axis. Serial peeling of a tangential section parallel to a sporophyll, extending from the surface of the cone to near the axis, was conducted on the remaining portion of slab E, followed by serial peeling perpendicular to the sporophyll from the surface of the cone to the center of the axis.

Slab C of the strobilus was trimmed with a rock saw, then mounted on a Buehler Isomet low-speed saw (Buehler, Lake Bluff, Illinois, USA) and cut into serial wafers, each 0.7 mm thick, using a 0.8 mm-wide diamond blade. Sections were mounted on glass slides under coverslips using Eukitt (Sigma-Aldrich Corp., St. Louis, Missouri, USA), studied primarily in reflected light, and photographed using a Zeiss Tessovar (ZEISS United States, Dublin, California, USA) with a Canon EOS D40 digital SLR camera. Type and figured specimens have been deposited at the Institute of Botany of the Chinese Academy of Sciences in Beijing, China.

Tomographic reconstruction—Three-dimensional reconstructions were based on tomographic datasets created from the optical photography of the mounted slides; subsequent manual alignment used SPIERSAlign (Sutton et al., 2012). The datasets were imported into SPIERSEdit (Sutton et al., 2012), where separation of the fossil from the surrounding matrix was achieved through a combination of thresholding and masking. Individual 'masks' were assigned to distinct anatomical structures that were rendered as separate isosurfaces. This process allowed the production of accurate false-color models that emphasized the spatial relationships among the anatomical structures, which could then be virtually manipulated within three-dimensional-space using SPIERSView (Sutton et al., 2012; Appendix S1, see Supplemental Data of this article). Blender was subsequently used to produce rendered raytraced images and animations (Garwood and Dunlop, 2014; Appendix S2).

RESULTS

Brief description of **Plagiozamites oblongifolius**—These megaphyllous leaves consist of a linear rachis that bears in two opposing rows numerous alternating pinnae, each elliptic-oblong to oblong and multiveined (Guo et al., 1990; Fig. 2A). The specimen figured by Guo et al. (1990) is 71 mm long and incomplete both basally and apically. The comparatively small (5 mm diameter) rachis supplies the pinnae via traces emitted from the margins of the distinctive inverted, omega (Ω)-shaped vascular bundle (Guo et al., 1990; Fig. 2B). Large secretory cavities are abundant within the cortex of the rachis (Guo et al., 1990) and the vascular bundle consists of metaxylem

tracheids showing scalariform pitting. The three-dimensional rachises found by us at Huopu mine are slightly smaller (ca 4 mm in diameter) than those of the compression leaves originally assigned to *P. oblongifolius*, but are anatomically near-identical, united by inverted Ω-shaped vascular bundles that are 6–7 tracheids thick (Fig. 2C).

Detailed description of **Dorsalistachya quadrisegmentorum**—*Introductory note*—Throughout most of this paper we have used the terms strobilus/cone and sporophyll in the manner that they have traditionally been applied to noeggerathialean reproductive organs. However, in the first section of the Discussion, we reinterpret the homologies of those organs with regard to *Dorsalistachya*. We argue that the "strobilus" is more likely a highly complex, strongly three-dimensional sporophyll and its similarly complex lateral appendages (i.e., traditional "sporophylls") are therefore homologous with vegetative pinnae. Most of the information in the following description is derived from the holotype, with additional insight from the three-dimensional model (Appendix S1 and S2).

Gross morphology—The partial strobilus selected by us as the holotype has a length of 115 mm, constituting a minimum length for the strobilus as neither the pedicel nor the strobilar apex has been preserved. When viewed in transverse section, the cone is almost isodiametric distally (ca 8 mm: Fig. 3A), but more proximally it appears moderately elliptical, ca 12 × 8 mm (Fig. 3B), the shorter (vertical) diameter probably being a result of postburial compression.

Axis—The strobilus axis is 2–3 mm in diameter (Fig. 3A, B) with a centrally located vascular bundle that in transverse section is unequivocally Ω-shaped (Fig. 3C–E) and wider than high, diminishing from 0.8–1.0 mm × ca 0.8 mm proximally (Fig. 3D, E) to 0.6 mm × 0.4 mm distally (Fig. 3C). The xylem strand is 5–10 tracheids high. Protoxylem is located at the two lateral margins of the vascular bundle and is mesarch (Fig. 3D, E). Metaxylem tracheids are nearly isodiametric or slightly radially elongated, 15–25 μm in diameter, apparently exhibiting scalariform thickenings (Fig. 4B). Secondary xylem is absent.

The cortex can be divided into two zones. The outer zone consists of parenchymatous cells 30–70 μm in diameter that are nearly isodiametric or slightly tangentially elongated. Two cortical strands composed of smaller sclerenchymatous cells 25–45 μm in diameter occur on opposite sides of the axis, occupying the plane of bilateral symmetry defined by the vascular trace (Fig. 3C–E). The inner zone of the cortex is also composed of parenchymatous cells but they are on average slightly smaller than those of the outer zone. All cortical cells are elongated parallel to the axis (Fig. 4A). Large secretory bodies are common and apparently randomly distributed throughout this zone. They appear circular or more often elliptical in shape in transverse section, varying considerably in size between 60 × 80 μm and 180 × 300 μm (Figs. 3D, E, 4A); longitudinal sections show that they vary in length from 350 μm to more than 2 mm in length (Fig. 4A). The surface of the axis expands outwards to form many stellate protuberances (Figs. 3B, 4C). These protuberances have a maximum length of 0.5 mm. In transverse section, epidermal cells appear rectangular, square, or columnar in outline, 15–20 × 20–25 μm; some have thickened anticlinal walls (Fig. 3C–E).

Sporophyll traces diverge from the two margins of the vascular bundle, either as a pair or a single trace that rapidly divides to form a pair (Fig. 3C, arrows). Traces extend distally through the cortex in
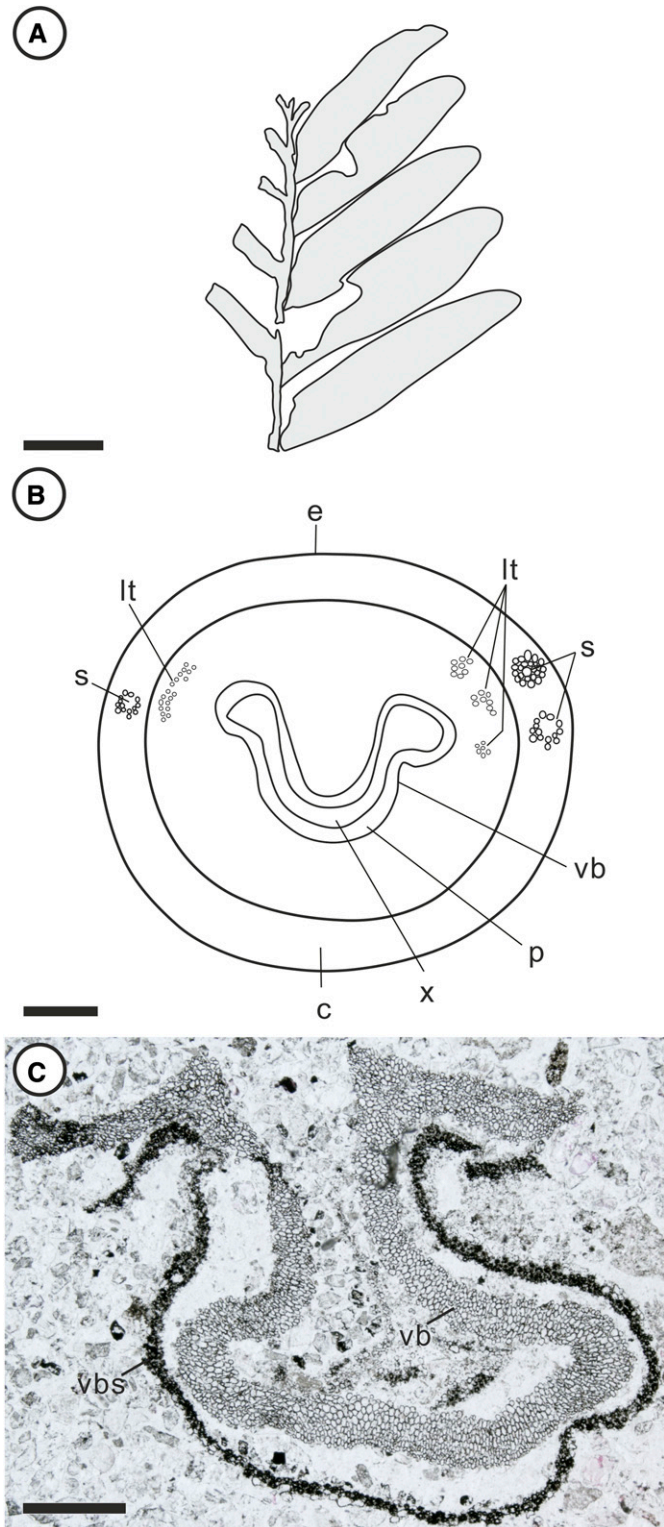
FIGURE 2 Structure of the leaf and rachis of *Plagiozamites oblongifolius*. (A) Outline drawing of leaves with central rachis and bearing alternate, oblong pinnules in two opposing rows. Scale bar = 20 mm. (B) Rachis anatomy of *P. oblongifolius* showing an inverted Ω-shaped vascular bundle (vb), opposite leaf traces (lt), xylem (x), phloem (p), cortex (c), epidermis (e), and position of an exemplar secretory cavities (s). Scale bar = 1 mm. (C) Isolated Ω-shaped vascular bundle (vb) and sclerotic

a nearly vertical course for one internode (i.e., for a distance of ca 3.0–3.5 mm) before entering the sporophyll at the succeeding node (see Fig. 7B).

Sporophyll—Sporophylls are half-disciform and are attached to the axis distichously and alternately (Figs. 3A, B, 4A, 5A–G, 6A, B). Each sporophyll is deeply divided into four segments (Figs. 3B, 6A, B). Each segment extends perpendicular to the cone axis for 2.5–3.0 mm as a proximal lamina before bifurcating to form two distal laminae that immediately and abruptly curve distally to parallel the cone axis (Figs. 3A, B, 4A, 5A–G, 6A, B, 7A, B). Viewed laterally, the distal lamina is 3–3.5 mm long, of which 0.5–1.0 mm is a proximally oriented heel (Figs. 4A, 5A, B, 6C, D, 7A).

The proximal lamina ("segment") expands distally from 1.2–1.5 mm to ca 2 mm in width (Figs. 7A, 8A). It extends adaxially into two conspicuously raised lateral margins separated by a shallowly concave central region (Figs. 7A, 8A). Narrow abaxial ridges 0.8–1.0 mm in height (Fig. 7A) extend radially near the margins of the proximal lamina, reaching the base of the distal lamina (Fig. 8B).

Hypodermal tissue is well developed on the adaxial surface of the proximal lamina. Along its margins the hypodermis consists of several layers of small sclerenchymatous cells 20–40 μm in diameter, but when the hypodermis is traced inward the cells become larger and more elongated; they are 40–50 μm high, 80 μm in tangential direction, and up to 200 μm in radial direction, with thick but loosely constructed walls (Fig. 7A, C). The mesophyll consists of comparatively light-colored, tangentially isodiametric, and radially elongated parenchymatous cells (Fig. 7D). Typically, elliptical idioblasts 30–40 μm in diameter are dispersed throughout the mesophyll (Fig. 7D). Cells of the lower epidermis are rectangular in transverse section and rectangular, polygonal, or irregular in periclinal section. The anticlinal walls of some cells are thickened and/or sinuous (Fig. 7E). No unequivocal stomata have been documented, though one possible stoma was observed on the abaxial surface of a sporophyll adjacent to a microsporangium (Fig. 9E).

The four proximal laminae of each segment are united only close to the junction with the cone axis (Figs. 3A, B, 6A, B, 7A, 8A, B), where a longitudinally elongated body of cells resembling those in the center of the adaxial hypodermis extends for ca 500–600 × 350–370 μm (Fig. 7A).

The distal lamina is ca 2 mm wide at its base, and is parallel-sided for approximately one-third of its length before tapering distally to a pointed apex (Fig. 7F). The thickness of the lamina is only 0.2–0.3 mm at its base, but increases to 0.8–1.5 mm midway along its length (Fig. 7G–J). Transverse sections of the basal portion of the distal lamina are complex in shape with margins that vary considerably in orientation and acuteness (Figs. 3A, B, 6A–D, 7A, I, J, 8A, B), whereas more distal portions of the lamina tend to have a more consistent transverse section that is either subtriangular or shallowly concave when viewed from the exterior of the cone (Figs. 3A, B, 6A, C, D, 7A, F–H). The mesophyll is less well-preserved in the basal portion of the distal lamina than in the apical portion, where it clearly consists of a mixture of parenchymatous and occasional sclerenchymatous cells (Fig. 7G–J). Parenchymatous cells are large

vascular bundle sheath (vbs) in the rachis of *P. oblongifolius* from Huopu coal mine, Guizhou Province. Slide WP2-0212. Scale bars = 1 mm. Figs. 2A, B modified after Guo et al. (1990).
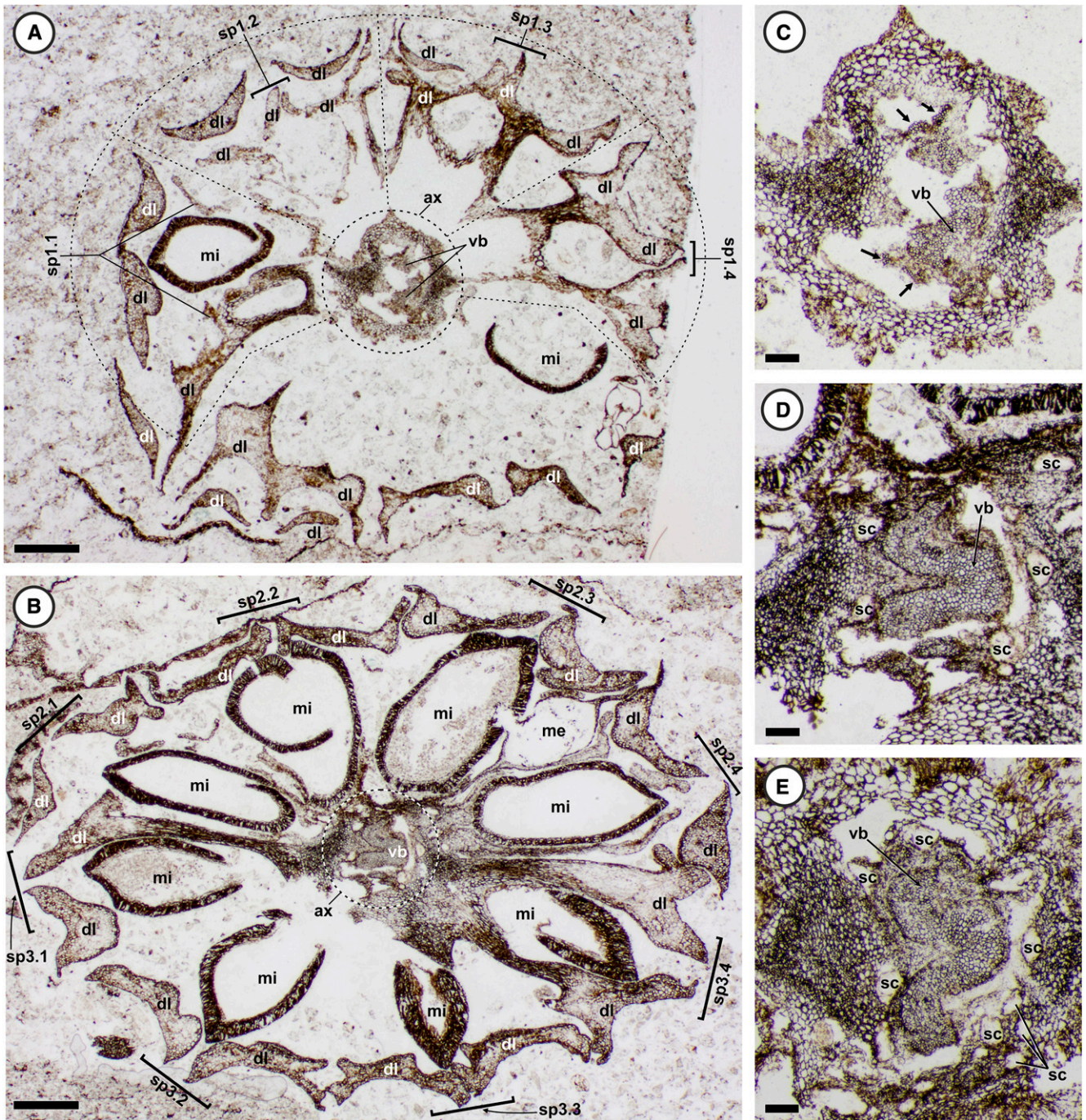
FIGURE 3 Anatomy and organization of *Dorsalistachya quadrisegmentorum.* (A) Transverse section through upper part of strobilus showing the axis (ax) with an Ω-shaped vascular bundle (vb) that has split post-mortem, and sporophylls at different levels with microsporangia (mi). Each sporophyll is divided into four segments (sp1.1–4; dashed lines), each of which divides into two distal laminae (dl) that curve upwards. Slide WP2-0208. Scale bar = 1 mm. (B) Transverse section through lower part of strobilus showing the axis (ax) with an Ω-shaped vascular bundle, and two sporophylls at different levels. Each sporophyll is divided into four segments (sp2.1–4 and sp3.1–4), each of which divides into two distal laminae (dl) that curve upwards. Each segment bears a single microsporangium (mi) while sporophyll 2 (sp2) also bears a single winged megasporangium (me) between adjacent microsporangia. Slide WP2-0271 E/Top (37). Scale bar = 1 mm. (C–E) Series of transverse peels showing the changes in axial anatomy and morphology from the apex toward the base. All scale bars = 200 μm. (C) Enlargement of Fig. 3A showing the Ω-shaped vascular bundle (vb) within the axis; arrows indicate sporophyll traces diverging from the periphery of the Ω bundle. Slide WP2-0208. (D) Enlargement of Fig. 3B showing the Ω-shaped vascular bundle (vb) surrounded by secretory channels (sc). Note increase in vascular bundle size compared with Fig. 3D. Slide WP2-0271 E/Top (37). (E) Transverse section through basal part of the strobilus showing the Ω-shaped vascular bundle (vb) surrounded by secretory channels (sc); note the slight increase in vascular bundle width compared with Fig. 3D. Slide WP2-0277.

FIGURE 4 Anatomy and organization of *Dorsalistachya quadrisegmentorum*. (A) Longitudinal section through strobilus showing strobilus axis (ax) and vascular bundle (vb), vertically elongated secretory channels (sc), and alternate rows of sporophylls on opposite sides of the strobilus. Sporophylls extend from the axis forming a 2.5–3.0 mm subhorizontal lamina (hl), to which microsporangia (mi) are attached on the abaxial (lower) surface, before abruptly turning upwards to form a 3.0–3.5 mm distal lamiae (dl); the base of the lamina at this point extends downward for a length of 0.5–1.0 mm. Slide WP2-0275 (X2 53). Scale bar = 1 mm. (B) Higher magnification of the Ω-shaped vascular bundle in longitudinal section showing tracheid walls bearing spiral and scalariform thickenings. Slide WP2-0275 (X2 53). Scale bar = 50 μm. (C) Transverse section of the strobilus axis showing stellate-shaped protuberances (arrowed), Ω-shaped vascular bundle (Ω vb), cortex (cx) and microsporangia (mi). Slide WP2-0203. Scale bar = 200 μm.

and typically isodiametric with a diameter of 40–80 μm, though in some places they are somewhat radially elongated (Fig. 7G, H). In longitudinal section parenchymatous cells appear slightly vertically elongated, rectangular and polygonal in shape (Fig. 7F). One or two layers of mesophyll beneath the abaxial epidermis consist of small and mostly isodiametric cells. Secretory cavities and/or idioblasts are often present in the basal portion of the distal lamina, but are absent from the remainder (Fig. 7F–H). The small, terete vascular bundle is generally located in the center of the lamina, though in some sections it appears closer to the adaxial surface (Fig. 7F–J).
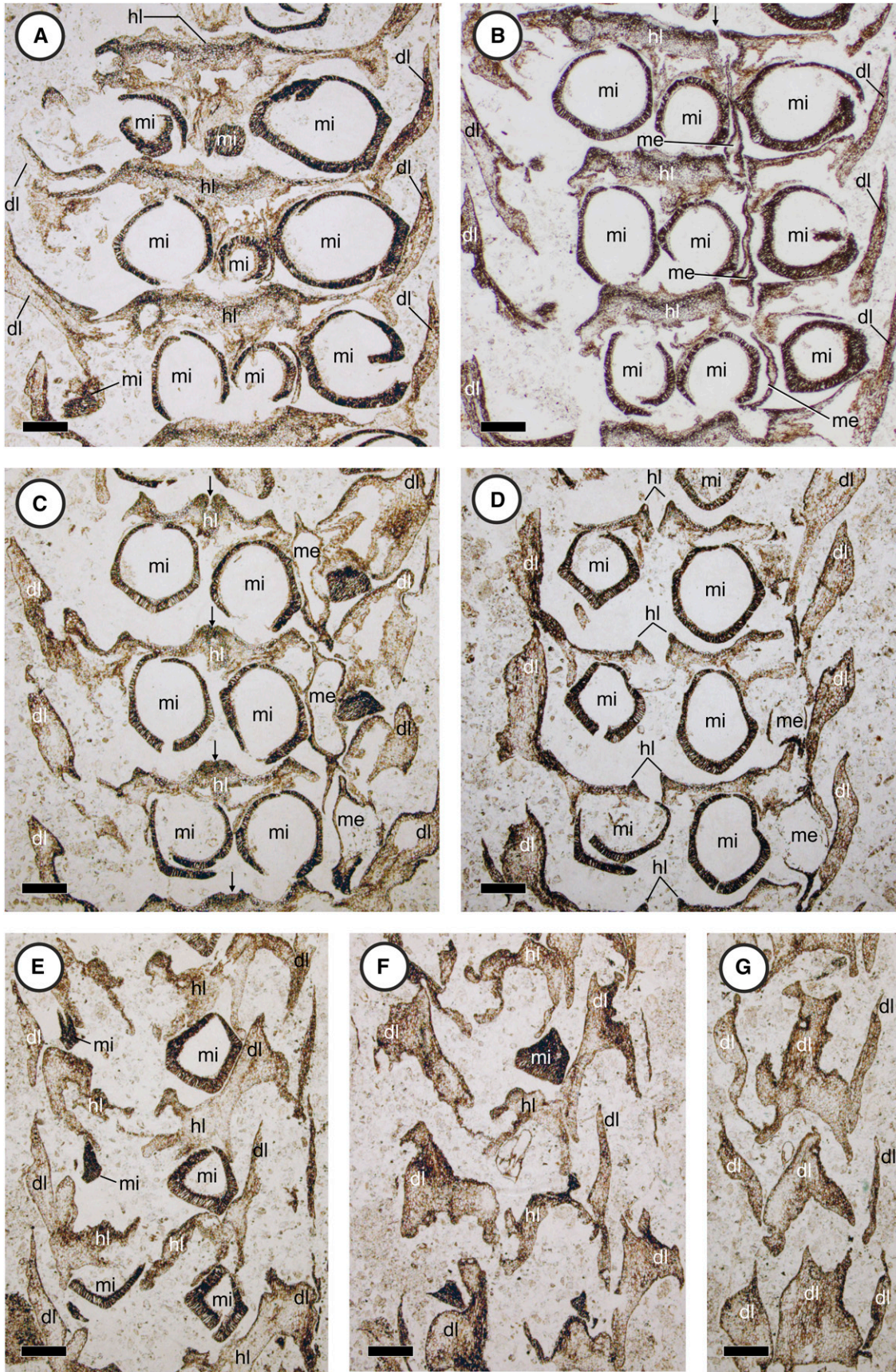
Microsporangia and microspores—In all sections of the strobilus, microsporangia are typically seen close to, or in some cases in organic attachment with, the abaxial surface of the proximal lamina close to its boundary with the strobilus axis (Figs. 4A, 7B, 9A, D, E). In most cases a gap separates the microsporangium from the upper surface of the underlying (proximal) sporophyll segment (Figs. 4A, 5A–E). Each segment bears a single microsporangium on its proximal lamina, such that in total four microsporangia are present on each sporophyll. Because they are positioned equidistant from the cone axis, the four sporangia are seen to be arranged in a shallow arc when viewed in transverse section (Figs. 3A, B, 6A, B).

Individual microsporangia are radially elongated; they reach ca 3 mm long, ca 1.5 mm wide, and up to 2 mm high (Figs. 3A, B, 4A, 5A–G, 6A, B, 9A–C, 10A–E). The proximal area of the microsporangium is subglobose (Figs. 9C, 10A, D, E), whereas the distal area is narrower and more prismatic (Figs. 9C, 10B, D, E). The adaxial surface is rounded, whereas the abaxial surface and lower regions of the lateral surfaces are expanded to form three radially aligned ridges—one median and two lateral (Figs. 9B, 10B–D). Approximately 1.5 mm from the apex of the microsporangium, the proximal abaxial surface is truncated at ca 28 degrees relative to the base of the microsporangium to form an aperture 0.5 × 0.7 mm (Figs. 9A, 10A, C, D). We were unable to detect vascular tissue supplying individual sporangia.

The sporangium wall consists of two zones (Fig. 9F). The outer zone is a single layer of large columnar cells 60–200 μm in radial diameter that are characterized by extremely thick and dark-colored walls (Fig. 9F, G). Overall thickness increases from the proximal end to the distal end and from the upper surface to the lower surface (Fig. 9A–C), where it is thinnest along the central ridge. Viewed in periclinal section, cells of the outer wall appear elongate, their long axis paralleling the long axis of microsporangium; the wall appears to be perforated by micropores (Fig. 9G). The inner zone of the sporangial wall consists of 2–5 layers of cells. Individual cells are 15–30 μm in diameter; in transverse section they appear isodiametric at the ridge but elongated elsewhere on the sporangium (Fig. 9C, F), whereas in longitudinal section all cells appear elongated (Fig. 9A, B).

Dehiscence probably took place along the proximal lower surface of the microsporangium through the open aperture (Figs. 9A,
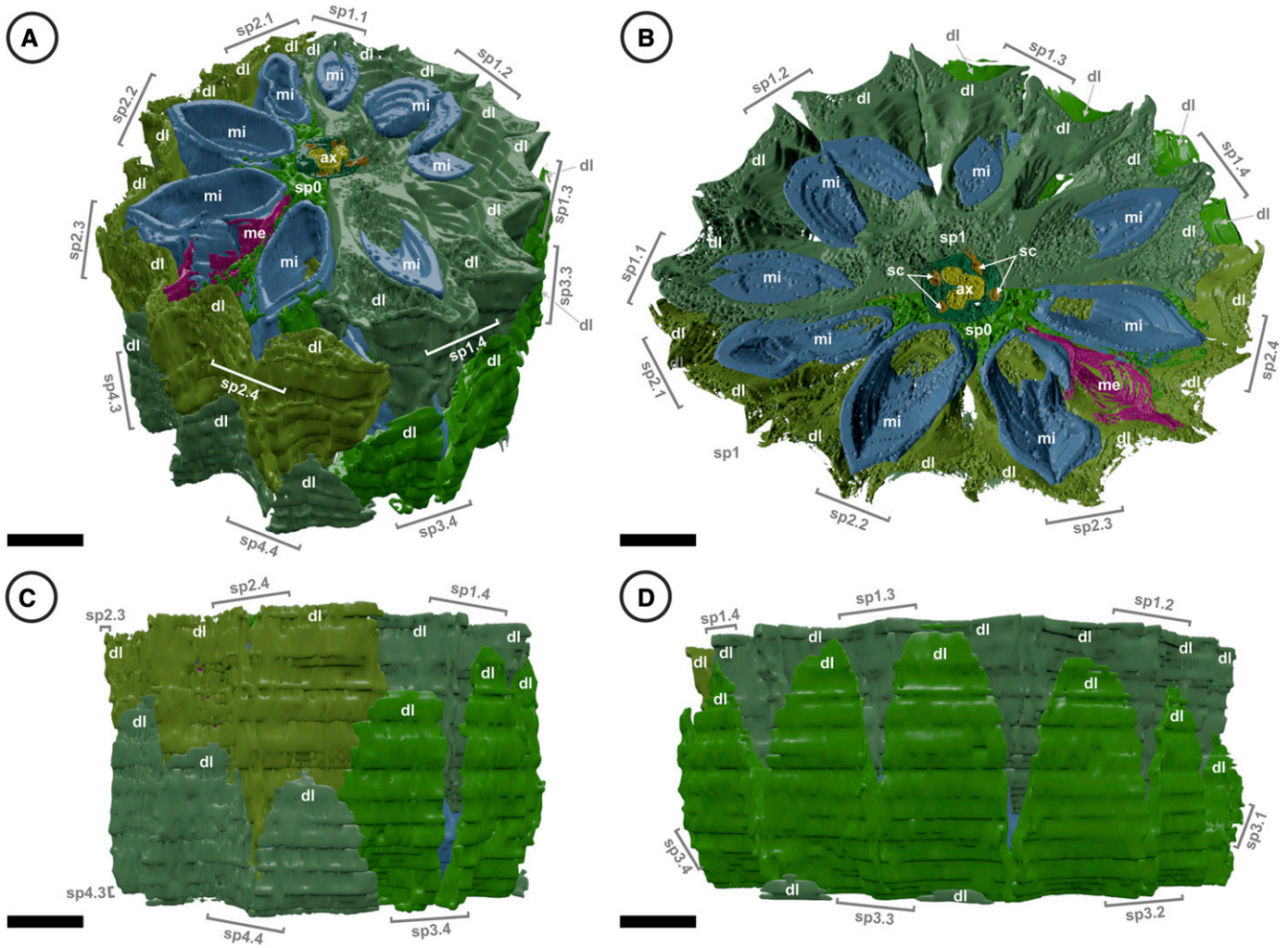
FIGURE 6 Raytraced three-dimensional reconstructions of *Dorsalistachya quadrisegmentorum*. (A) Oblique apex projection showing distribution of microsporangia (mi) and megasporangia (me) within the sporophylls (sp0–sp4) that surround the central axis (ax). Also note the alternating vertical arrangement of the sporophylls, which terminate in distal laminae (dl). (B) Transverse projection of model viewed from the apex showing the distribution of microsporangia (mi) and megasporangia (me) across the sporophylls. Within the axis four secretory channels (sc) surrounding the Ω-shaped vascular bundle (vb) are shown. The most prominent sporophylls (sp1, sp2) best illustrate the division into four segments (sp1.1–4, sp2.1–4), the distal part of each segment further dividing into two distal laminae. (C) Projection showing the vertical face of the strobili showing the alternating vertical arrangement of the half-disciform sporophylls. (D) Projection showing the vertical face of the strobili tangentially from the axis showing arrangement of the half-disciform sporophylls. All scale bars = 1 mm. Also see Appendix S1 and S2 (see Supplemental Data with the online version of this article).

10A, C, D). Although numerous sporangia are split along a thinning of their wall adaxially, toward the midlongitudinal region and along the ridges, this is believed to represent a post-mortem taphonomic phenomenon (e.g., Figs. 3A, B, 5, 6B, 9B). Most of the presumed microsporangia no longer contain microspores, whereas in most of the remainder the remains of the microspores are taphonomically fragmented (Figs. 9C, 11A). The best-preserved microspores are nearly spherical, circular, or rounded-triangular in

outline in polar view, and ca 30 μm in diameter. They possess a comparatively small trilete suture and apparently lack any other surface ornamentation (Figs. 9H, 11A).

According to Permo-Triassic miospore specialist Liu Feng (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, personal communication, 2016), the closest (though imperfect) named comparators among dispersed spore-species are *Patellisporites meishanensis* Ouyang (1962) and

FIGURE 5 Anatomy and organization of *Dorsalistachya quadrisegmentorum*. (A–G) Sequential serial peels, showing tangential longitudinal sections of three rows of sporophylls, through their subhorizontal laminae (hl) to their distal laminae (dl). Four vertical rows of segments at the point where they separate (arrowed in B and C) are shown, together with microsporangia (mi) and a short vertical row of megasporangia (me). Note that microsporangia (mi) are attached on the abaxial surface, leaving a gap to the upper surface of the lower sporophyll subhorizontal part. Slides A–G: WP2-0248 (u/24), WP2-0247 (u/22), WP2-0245 (u/19), WP2-0243 (u/15), WP2-0241 (u/11), WP2-0240 (u/8), WP2-0239 (u/7). All scale bars = 1 mm.
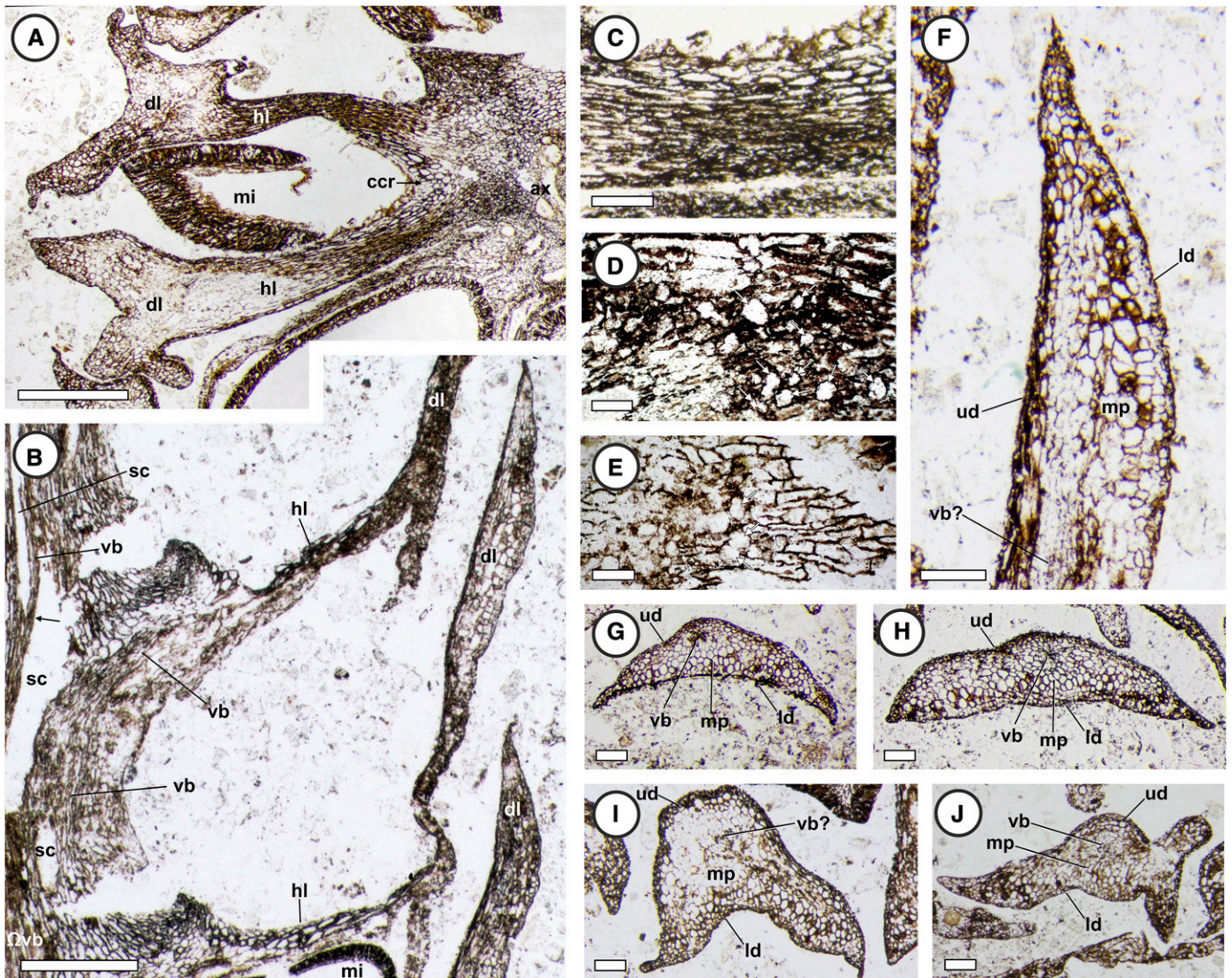
FIGURE 7 Anatomy and organization of *Dorsalistachya quadrisegmentorum* sporophylls. (A) Transverse section showing the anatomy of one quarter of a sporophyll from the proximal attachment to the axis (ax) and the bifurcation into two subhorizontal laminae (hl) at the concave central region (ccr), which encloses a single microsporangium (mi). Each horizontal lamina (hl) divides to produce a pair of distal laminae (dl). Slide WP2-0271 E/Top (37). Scale bar = 1 mm. (B) Longitudinal section through sporophylls showing the anatomy from the axial Ω-shaped vascular bundle (Ωvb) with its secretory channels (sc), through the subhorizontal lamina (hl) to its distal lamina (dl). Vascular bundles (vb) for the sporophyll separate from the axial vascular bundle (Ωvb) one internode (arrow) below the point of entry at the next internode, and then travel along the center of the subhorizontal lamina (hl). Slide WP2-0275 (53). Scale bar = 1 mm. (C) High magnification image showing the hypodermal cells of the subhorizontal lamina in transverse section. At the lateral edge the hypodermis consists of several layers of small sclerenchymatous cells. The cells of the central zone are larger and tangentially elongated. Slide WP2-0271 E/Top (37). Scale bar = 200 μm. (D) High magnification image showing the mesophyll in transverse section. Consisting of parenchymatous cells that are tangentially isodiametric and radially elongated and isolated; round-rectangular idioblasts are dispersed throughout the mesophyll (arrows). Slide WP2-0248. Scale bar = 100 μm. (E) High magnification image showing lower epidermis cells in transverse section. Arrows indicate idioblasts. Slide WP2-0233. Scale bar = 100 μm. (F) Longitudinal section through distal lamina showing the hypodermis (upper dermis = ud), mesophyll (mp), and abaxial epidermis (lower dermis = ld), with putative vascular bundle (vb). Slide WP2-0275 (53). Scale bar = 200 μm. (G–J) Transverse sections through the distal lamina showing cellular anatomy from the apex to the base. The hypodermis (upper dermis = ud), mesophyll (mp), and abaxial epidermis (lower dermis = ld) surround a single vascular bundle (vb) in the center of the lamina. All scale bars = 200 μm. (G) Point near apex. Slide WP2-0208. (H) Midpoint between apex and the subhorizontal lamina. Slide WP2-0271 E/Top (37). (I) Point above the subhorizontal lamina. Slide WP2-0271 E/Top (37). (J) Point below the subhorizontal lamina showing the convoluted shape of the basal protrusion. Slide WP2-0271 E/Top (37).

Densosporites paranulatus Ouyang (1986); the zona is equatorial in the latter but displaced toward the proximal pole in the former, making *Patellisporites* a better match with the microspores observed in *Dorsalistachya*. *Patellisporites meishanensis* is common throughout the Wuchiapingian (upper Permian) of China, extending sporadically into the lower Triassic, and should be sought in other noeggerathialean fossils. *Patellisporites* has not previously been recorded in other noeggerathialean cones.
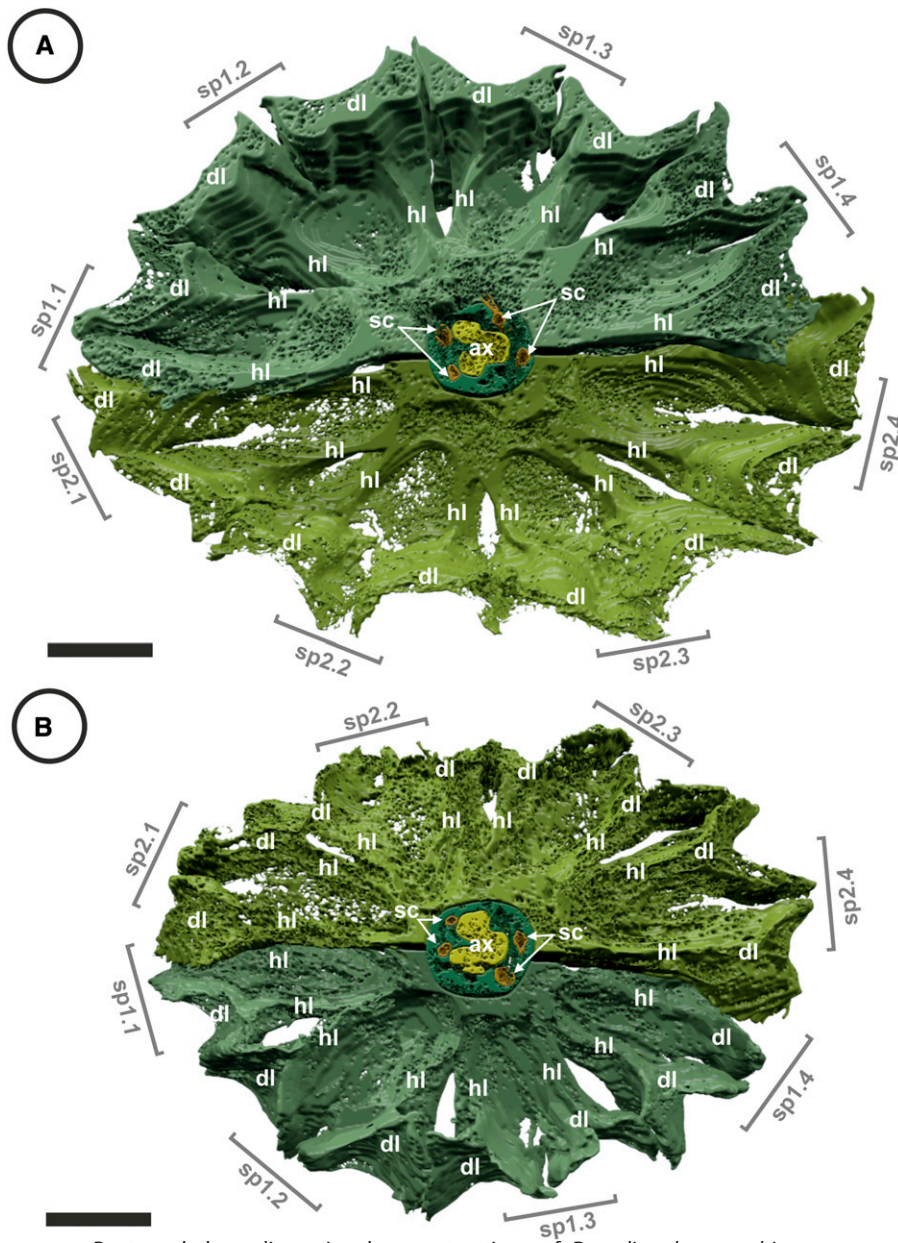
FIGURE 8 Raytraced three-dimensional reconstructions of *Dorsalistachya quadrisegmentorum* showing sporophyll morphology with digital removal of the microsporangia and megasporangia. (A) Slightly oblique projection of model viewed from the apex showing the upper surface morphology, subhorizontal (hl) and distal laminae (dl) of two sporophylls (sp1, sp2) surrounding the axis (ax), which contains four secretory channels (sc). The sporophylls show the division into four segments (sp1.1–4, sp2.1–4), the distal part of each segment further dividing into two distal laminae. (B) Slightly oblique projection of model viewed from the base showing the lower surface morphology of the two sporophylls (sp1, sp2) seen in A. All scale bars = 1 mm. Also see Appendix S1 and S2 (see Supplemental Data with this article).

Megasporangia and megaspores—The majority of sporophylls bear only microsporangia, but the remainder produce one megasporangium alongside four microsporangia (Figs. 3B, 5B, D). Where present, the megasporangia occupy the space between the horizontal lamina and distal lamina of the sporophyll holding the third and fourth microsporangia (Figs. 3B, 5B–D, 6A, B). When the strobilus is viewed laterally, megasporangia are seen to be distributed in short, vertical rows of three or four megasporangia,

the rows apparently being distributed randomly throughout the strobilus.

The megasporangium is peripterous, the wing being moderately well developed and 0.7–0.9 mm wide (Figs. 10F, G, 11A–C). The dimensions of the megasporangium resemble those of the microsporangium, though the cavea (void) surrounding the former is much smaller than that surrounding the latter. The cavea of the megasporangium approximates 1.5 mm in radial direction, 1 mm in tangential direction, and up to 2 mm in vertical direction (Figs. 10F, G, 11A, B); this allows the megasporangium to become vertically elongated, whereas the microsporangium is radially elongated. Unfortunately, we were unable to discern details of the attachment to the sporophyll.

The megasporangium wall is bilayered and 50–150 µm thick. The dark-colored columnar cells that form the outer wall have a radial diameter of 8–20 µm, whereas the inner wall consists of approximately six layers of cells each 2–10 µm in radial diameter (Fig. 11C). Putative megaspores within the megasporangia are typically poorly preserved and fragmentary (e.g., Fig. 11A); it is the approximate alignment of the fragments (Fig. 11D) to describe a crude circle within some megasporangia that implies the presence of only one functional megaspore per megasporangium.

SYSTEMATICS

Phylum **Tracheophyta** Sinnott (1935) ex Cavalier-Smith (1998).

Subphylum **Euphyllophytina** sensu Crane & Kenrick (1997).

?Class (paraphylon) **Progymnospermopsida** C.B. Beck (1960b).

(arguably incertae sedis at Class level; see Discussion).

Order **Noeggerathiales** sensu Němejc (1931).

Emended diagnosis—Heterosporous plants with compact, pedunculate, bisporangiate strobili. Sporophylls usually emitted linearly rather than helically, bipartite. Sporangia sessile, attached to adaxial (or rarely abaxial) surface of sporophyll. Strobilar axis (where known) with bilateral vascular bundle. Foliage (where known) pinnate and multiveined.

Family **Discinitaceae** W. Remy & R. Remy (1977), emend. S.J. Wang & A.R.T. Spencer.
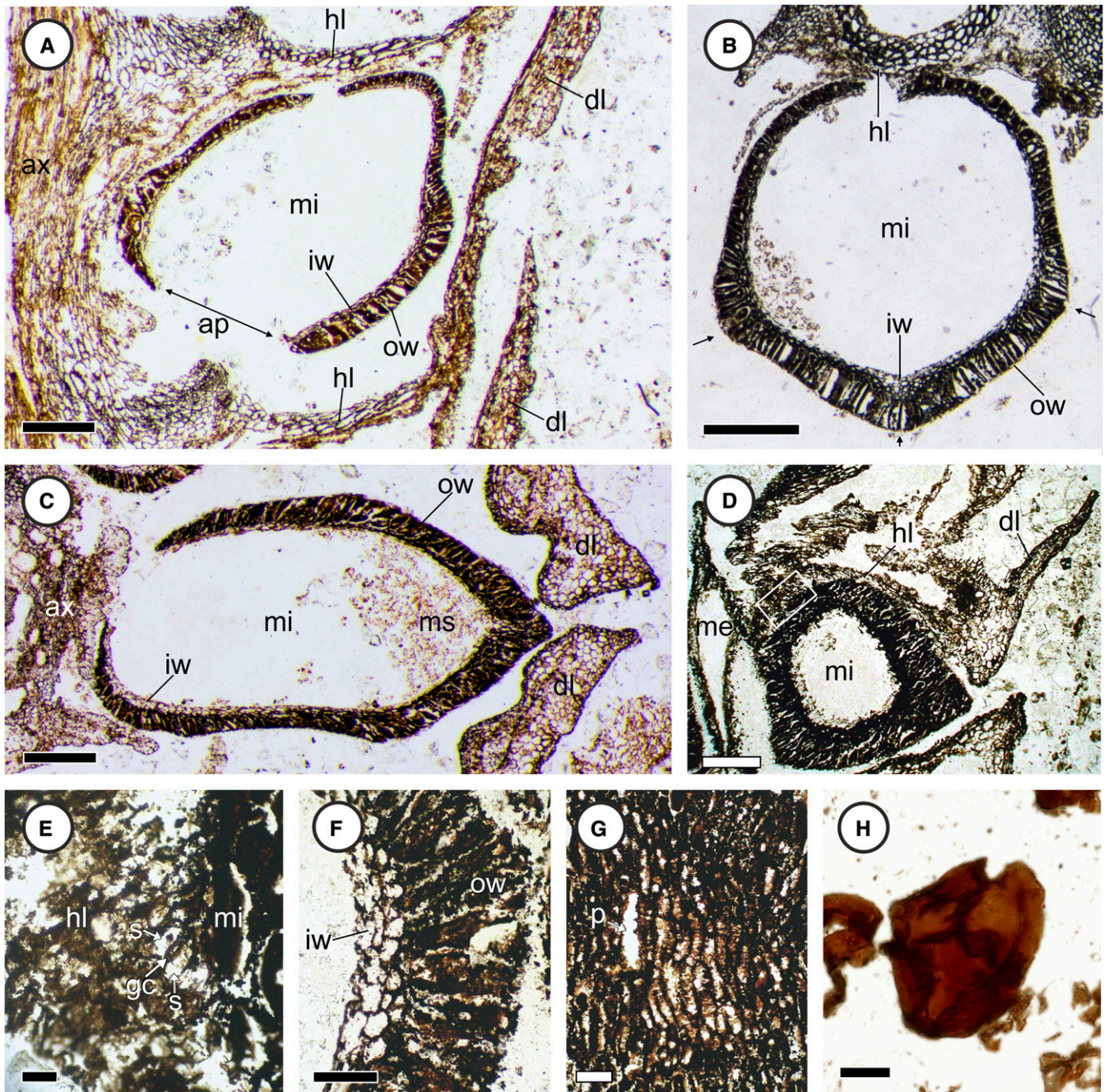
FIGURE 9 Anatomy and morphology of the microsporangium of *Dorsalistachya quadrisegmentorum*. (A) Longitudinal section through a single microsporangium (mi), showing the attachment to the horizontal lamina (hl) above, the proximal aperture (ap) facing the axis (ax), and the inner (iw) and outer (ow) microsporangial walls. Slide WP2-0271 E/Top (53). Scale bar = 0.5 mm. (B) Tangential section through a single microsporangium (mi) containing microspores, showing the attachment to the horizontal lamina (hl) above, the inner (iw) and outer (ow) microsporangial walls, and the three ribs (arrows). Slide WP2 0247 (u/18). Scale bar = 0.5 mm. (C) Transverse section through a single microsporangium (mi), showing the inner (iw) and outer (ow) microsporangial walls, and the remaining microspores (ms) distally. Slide WP2-0271 E/Top (37). Scale bar = 0.5 mm. (D) Obliquely longitudinal section of a sporophyll showing the horizontal lamina (hl) to distal lamina (dl), with a microsporangium (mi) attached to the horizontal lamina lower surface. A single megasporangium (me) is also present. White boxed area is enlarged in Fig. 9E. Slide WP2-0246. Scale bar = 0.5 mm. (E) Enlargement of boxed area in Fig. 9D showing the organic connection of the microsporangium (mi) to the horizontal lamina (hl) of a segment. A single possible stoma possesses putative paired guard cells (gc) and subsidiary cells (s). Slide WP2-0246. Scale bar = 50 μm. (F) Enlargement of a part of transverse section of the microsporangium showing the detail of the sporangial wall, divisible into outer wall (ow) and inner wall (iw). Slide WP2-0264. Scale bar = 100 μm. (G) Paradermal section through the sporangium wall showing longitudinally elongate cells and micropores (p) through wall. Slide WP2-0248. Scale bar = 100 μm. (H) High magnification image of a well-preserved microspore showing the trilete mark. See Fig. 11A for location of spore. Slide WP2 0271 E/Top (36). Scale bar = 10 μm.
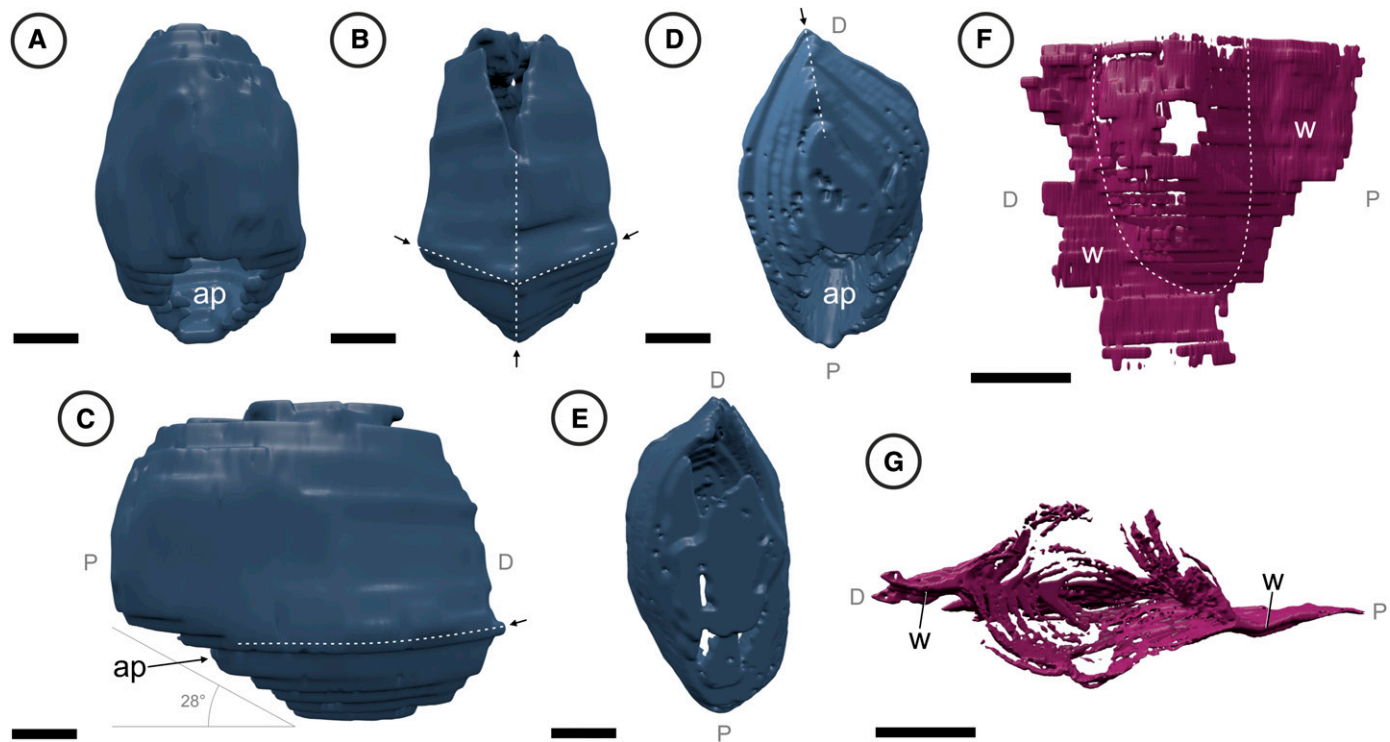
FIGURE 10 Raytraced three-dimensional reconstructions of *Dorsalistachya quadrisegmentorum* showing morphology of the microsporangia and megasporangia. (A–E) Microsporangia. (A) View of proximal surface, showing the basal aperture (ap). (B) View of distal surface; arrows and dashed lines indicate the three ridges. (C) Lateral view with the proximal (P) surface to the left and distal (D) surface to the right; the basal aperture (ap) truncates the proximal surface at an angle of ca 28°. The arrow and dashed line indicate a single ridge that circumscribes the microsporangium. (D) Basal view showing the abaxial surface from proximal (P) to distal (D) with the midline ridge (arrow and dashed line) and the basal aperture (ap). (E) Adaxial view showing the top surface from proximal (P) to distal (D). All scale bars = 500 µm. (F, G). Megasporangia. (F) Lower portion of a single megasporangium showing the wings (w) in both proximal (P) and distal (D) directions. The dashed line indicates the position on the internal cavity. (G) View of the lower portion seen in Fig. 10F from the apex showing the cross-sectional shape. Both scale bars = 0.5 mm. Also see Appendix S1 and S2 (see Supplemental Data with this article).

Emended diagnosis—Sporophylls whorled; proximal part of sporophyll strongly discoid, distal part of sporophyll upturned and dissected into small laminae. Sporangia attached to the adaxial surface of the proximal part, numerous, arranged in several rings.

Genera—*Discinites* Feistmantel (1880), *Saarodiscites* Hirmer (1940).

Satellite genera—*Yuania* Sze (1953), *Palaeopteridium* Kidston (1923), *Saaropteris* Hirmer (1940).

Note—Specimens of this family are all preserved as compression–impressions so their anatomy is unknown. *Russellites* Mamay (1968), obtained from the Cisuralian (lower Permian) of Texas and previously considered to belong to the family, is now recognized as being a junior synonym of *Yuania* (Wang and Chaney, 2010). Wang and Wang (1986) described *Discinites sunjiagouensis* Z.-Q. Wang & L.-X. Wang from the latest Permian Sunjiagou Formation in North China. However, as the sporophylls of this species are half-discs, they more likely belong within the genus *Lacoea* C.B. Read of the family Noeggerathiaestrobaceae.

Family **Tingiostachyaceae** Z. Gao & B.A. Thomas (1987), emend. S.J. Wang & A.R.T. Spencer.

Emended diagnosis—Sporophylls spiral or whorled; proximal part of sporophyll vaguely disc-shaped or dissected into segments, distal part of sporophyll upturned and dissected into small laminae. Sporangia attached to the adaxial surface of the proximal part, few, arranged in a single ring.

Genera—*Tingiostachya* Kon'no (1929), *Paratingiostachya* Sun et al. (1999), strobili of the whole-plant *Paratingia wudensis* J. Wang et al. (2009) + *Tingia unita* J. Wang (2006) + *Plagiozamites oblongifolius* Halle (1927).

Satellite genera—*Tingia* Halle (1954), *Paratingia* Zhang (1987), *Plagiozamites* Zeiller (1894).

Note—Specimens of this family are all preserved as compression–impressions so their anatomy is unknown. The spiral arrangement attributed to the sporophylls is contentious. On the basis of a large collection of strobili of *Paratingia*, Wang et al. (2012) documented whorled sporophylls that were partially fused proximally but distally dissected into small laminae. Similarly, a large proportion of known specimens of the strobili of *Tingia* demonstrate that the sporophylls are whorled rather than spiraled. This topic will be the subject of a subsequent paper produced by some of the present authors (J. Wang et al., unpublished manuscript).
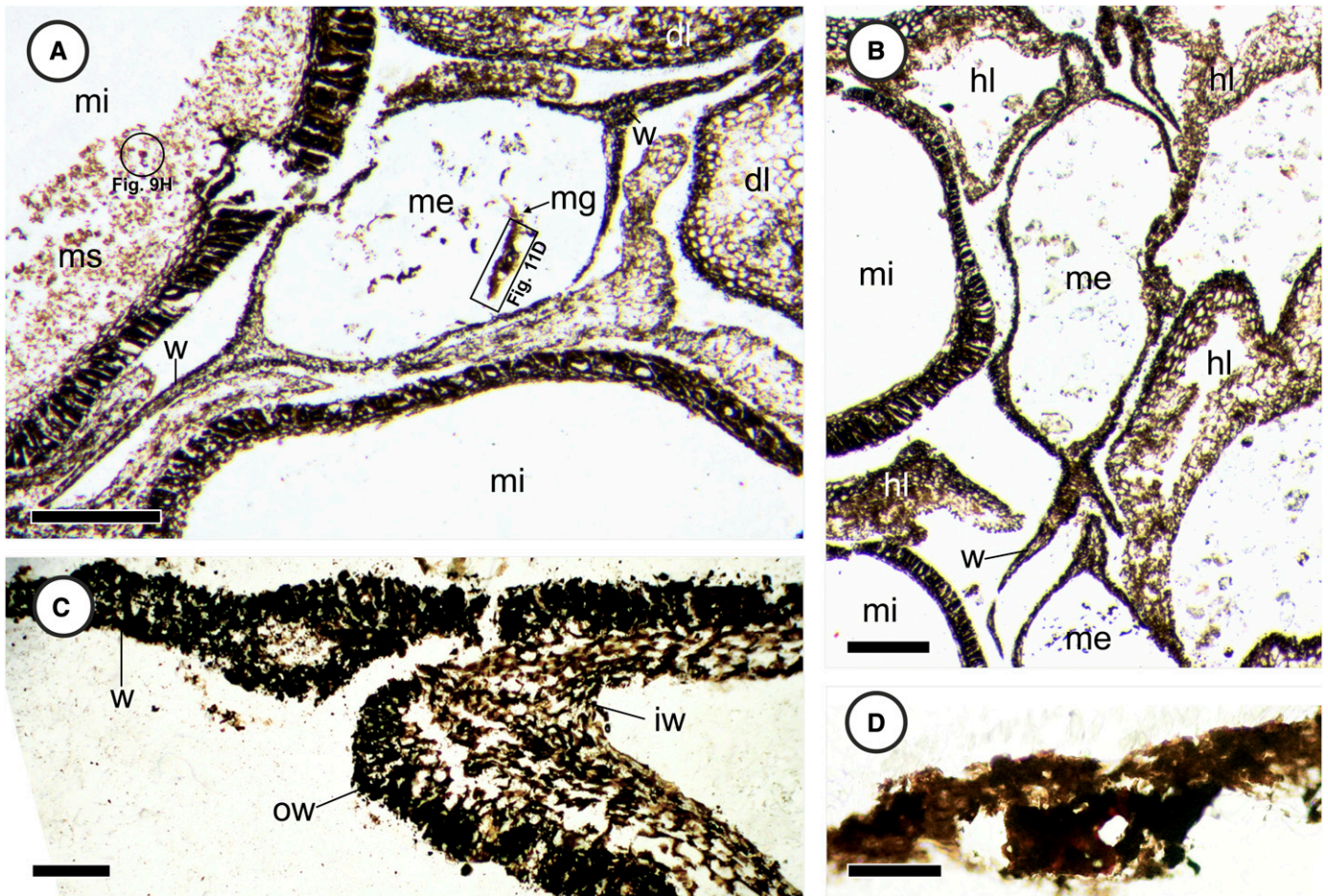
FIGURE 11 Anatomy and morphology of the megasporangia of *Dorsalistachya quadrisegmentorum*. (A) Transverse section through a single megasporangium (me), positioned between two microsporangia (mi). The megasporangium displays two wings (w) in the proximal and distal direction and contains the remains of a single megaspore (mg). Slide WP2-0271 E/Top (36). Scale bar = 0.5 mm. (B) Tangential section through a single megasporangium, showing the elongate shape and possible bifurcating wings at the base (w). Slide WP2 0247 (u/18). Scale bar = 0.5 mm. (C) Enlargement of a part of the megasporangium showing the detail of the sporangial wall and wing, differentiating inner wall zone (iw) and outer wall zone (ow). Slide WP2-0265. Scale bar = 100 μm. (D) Enlargement of a piece of fragmented megasporangium shown in Fig. 11A. Slide WP2-0271 E/Top (36). Scale bar = 50 μm.

Family **Noeggerathiaestrobaceae** (= Noeggerathiaceae) Němejc (1963), emend. S.J. Wang & A.R.T. Spencer.

Emended diagnosis—Sporophylls distichous; proximal part of sporophyll semicircular, distal part upturned and dissected into small laminae. Sporangia attached to adaxial surface of proximal part, numerous, arranged in several rings.

Genera—*Noeggerathiaestrobus* O. Feistmantel (1872); *Archaeonoeggerathia* W. Remy and R. Remy (1986); *Lacoea* C.B. Read (1946).

Satellite genera—*Noeggerathia* Sternberg (1821); *Palaeopteridium* Kidston (1923); *Conchophyllum* Schenk (1883).

Note—Specimens of this family are all preserved as compression–impressions so their anatomy is unknown. As mentioned above, *Discinites sunjiagouensis* sensu Z.-Q. Wang and L.-X. Wang (1986) belongs within *Lacoea* C.B. Read.

Family **Dorsalistachyaceae** S.J. Wang & A.R.T. Spencer, fam. nov.

Diagnosis—Sporophylls distichous, alternate; proximal part of sporophyll semicircular, dichotomous, distal part upturned. Sporangia abaxial, arranged in a single crescent. Microsporangia with proximal lower surface dehiscence. Vascular bundle of strobilar axis (and petiole and rachis of correlated foliage) bilaterally symmetrical, sporophyll traces diverging from the two opposed margins. Secretory cavities within cortex of both strobilar axis and sporophyll.

Type genus—*Dorsalistachya* S.J. Wang & A.R.T. Spencer, gen. nov.

Satellite genus—*Plagiozamites* Halle (1927).

Note—This family presently consists only of anatomically preserved disarticulated organs that are clearly attributable to Noeggerathiales.

Dorsalistachya quadrisegmentorum S.J. Wang & A.R.T. Spencer, gen. et sp. nov.

Diagnosis—Strobilus slender, cylindrical, ca 10 mm in diameter. Vascular bundle of axis inverted Ω-shaped in transverse section;

metaxylem tracheids with scalariform thickenings; several longitudinal secretory cavities within cortex. Sporophylls divided into four vertically aligned segments that undergo one further division before curving upwards. Proximal portion of sporophyll horizontal, semicircular; medial portion dichotomous; distal portion lanceolate, concave, upturned but with downward projection. Sporophylls bearing four microsporangia occasionally also one megasporangium. Microsporangia radially elongated. Microspores trilete, unornamented. Megasporangia with well-developed wings, organized in short vertical rows randomly distributed throughout the strobilus.

Etymology—The genus epithet is derived from *dorsalis*, from the Latin *dors* for belly (referring to the attachment of sporangia to the abaxial side of the sporophyll) and *stachya*, from the Latin *stachys* (for ear of corn, referring to the comparatively slender cone). The species epithet refers to the sporophylls being divided into four segments and is derived from *quadri* (from the Latin *quattuor*, for four), and *segmentorum* (from the Latin *segmentum*, for segments).

Holotype here designated—HP2007-1-A (slabs HP2007-1 B–F; serial wafers from slab HP2007-1 C; acetate peels in transverse, tangential, and median longitudinal sections from slab HP2007-1E). Figures 3–11.

Age—Wuchiapingian–Changhsingian stages of the Lopingian Epoch (late Permian Period).

Location—Xuanwei Formation, Huopu coal mine, Guizhou Province, southwestern China.

Depository—Institute of Botany, Chinese Academy of Sciences, Beijing, China.

DISCUSSION

I. The nature of *Dorsalistachya*

Homology assessments—The *Dorsalistachya* "cone" is consistent with those of previously described Noeggerathiales in size and shape, and in having alternating rather than whorled or helically inserted sporophylls (Němejc, 1931; Browne, 1933; Beck, 1981; Wang, 2008; Wang et al., 2009, 2012). Nonetheless, it diverges considerably in gross architecture from the reproductive organs of any other known plant. Its most noteworthy features are: (1) the bilateral rather than radial symmetry of the vasculature of the central axis; (2) the strongly three-dimensional dichotomies undergone by the "sporophyll"; and (3) the abaxial attachment on the "sporophylls" of the globose sporangia. Indeed, features (1) and (2) are sufficiently divergent to challenge the conventional descriptive terminology that we have applied in earlier sections of this paper. We should also note at the outset that our assumption that these structures are not fertile zones resembling positionally those of the progymnosperm *Cecropsis* (Stubblefield and Rothwell, 1989) is based only on comparison with cones of other noeggerathialeans lacking anatomical preservation.

(1) As the cone appears near circular in outline toward its distal end when viewed in transverse section, it appears superficially to be radially symmetrical. When considering the compact concentrations of reproductive organs that are collectively termed cones/strobili in other plant groups, radial symmetry (or a condition only slightly divergent from radial symmetry) is in practice a defining property of the term "cone", along with occupying a terminal position on the subtending axis. Radial symmetry characterizes the cones found in many zosterophyllopsids, lycopsids, sphenopsids, cycadopsids, coniferopsids, and bennettitaleans, and until the current study, it was also thought to reliably characterize noeggerathialeans. However, that assumption was based entirely on compression–impression material lacking evidence of vascular architecture. The omega-shaped vascular strand of the "cone" axis of *Dorsalistachya* is strongly bilaterally symmetrical, and when examined in detail from a dorsiventral viewpoint, it becomes evident that the "sporophylls" are emitted not helically but rather distichously and oppositely and alternately, in accordance with the bilateral symmetry of the vasculature. Thus, the cones are fundamentally bilaterally symmetrical, even though the three-dimensionality of the "sporophylls" gives the superficial appearance of radial symmetry. Given these characteristics, it might be more appropriate to describe *Dorsalistachya* as a "pseudostrobilus" rather than a strobilus.

(2) The broadly similar diameter, outline, and trace shape of the rachis of the *Plagiozamites* megaphyll and the "cone axis" of *Dorsalistachya* strongly suggests homology of the leaf and the pseudostrobilus. If so, the "strobilar axis" would be more appropriately described as a pseudostrobilar rachis, and despite its complexity, the pseudostrobilus would strictly represent a single sporophyll (G. W. Rothwell, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon, USA, personal communication, 2015). This would mean that each of the numerous quadrifurcate "sporophylls" (described above in the diagnosis) borne on each pseudostrobilar rachis is strictly homologous with a pinna, despite the fact that the pinna-homologs are much smaller than the vegetative pinnae and have radically different morphologies that extend into three dimensions rather than just two.

(3) Each pinna-homolog of *Dorsalistachya* generates four abaxial sporangia. The abaxial position occupied by the microsporangia was unexpected because many previous reports of noeggerathialean fossils that lack anatomical preservation have interpreted sporangial attachment as adaxial (Browne, 1933; Boureau, 1964; Bierhorst, 1971; Bateman and DiMichele, 1994). Although Hirmer and Guthörl (1940) initially considered sporangia in the noeggerathialean strobilus *Saarodiscites* to be attached abaxially, their view was subsequently challenged by Daber (1957), whose assertion of adaxial attachment became firmly established in the subsequent literature (Boureau, 1964). Adaxially positioned sporangia are typical of lycopsids and most sphenopsids (Bateman and DiMichele, 1994), but this character has not previously been reported for any eusporangiate fern or any progymnosperm. Critical re-evaluation of sporangial insertion in other noeggerathialean strobili, in search of other taxa possessing abaxial sporangia, is now clearly warranted. It seems to us most likely that the abaxial sporangia represent a condition that was evolutionarily derived from an adaxial ancestor via ectopic expression (e.g., Frohlich, 2002).

Heterosporous features—Although several species of noeggerathialean strobilus had already been shown to be heterosporous (Němejc, 1937; Bek and Šimůnek, 2005), the mode of expression of heterospory within the Huopu strobilus is exceptional. Microsporangia dominate numerically over megasporangia in most heterosporous pteridophytes that do not segregate the two genders of sporangia into separate cones (Bierhorst, 1971; Bateman and DiMichele, 1994), but it is remarkable for the two "genders" of sporangium

to differ as radically in morphology and anatomy as they do in *Dorsalistachya* (Bateman and DiMichele, 1994).

Indeed, the vertical rows of megasporangia within the strobilus appear to have been added as a developmental afterthought, squeezed in between a symmetrical array of microsporangial rows; this pattern is particularly evident when the cone is viewed in transverse section (Figs. 3B, 5A–D, 6A, B). It is tempting to view this peculiar architecture as a teratological phenomenon (Bateman and DiMichele, 2002; Rudall et al., 2011), but this interpretation is contradicted by the unequivocal presence of the megaspore within. Also, expression of megasporangia in vertical rows within bisporangiate cones has occasionally been observed in the extant lycopsid *Selaginella* P. Beauv., some authors arguing that it reflects gravitational pooling of auxin within horizontally oriented cones (e.g., Horner and Arnott, 1963). Although we do not know the orientation of the strobili or the structure of the *Dorsalistachya* plant, as the fossils were found fragmented, reconstructions of noeggerathialeans based on articulated plants preserved in situ by volcanic ash from the Cisuralian (lower Permian) of China demonstrate that their cones were held vertically and positioned in the center of a previously vegetative rosette of branches (Wang et al., 2009, 2012).

Bateman and DiMichele (1994) estimated that the monomegasporous level of heterospory had been achieved independently by five different land-plant lineages: (1) selaginellalean plus isoetalean lycopsids; (2) some extinct equisetalean sphenopsids; (3) leptosporangiate hydropterid water-ferns: (4) derived progymnosperms plus seed-plants; and (5) possibly the noeggerathialean compression/impression genus *Discinites* (Němejc, 1937; Bek and Šimůnek, 2005), which Bateman and DiMichele tentatively ascribed to the progymnosperms. Monomegaspory within the strobili of *Dorsalistachya* clearly demonstrates that during the Permian the Noeggerathiales had reached a level of reproductive sophistication similar to that achieved by lycopsids and sphenopsids in the preceding Carboniferous Period. In particular, the Mississippian sphenopsid *Protocalamostachys farringtonii* R.M. Bateman was able to develop both megasporangia and microsporangia in different sporangia borne on the same quadripartite sporangiophore (Bateman, 1991). Also, by the Pennsylvanian, the sphenopsid *Calamocarpon insignis* Baxter had achieved monomegaspory (Bateman and DiMichele, 1994), albeit in cones that were more strongly and more conventionally developmentally canalized; its megasporangia are typically concentrated toward the base of most bisporangiate cones and matured earliest, whereas we infer simultaneous maturation in the *Dorsalistachya* cone.

Functional morphology—A winged sporangium of this nature is unique to the cone of the *Dorsalistachya* plant. The monomegaspory and wing cause the megasporangium to superficially resemble a seed, though this appearance is misleading; it possesses neither megasporangial modification for reception and retention of the male gametes prior to fertilization nor an enclosing integument (Bateman and DiMichele, 1994; Hilton and Bateman, 2006). The closest analog among pteridophytes is found in some of the more derived isoetalean clubmosses, but here the wing extends horizontally rather than vertically and originates from the tissue of the sporophyll rather than the sporangium.

We suggest that the winged megasporangium of *Dorsalistachya* assisted wind dispersal in a similar way to bona fide winged seeds (Greene and Johnson, 1989) such as those of contemporaneous cordaitaleans (Wang et al., 2003)—a conclusion supported by the

apparent absence of dehiscence structures in the megasporangia that would have allowed release of the megaspore alone. However, it would have been necessary to first shed the sporophylls that tightly envelop the winged megasporangia (Figs. 3B, 5A–C, 6A, B) before the megasporangia could disperse. We have observed within the Huopu mine succession isolated sporangia and sporophylls, together with cone axes that have retained only the basal parts of the sporophyll lamina, though we cannot be certain that the disassembly of these cones was the result of routine abscission rather than post-mortem taphonomic processes (Neregato et al., 2016).

Although the apparent demise of the last noeggerathialeans in the Triassic (Boureau, 1964; Sun et al., 1995; Taylor et al., 2009) may have been the result of competition with ascendant groups such as conifers, it is possible that it can be at least partly attributed directly to their heterosporous life history. Heterospory is largely a feature of hydrophilic plants (Bateman and DiMichele, 1994), which are comparatively vulnerable to restricted availability of free water. Although the Noeggerathiales survived the end-Permian extinction, they had passed their Permian acme and were already declining in species numbers (Greene and Johnson, 1989; Bond et al., 2010). They were primarily restricted to low-latitude wetlands in southern Cathaysia that suffered aridification during the Triassic (Zhao et al., 1980; Sun et al., 1995), the drying climate being the most likely key to the extinction of these wetland plants.

II. Comparisons of *Dorsalistachya* with previously described taxa— When attempting to assign a species to higher taxa it is important to distinguish between the circumscriptions of those taxa, the evolutionary relationships among them, and the respective formal ranks to which they are assigned. All three properties are linked and require a comparative approach, but they should not be conflated. When attempting to place the genus *Dorsalistachya*, it is important to note that an entirely passive approach, simply placing the genus in a pre-existing taxonomic pigeonhole, may be deemed inappropriate with respect to limited current understanding of the most likely pigeonhole, Noeggerathiales.

Noeggerathialeans have been viewed by previous authors variously as sphenopsids, eusporangiate ferns, leptosporangiate ferns, progymnosperms, or none of the above (i.e., constituting a Class-level taxon in their own right). Thus, it is not surprising that the rank attributed to the group has also varied wildly, fluctuating between Phylum/Division (Zimmermann, 1959; Boureau, 1964), Class, and more commonly Order. It is therefore essential that we ask whether *Dorsalistachya* is indeed most appropriately viewed as a noeggerathialean, and if so, to what degree circumscription of Noeggerathiales should be modified to accommodate the new cone and what taxonomic rank is most appropriately occupied by the recircumscribed higher taxon.

Comparison with relevant Classes of vascular plants—*Classes readily dismissed as being of close affinity*—The strobilus described here as *Dorsalistachya* is both heterosporous and heterosporangiate (viable spores are bimodal in size, the two modes being produced in separate sporangia). The holotype cone produced both microsporangia and megasporangia, and thus deviated from the reproductive organization that characterizes coeval gymnospermous seed-plant groups such as early-diverging pteridosperms, cycads, ginkgos, and conifers—all plants that combine microsporangia and megasporangia only in rare teratological individuals (e.g., Rudall et al., 2011).

Moving on to consider pteridophytic groups, those capable of emulating *Dorsalistachya* by producing compact strobili include the more derived portion of the lycopsid clade, all sphenopsids, and (by definition) all noeggerathialeans. Strobilar axes of both lycopsids and sphenopsids have radially symmetrical steles that differ substantially from the bilateral inverted Ω-shaped vascular bundle observed in the axis of *Dorsalistachya*. Lycopsids are further differentiated from *Dorsalistachya* by their helically inserted sporophylls that bear sporangia on the adaxial surface of the sporophyll, rather than being distichous with abaxial sporangia. Sphenopsids are further differentiated from *Dorsalistachya* by possessing sporangiophores that are whorled and produce pedicellate sporangia on the adaxial surface, in contrast with the distichous, alternate sporophylls of *Dorsalistachya*.

Eliminating these higher taxa leaves us to consider only ferns and progymnosperms. Progymnosperms are an exclusively Paleozoic group that is most commonly treated taxonomically as a Phylum/Class but is also widely viewed as being paraphyletic and containing the likely ancestor of all seed-plants (e.g., Beck and Wight, 1988; Rothwell and Serbet, 1994). Morphological cladistic studies strongly suggest that the group lacks close living relatives (e.g., Doyle and Donoghue, 1986; Hilton and Bateman, 2006), which leaves its classification largely a matter for debate among paleobotanists. By contrast, 'ferns' sensu Kenrick and Crane (1997) (i.e., nonsphenopsid monilophytes) retain a relatively good taxonomic representation in the extant flora that permits construction of molecular phylogenies (Pryer et al., 2004; Rai and Graham, 2010; Lehtonen, 2011; Grewe et al., 2013; Knie et al., 2015). Admittedly, several morphologically divergent higher taxa of Paleozoic ferns sensu lato—a much broader and less cohesive phylogenetic grouping than nonsphenopsid monilophytes studied by neobotanists—also lack close living relatives (e.g., Iridopteridales, Cladoxylales, Zygopteridales, Stauropteridales), but none of these groups bears a close resemblance to *Dorsalistachya*.

Ferns sensu lato—Sporangium morphology alone is sufficient to reject a close relationship between *Dorsalistachya* and leptosporangiate ferns, thereby restricting comparison to the morphologically and taxonomically diverse paraphyletic group informally termed "eusporangiate ferns". Driven primarily by molecularly determined phylogenies, most recent classifications based on extant ferns have circumscribed four groups of equal rank, three of them eusporangiate—Equisetopsida (representing "Sphenopsida" as discussed in the preceding paragraphs), Psilotopsida (Psilotales plus Ophioglossales), and Marattiopsida—and one leptosporangiate—Polypodiopsida. Circumscription into these four major groups has become widely accepted, the main outstanding difference of taxonomic opinion being whether these four extant monophyletic taxa are better treated as Subclasses (e.g., Christenhusz and Chase, 2014) or Classes (e.g., Smith et al., 2006). However, the molecular phylogenetic relationships among the four groups actually remain equivocal, other than reliably agreeing that Marattiopsida are sister to Polypodiopsida (cf. Pryer et al., 2004; Rai and Graham, 2010; Lehtonen, 2011; Grewe et al., 2013; Knie et al., 2015). Confidence in inferred relationships among higher taxa of ferns deteriorates further when considering the few more radical morphological phylogenies that have incorporated extinct fern groups (e.g., Rothwell and Nixon, 2006).

Many morphological differences separate Marattiopsida from *Dorsalistachya*, not least the absence of any feature that even vaguely resembles a reproductively specialized cone; Marattiopsida simply bear the (reliably homosporous) eusporangia on the abaxial surface of otherwise normal ultimate pinnae of their large, highly pinnate fronds. All Psilotopsida are small, herbaceous, rhizomatous plants that are reliably homosporous. Although unequivocal fossil evidence of the group does not extend further back in time than the earliest Cenozoic (Rothwell and Stockey, 1989), molecular clock methods suggest that they diverged from other pteridophytes at some point between the late Devonian and late Pennsylvanian (Rothfels et al., 2015). Psilotales lack any structure that could legitimately be termed a cone, instead bearing sporangia at the junction of the fertile pinna and stem, either singly or in clusters of three. Comparison with Ophioglossales appears more encouraging, as the eusporangia of *Ophioglossum* L., *Helminthostachys* Kaulf., *Mankyua* B.Y. Sun, M.H. Kim & C.H. Kim, and *Botrychium* Sw. appear to be borne on at least distally naked axes—they form compact, bilaterally symmetrical structures that resemble cones and are generally termed "fertile pinnae", "fertile pinnules" or, less specifically, "fertile spikes" (though the term "cone" could not legitimately be applied if the sporangia are actually borne on very narrow laminae: G. W. Rothwell, personal communication, 2016). In addition, *Botrychium* is also famously the only genus of extant ferns to show putative secondary cambial activity (Stevenson, 1980), though its "secondary xylem" is viewed by some workers merely as aligned metaxylem representing exceptionally slow but nonetheless determinate growth (Rothwell and Karrfalt, 2008). Until the advent of molecular phylogenetics, these observations led to occasional suggestions that Ophioglossales were direct descendants of Paleozoic progymnosperms (Kato, 1988). Overall, *Dorsalistachya* could credibly be viewed as an early-divergent ophioglossalean.

Nonetheless, there are sufficient morphological differences evident between *Dorsalistachya* and any of the four Classes/Subclasses of extant ferns that we remain uncomfortable assigning *Dorsalistachya* (and other noeggerathialeans) to any of the four, implying that if we chose to regard noeggerathialeans as ferns, they are arguably best treated as a separate higher taxon at a rank equivalent to those occupied by the four extant groups. In the light of the range of characters documented in *Dorsalistachya*, we were indeed initially inclined to treat the noeggerathialeans as a Class of comparatively complex and specialized eusporangiate ferns. Only later did we reconsider, with greater care, the range of morphologies shown by the various previously described progymnosperm groups.

Progymnosperms—The progymnosperms are most commonly described as the Class Progymnospermopsida, encompassing three Orders: (1) the mid–upper Devonian Aneurophytales; (2) mid–upper Devonian Archaeopteridales (Beck, 1960a, 1960b, 1962); and (3) comparatively poorly known Mississippian Protopityales (Walton, 1958; Beck, 1960b; Smith, 1962) (reviewed by Bonamo, 1975; Beck, 1976; Beck and Wight, 1988; Stubblefield and Rothwell, 1989). Some authors recognize a fourth Order, Cecropsidales, established comparatively recently on the basis of a single anatomically preserved upper Pennsylvanian reproductive foliate axis described by Stubblefield and Rothwell (1989). The Aneurophytales are widely regarded as the most primitive group of progymnosperms, possessing lobed protosteles rather than sympodial protosteles or eusteles, and a sparganum-type rather than a dictyoxylon-type cortex. More importantly in the present context, their sporangia are

terminal on naked axes, dehisce along only one side, and are reliably homosporous. They thus diverge greatly from *Dorsalistachya*; moreover, the *Plagiozamites* fronds associated with *Dorsalistachya* bear little resemblance to the small, three-dimensional "pre-fronds" that characterize aneurophytaleans.

Unsurprisingly, the Devonian Aneurophytales contrast most strongly with the more recent (Pennsylvanian) Cecropsidales (Stubblefield and Rothwell, 1989). Both taxa have globose sporangia, though those of *Cecropsis* have an apical dehiscence resembling that of the early divergent lineage leading to the "fern" *Botrychium*. Both taxa also share the characteristic of having reached the mono-megasporangiate grade of heterospory, but this grade has been achieved by a minimum of six different lineages of vascular land plant (Bateman and DiMichele, 1994). Moreover, the small clusters of sporangia borne on the sporophylls of *Cecropsis* are evenly distributed on the adaxial rather than abaxial surface, and the highly invaginated sporophylls are borne among—and otherwise identical to—the sterile leaves; both kinds of determinate organs are subtended by a slender but nonetheless woody branch. The *Cecropsis* plant unquestionably lacked bona fide strobili.

Intermediate in age, and arguably also in morphology, to the Aneurophytales and Cecropsidales are the two remaining progymnosperm orders. The Archaeopteridales differ in only few characters from Cecropsidales but are less similar to *Dorsalistachya* in several reproductive characters. Protopityales have achieved at best a substantially lower grade of heterospory and bear fusiform sporangia in similar fashion to aneurophytaleans (Walton, 1958; Smith, 1962; Bateman and DiMichele, 1994). Their branches do share with *Dorsalistachya* and *Plagiozamites* the feature of having vascular systems that are bilaterally organized, though the two taxa differ considerably in the details of their vascular architecture. Crucially, none of the four recognized Orders of progymnosperms bore cones. Thus, if noeggerathialeans (not least *Dorsalistachya*) were to be viewed as progymnosperms, they would most logically constitute a separate Order within the Class—an Order that may prove to be delimited by possession of fertile organs that consist entirely of a single leaf homolog.

***Comparison with other noeggerathialean genera*—**All strobili previously assigned to the Noeggerathiales (*Noeggerathiaestrobus*, *Tetraphyllostrobus* Gao & Zodrow, *Archaeonoeggerathiostrobus*, *Tingiostachya*, *Discinites*, *Lacoea*, *Saarodiscites*, and *Paratingiostachya*) were preserved as compression–impressions and therefore lacked anatomical preservation. They resemble *Dorsalistachya* in being compact and heterosporangiate, with sporophylls (often distichous) bearing sessile sporangia. Although each of these cone-genera clearly shares some similarities with the present strobilus, each also appears distinct from it (Table 1).

Sporophylls are spiral or whorled in *Tingiostachya* and *Paratingiostachya* (Gao and Thomas, 1987; Sun et al., 1999; Wang, 2006; Wang et al., 2009), or decurrent–disks in *Saarodiscites* and *Discinites* (Hirmer, 1940; Boureau, 1964; Bek and Šimůnek, 2005), contrasting with the distichous arrangement of *Dorsalistachya*. The sporophylls of *Tetraphyllostrobus* are decussate and each bears up to 50 sporangia (Gao and Zodrow, 1990), whereas the present strobilus consists of distichous sporophylls, each bearing only four microsporangia. Although *Lacoea* and *Noeggerathiaestrobus* bear distichous semicircular sporophylls comparable with those of *Dorsalistachya*, each sporophyll bears a much greater number of sporangia, and they are arranged in several rings on the adaxial surface (Read, 1946;

Leary, 1973, 1980; Leary and Pfefferkorn, 1977; Šimůnek and Bek, 2003) rather than in a single ring on the abaxial surface. In *Saarodiscites* the distal margin of the sporophyll is reputedly turned downward (Hirmer, 1940; Daber, 1957; Šimůnek and Bek, 2003); if correctly interpreted, this is a unique feature within Noeggerathiales. Lastly, none of the previously recognized cones produced megasporangia that are winged, and none conclusively bore sporangia abaxially.

We conclude that the present strobilus is a bona fide member of the Noeggerathiales, but deviates considerably from the circumscriptions of all the previously described genera, prompting us to establish the new genus *Dorsalistachya*.

***Comparison with other noeggerathialean families*—**Three families (or Orders according to Boureau, 1964) have previously been recognized within Noeggerathiales. Members of the Discinitaceae have whorled sporophylls. Each sporophyll consists of a near-horizontal disc-shaped proximal part and an upturned (at least partially dissected) distal part; the sporophyll bears numerous sporangia that are arranged in several rings (Remy and Remy, 1977; Gao and Thomas, 1994). Tingiostachyaceae are characterized by helical or whorled sporophylls. The proximal part of the sporophyll is disc-shaped or dissected into segments, whereas the distal part is upturned and dissected into smaller laminae; sporangia are arranged in a single ring (Gao and Thomas, 1987; Wang, 2006; Wang et al., 2009). By contrast, Noeggerathiaestrobaceae bear sporophylls distichously; the proximal part of the sporophyll is semicircular, the distal part upturned and dissected into small laminae; the sporangia are arranged in several rings (Němejc, 1963). The primary justification for recognizing the new family, Dorsalistachyaceae, is that all three pre-existing families have adaxial sporangia, whereas insertion is abaxial in *Dorsalistachya quadrisegmentorum*.

CONCLUSIONS

We have shown that noeggerathialeans were capable of achieving a level of reproductive sophistication that is comparable with those of the most 'advanced' late Paleozoic lycopsids and sphenopsids, and greater than that achieved by any other group of eusporangiate ferns. In parallel with several groups of seed plants, they appear to have evolved wind-dispersed propagules. And in parallel with ferns of the eusporangiate Marattiopsida and leptosporangiate Cyatheaceae, they evolved the tree-fern growth habit that allowed them to reach at least 10 m in height (Wang et al., 2009, 2012). But like so many groups that rise to ecological (co)dominance, their success was short-lived when viewed on a geological timescale.

We can only offer a less concrete answer to the key question 'Just what *are* Noeggerathiales?' The bilateral organization of their shoots alone is sufficient to distinguish them from the radial symmetry that characterizes the shoots of all sphenopsids (Browne, 1933; Boureau, 1964; Taylor et al., 2009) and most progymnosperms (Beck, 1981)—indeed, it also challenges our very concepts of strobilus and sporophyll. Based on the present (limited) evidence, the most credible comparisons are with the psilopsid ferns (especially the extant ophioglossalean genera *Botrychium* and *Helminthostachys*) on the one hand and the more derived cecropsidalean and protopityalean progymnosperms on the other. Studies that require comparison of a potentially crucial fossil with members of not one but two taxonomic Classes may at first glance appear to be the epitome of ignorance, but in truth, the phylogenetic

TABLE 1. Comparison of noeggerathialean strobili.

Genus	Saarodiscites	Discinites	Tingiostachya	Archaeonoeggerathiostrobus	Lacoea	Tetraphyllostrobus	Paratingia wudensis[1]	Tingia unita[1]	Noeggerathiostrobus	Paratingiostachya	Dorsalistachya
Family	Discinitaceae	Discinitaceae	Tingiastachyaceae	?Noeggerathiaestrobaceae	Noeggerathiastrobaceae	?Noeggerathiaestrobaceae	Tingiastachyaceae	Tingiastachyaceae	Noeggerathiaestrobaceae	Tingiastachyaceae	Dorsalistachyaceae
Epoch/Age	Carboniferous (Middle Pennsylvanian)	Carboniferous–Permian	Carboniferous–Permian	Carboniferous (Mississippian–Lower Pennsylvanian)	Carboniferous (Pennsylvanian)	Carboniferous (Upper Pennsylvanian)	Early Permian	Early Permian	Pennsylvanian–Permian (Cisuralian)	Permian (Cisuralian)	Permian (Lopingian)
Strobilus shape	Cylindrical, tapering top and bottom	Cylindrical	Cylindrical?	?	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical
Peduncle	?	?	Bears pinnae; forked, each branch bearing a strobilus	?	?	?	Lacks pinnae	Lacks pinnae	Bears Noeggerathia pinnae	?	?
Strobilus length (mm)	50–200[6]	>210	ca 130	?	?	ca 30–35	>120	>200	100–200 (incomplete)	80	115 (incomplete)
Strobilus diameter (mm)	45–50	15–70	80–120	?	<20	8–10	15	20–25	28–38	10–14	ca 10
Axis diameter (mm)	?	2–10	Slender	?	?	0.7	?	?	2.0–2.6	2.0	1.5
Sporophyll arrangement	Decurrent disk?	Decurrent disk	Helical or verticillate (unfused)	?	Distichous, opposite	Decussate (whorls overlapping slightly)	Decurrent disk (somewhat overlapping)	Verticillate	Weakly distichous, alternate	Helical or verticillate, perpendicular	Distichous, alternate
Sporophyll spacing (mm)	5.0–6.0	4.0–7.0	?	?	1.6	2.0–3.0	?	?	4.5–8.0	?	1.0
Sporophyll orientation and shape	Proximal part discoidal, flat, distal margin downturned up to 8 cm	Proximal part discoidal, flat; distal margin upturned to parallel axis, dentate or entire	Perpendicular to axis	Relatively long and narrow, flabelliform, radially corrugate and/or ribbed; distal margin sharply upturned, basally connate, margin sinuous and/or dentate	Semicircular, fringing laciniate border	Incurved, flabelliform; 4–5 veins terminating in an undulate distal margin	Distal margin upturned to parallel axis, deeply dentate	Perpendicular to axis	Semicircular, margin dentate	Linear to linear-lanceolate, distal margin upturned to parallel axis	Semicircular in outline, dividing to produce four dorsiventrally flattened segments that undergo one further division before curving upwards, but with distal heels that project abaxially; lateral abaxial ridges flank microsporangia
Bisporangiate	Yes?	Yes	Yes?	?	Yes	?	Yes	Yes	Yes	?	Yes
No. of microsporangia per sporophyll	?	30–1400[7]	1?	ca 30–65	10+	ca 45–65	10–14	8–10 sporangia and sporophylls on a whorl	?	?	4 (single sporangium per sporophyll)

TABLE 1, *continued*

Genus	Saardiscites	Discinites	Tingiostachya	Archaeo-noeggerathio-strobus	Lacoea	Tetraphyllostrobus	Paratingia wudensis[1]	Tingia unita[1]	Noeggerathio-strobus	Paratingio-stachya	Dorsalistachya
Microsporangium shape in outline	?	Oval/circular	Circular	Oval	Elliptical	Circular-reniform[4]	Elliptical (apex and base slightly contracted)	Elliptical	Oval	Circular/elliptical	Oval-ellipsoidal
Microsporangium size	2.5 mm long, 1.5 mm wide	?	1.0–1.5 mm diameter	1.0–1.2 mm long	1.5 mm diameter, 4.0 mm long	0.6–0.8 mm long	2.0–3.0 mm diameter, 5.0–7.0 mm long	2.0–4.0 mm diameter, 5.0–7.0 mm long	?	?	1.5 mm diameter, 3.0 mm long
Microsporangium dehiscence	?	Longitudinal	?	?	?	?	Longitudinal	Longitudinal	?	?	Proximal lower surface
Microsporangium attachment	?	Short, robust "sporangiophore"	Sessile	Sessile	?	?	Sessile	Sessile	Sessile	?	Sessile
Microsporangia arrangement on sporophyll	?	Radial, adaxial attachment to proximal portion of sporophyll	Adaxial attachment to proximal portion of sporophyll	Adaxial attachment to inflexed margin	Spiral	3–4 rows, 15 per row, lower sporangia overlapping upper	Single ring, adaxial	Adaxial	Adaxial, in 3–5 rows	?	Solitary row, abaxial
Microspore type(s)	?	Calamospora-type, Pteroretis primum, Vestispora laevigata, Calamospora laevigata	?	?	Calamospora cf. liquida, Punctatisporites	Laevigatosporites minor	Calamospora, Punctatisporites	Punctatisporites	Verrucosisporites microtuberosus, Calamospora-type, Cyclogranisporites, Punctatisporites	?	?
Megasporagium shape	?	?	?	?	?	?	Circular/subcircular, with equatorial expansion	?	?	?	Bilaterally flattened, with dorsiventral wings
Megasporagium size	?	?	?	?	?	?	1.0–1.3 mm diameter	?	?	?	2.0 x 1.0 x 1.5 mm
No. of megasporangia per sporophyll	16?	ca 16 (where present)	?	?	?	?	?[5]	?	?	?	1 (where present, arranged vertically)
Megaspore type(s)	?	Calamospora-type	?	?	Calamospora-type	?	Equatorial bulge	Circular/elliptical, >1.0 mm in diameter	Calamospora	?	?[3]
Preservation	Compression/impression	Compression/impression	Compression/impression	Compression/impression	Compression/impression	Compression/impression (coalified)	Compression/impression (in tuff)	Compression	Compression	Compression/impression	Anatomical preservation via carbonate permineralization
Known localities	Germany, Czech Republic	Belgium, China, Czech Republic, France, Germany, Saudi Arabia, USA	China, Korea, Oman	Belgium, Czech Republic, Germany	USA	Canada	China	China	Czech Republic, Germany	China	China

TABLE 1, *continued*

Genus	Saarodiscites	Discinites	Tingiostachya	Archaeo-noeggerathio-strobus	Lacoea	Tetraphyllostrobus	Paratingia wudensis[1]	Tingia unita[1]	Noeggerathio-strobus	Paratingio-stachya	Dorsalistachya
Assigned species	S. guthoerlii	D. bohemicus, D. delectus, D. dentilongus, D. egregious, D.? fimbriata, D. hlizae, D. jongmansi, D. nemejcii, D. major, D. orientalis, D. raconicensis, D. sinensis, D. sunjiaquouensis	T. tetralocularis, T. mingshanenis, T. santianensis	A. schatzlarensis, A. gothanii	L. seriata	T. broganensis	P. wudensis[1]	T. unita[1]	N. bohemicus, N. vicinalis, strobilus of Noeggerathia zamitoides[2]	P. cathaysiana	D. tetrasegmentus
Foliage associated with fructification	Saaropteris guthörlii?	Palaeopteridium, Yuania, Russellites?	Tingia?	?	Palaeopteridium?	?	Paratingia	Tingia	Noeggerathia	Paratingia	Plagiozamites oblongifolius
References	Hirmer, 1940; Daber, 1957; Němejc, 1963; Boureau, 1964	Grand'Eury, 1877; Němejc, 1937, 1941; Hirmer, 1940; Arnold, 1944, 1949; Mamay, 1954; Remy and Remy, 1956; Stockmans and Mathieu, 1957; Boureau, 1964; Potonié, 1965; Bohlin, 1971; Gu and Zhi, 1974; Liu and Shen, 1978; Zhao et al., 1980; Gao and Thomas, 1994; Mei et al., 1996; Wang, 2000; Wang and Shen, 2000; Wang et al., 2004; Bek and Šimůnek, 2005	Kon'no, 1929; Browne, 1933; Stockmans and Mathieu, 1939, 1957; Boureau, 1964; Gao and Thomas, 1987; He et al., 1996; Mei et al., 1996; Berthelin et al., 2003	Remy and Remy, 1986; Leary, 1988; Šimůnek and Bek, 2003	Read, 1946; Leary, 1973, 1980	Gao and Zodrow, 1990	Wang et al., 2009, 2012	Wang, 2006	Geinitz, 1865; O. Feistmantel, 1872, 1879; Weiss, 1879; Sterzel, 1918; Němejc, 1928; Hirmer, 1940; Halle, 1954; Remy and Remy, 1956; Boureau, 1964; Šimůnek and Bek, 2003	Sun et al., 1999	Present paper

Notes: ? = Unknown/Uncertain state. [1]Noeggerathialean plant with leaves and unnamed strobili attached; [2]Strobilus mentioned by Sterzel (1918) but not formally named; [3]Single functional megaspore of unknown type; [4]Based on Pl. I, 5 and Fig. 4 of Gao and Zodrow (1990); [5]Megaspores were found scattered on the surface of the strobili and in situ within megasporangium by Wang et al. (2009, figs. 37–41); [6]Maximum length estimation by Boureau (1964). [7]Upper range value reported in *Discinites* cf. *raconicensis* by Bek and Šimůnek (2005).

distance separating progymnosperms from the early divergent eusporangiate ferns is not great. Moreover, relationships among the basally divergent fern groups remain highly contentious, especially when (a) extinct groups are taken into account, and (b) some phylogeneticists have formally treated the recognized Orders of progymnosperms as plesions, together forming a (most likely paraphyletic) group located phylogenetically between ferns sensu latissimo and seed-plants, but of uncertain relationships among themselves (e.g., Kenrick and Crane, 1997).

We also note that the circumscription of Progymnospermopsida per se has been much-debated throughout the last half-century (cf. Bonamo, 1975; Beck, 1976; Beck and Wight, 1988; Stubblefield and Rothwell, 1989), a fact that is hardly surprising when one considers that this group is defined by a supposedly unique combination of two character suites that are most definitely not unique to the group, specifically a bifacial vascular cambium (generating 'gymnospermous wood') plus free-sporing reproduction. We also acknowledge that we presently lack any evidence that the *Dorsalistachya* plant produced wood. It is not surprising that the *Dorsalistachya* cone and *Plagiozamites* frond both lack wood, as we regard these two organs as likely occupying the same hierarchical level within the growth architecture of the source plant (i.e., exhibiting positional homology); it is unlikely that wood would be present in one of these organs but absent from the other. Nonetheless, in regarding this source plant as potentially progymnospermous we would, by definition, be assuming that the stem and branches underwent secondary thickening—a hypothesis that can be tested only by finding these correlated organs in the fossil record (Bateman and Hilton, 2009).

We are now confident that noeggerathialeans (including *Dorsalistachya*) constitute a major group of vascular land-plants that lie within the general plexus of land plants encompassing eusporangiate ferns plus progymnosperms. Whether they lie within one of the "fern Classes", "progymnosperm Orders", or represent a separate Class outside either of these "grab-bag" taxa remains a matter for ongoing debate. To be constructive, that debate will need to be fueled by (a) new, more informative fossils, and (b) a morphological cladistic analysis that combines the most informative among the conceptually reconstructed fossils with relevant extant taxa. Such work is now underway.

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LITERATURE CITED

Arnold, C. A. 1944. A heterosporous species of *Bowmanites* from the Michigan Coal Basin. *American Journal of Botany* 31: 466–470.

Arnold, C. A. 1949. Fossil flora of the Michigan Coal Basin. *In* Fossil flora of the Michigan Coal Basin. Contributions from the Museum of Paleontology, University of Michigan, 131–269. University of Michigan Press, Ann Arbor, Michigan, USA.

Bateman, R. M. 1991. Palaeobiological and phylogenetic implications of anatomically-preserved archaeocalamites from the Dinantian of Oxroad Bay and Loch Humphrey Burn, southern Scotland. *Palaeontographica, Abteilung B, Paläeophytologie* 223: 1–59, 8 plates.

Bateman, R. M., and W. A. DiMichele. 1994. Heterospory: The most iterative key innovation in the evolutionary history of the plant kingdom. *Biological Reviews of the Cambridge Philosophical Society* 69: 345–417.

Bateman, R. M., and W. A. DiMichele. 2002. Generating and filtering major phenotypic novelties: neoGoldschmidtian saltation revisited. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution, 109–159. Taylor & Francis, London, UK.

Bateman, R. M., and J. Hilton. 2009. Palaeobotanical systematics for the phylogenetic age: Applying organ-species, form-species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole-plants. *Taxon* 58: 1254–1280.

Beck, C. B. 1960a. Connection between *Archaeopteris* and *Callixylon*. *Science* 131: 1524–1525.

Beck, C. B. 1960b. The identity of *Archaeopteris* and *Callixylon*. *Brittonia* 12: 351–368.

Beck, C. B. 1962. Reconstructions of *Archaeopteris*, and further considerations of its phylogenetic position. *American Journal of Botany* 49: 373–382.

Beck, C. B. 1976. Current status of the Progymnospermopsida. *Review of Palaeobotany and Palynology* 21: 5–23.

Beck, C. B. 1981. *Archaeopteris* and its role in vascular plant evolution. *In* K. J. Niklas [ed.], Paleobotany, paleoecology, and evolution, vol. 1, 193–230. Praeger, New York, New, York, USA.

Beck, C. B., and D. C. Wight. 1988. Progymnosperms. *In* C. B. Beck [ed.], Origin and evolution of gymnosperms, 1–84. Columbia University Press, New York, New York, USA.

Bek, J., and Z. Šimůnek. 2005. Revision of the cone genus *Discinites* from the Carboniferous continental basins of Bohemia. *Palaeontology* 48: 1377–1397.

Berthelin, M., J. Broutin, H. Kerp, S. Crasquin-Soleau, J.-P. Platel, and J. Roger. 2003. The Oman Gharif mixed paleoflora: A useful tool for testing Permian Pangea reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196: 85–98.

Bierhorst, D. W. 1971. Morphology of vascular plants. Macmillan, New York, New York, USA.

Bohlin, B. 1971. Late Palaeozoic plants from Yuerhhung, Kansu, China. Sven Hedin Foundation, Stockholm, Sweden.

Bonamo, P. M. 1975. The Progymnospermopsida: Building a concept. *Taxon* 24: 569–579.

Bond, D. P. G., J. Hilton, P. B. Wignall, L. G. Stevens, J. R. Ali, Y. Sun, and X. L. Lai. 2010. The Middle Permian (Capitanian) mass extinction on land and in the oceans. *Earth-Science Reviews* 102: 100–116.

Boureau, É. 1964. Traité de paléobotanique, III. Sphenophyta, Noeggerathiophyta. Masson et Cie, Paris, France.

Browne, I. 1933. The Noeggerathiae and Tingiae. The effects of their recognition upon the classification of the Pteridophyta: An essay and a review. *New Phytologist* 32: 344–358.

Cavalier-Smith, T. 1998. A revised six-kingdom system of life. *Biological Reviews of the Cambridge Philosophical Society* 73: 203–266.

Christenhusz, M. J. M., and M. W. Chase. 2014. Trends and concepts in fern classification. *Annals of Botany* 113: 571–594.

Crane, P. R., and P. Kenrick. 1997 [1996]. Problems in cladistic classification: Higher-level relationships in land plants. *Aliso* 15: 87–104.

Daber, R. 1957. Parallelisierung der Flöze des Zwickauer und des Lugau-Oelznitzer Steinkohlenreviers auf Grund paläobotanischer Untersuchungen. *Geologie* 19: 1–76.

Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. *Botanical Review* 52: 321–431.

Feistmantel, C. 1879. Über die Noeggerathien und deren Verbreitung in der Böhmischen Steinkohlenformation. *Sitzungsberichte der königlich Böhmischen Gesellschaft der Wissenschaften in Prag* 1879: 75–88.

Feistmantel, O. 1872. Fruchtstände fossiler Pflanzen aus der böhmischen Steinkohlenformation. 1. Hälfte: Equisetaceae und Filices. *Abhandlungen der königlichen Böhmischen Gesellschaft der Wissenschaften in Prag*, series 6, 5: 1–51, plates 1–6.

Feistmantel, O. 1880–1881. Fossil flora of the Gondwana System, II, The flora of the Damuda and Panchet Divisions. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, series 12, 3: 1–77, 1880; 79–149, 1881.

Frohlich, M. W. 2002. The Mostly Male theory of flower origins: Summary and update regarding the Jurassic pteridosperm *Pteroma. In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution, 85–108. Taylor & Francis, London, UK.

Galtier, J., and T. L. Phillips. 1999. The acetate peel technique. *In* T. P. Jones and N. P. Rowe [eds.]. Fossil plants and spores: Modern techniques, 67–71. Geological Society of London, London, UK.

Gao, Z., and B. A. Thomas. 1987. A re-evaluation of the plants *Tingia* and *Tingiostchya* from the Permian of Taiyuan, China. *Palaeontology* 30: 815–828.

Gao, Z., and B. A. Thomas. 1994. A new species of *Discinites* from the Lower Permian of China. *Review of Palaeobotany and Palynology* 81: 185–192.

Gao, Z., and E. L. Zodrow. 1990. A new strobilus *Tetraphyllostrobus broganensis* gen. et sp. nov. from the Upper Carboniferous, Sydney Coalfield, Nova Scotia, Canada. *Review of Palaeobotany and Palynology* 66: 3–11.

Garwood, R. J., and J. A. Dunlop. 2014. The walking dead: Blender as a tool for palaeontologists with a case study of extinct arachnids. *Journal of Paleontology* 88: 735–746.

Geinitz, H. B. 1865. Über einige seltene Versteinerungen aus der unteren Dyas und der Steinkohlen-Formation. *Neues Jahrbuch für Mineralogie. Geologie und Paläeontologie* 1865: 385–394.

Grand'Eury, M. 1877. Flore carbonifère du départment de Loire et du centre de la France. *Mémoires présentés par divers savants à l'Académie des Sciences* 24: 1–624, plates 1-34.

Greene, D. F., and E. A. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70: 339–347.

Grewe, F., W. Guo, E. A. Gubbels, A. K. Hansen, and J. P. Mower. 2013. Complete plastid genomes from *Ophioglossum californicum, Psilotum nudum*, and *Equisetum hyemale* reveal an ancestral land plant genome structure and resolve the position of Equisetales among monilophytes. *BMC Evolutionary Biology* 13: 8.

Gu, Z. and L. Zhi [eds.]. 1974. Palaeozoic plants from China. Fossil plants of China, vol. 1. Science Press, Beijing, China [in Chinese].

Guo, Y. T., B. L. Tian, and D. X. Han. 1990. The anatomical study of *Plagiozamites oblongifolius* and the systematic position of *Plagiozamites. Acta Botanica Sinica* 30: 799–804 [in Chinese with English abstract].

Halle, T. G. 1927. Palaeozoic plants from central Shansi. *Palaeontologica Sinica Series A*, 2(i). Geological Survey of China, Peking.

Halle, T. G. 1954. Notes on Noeggerathiineae. *Svensk Botanisk Tidskrift* 48: 368–380.

He, X. L., D. S. Liang, and S. Z. Shen. 1996. Research on the Permian Flora from Jiangxi Province, China. China University of Mining and Technology Press, Xuzhou, China. [in Chinese with English summary]

Hilton, J., and R. M. Bateman. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133: 119–168.

Hirmer, M. 1940. Noeggerathiineae. *In* M. Hirmer and P. Guthörl, Abt. 3, Filicales und Verwandte. *In* Hirmer, M, and W. Gothan [eds.], Die Karbon-Flora des Saargebietes. Palaeontographica, Supplement 9: 1-60.

Hirmer, M., and P. Guthörl. 1940. Abt. 3, Filicales und Verwandte. *In* Hirmer, M, and W. Gothan [eds.], Die Karbon-Flora des Saargebietes. Palaeontographica, Supplement 9, Lieferung 1: 1–44.

Horner, H. T., and H. J. Arnott. 1963. Sporangial arrangement in North American species of *Selaginella. Botanical Gazette (Chicago, Illinois, USA)* 124: 371–383.

Kato, M. 1988. The phylogenetic relationship of Ophioglossaceae. *Taxon* 37: 381–386.

Kenrick, P., and P. R. Crane. 1997. The origin and early diversification of land plants. Smithsonian Institution Press, Washington, District of Columbia, USA.

Kidston, R. 1923. Fossil plants of the Carboniferous rocks of Great Britain. *Great Britain Geological Survey Memoirs* 2(1–3): 1–276, plates 1-68.

Knie, N., S. Fischer, F. Grewe, M. Polsackiewicz, and V. Knoop. 2015. Horsetails are the sister group to all other monilophytes and Marattiales are sister to leptosporangiate ferns. *Molecular Phylogenetics and Evolution* 90: 140–149.

Kon'no, E. 1929. On genera *Tingia* and *Tingiostachya* from the Lower Permian and Permo-Triassic beds in northern Korea. *Japanese Journal of Geology and Geography* 6: 113–147.

Leary, R. L. 1973. *Lacoea*, a Lower Pennsylvanian noeggerathialian cone from Illinois. *Review of Palaeobotany and Palynology* 15: 43–50.

Leary, R. L. 1980. *Lacoea* with sporangia and *Calamospora*spores from Rock Island, Illinois. *Review of Palaeobotany and Palynology* 29: 23–28.

Leary, R. L. 1988. Additional specimen of *Archaeonoeggerathia gothani* Remy and Remy 1986 from the Namurian of Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre* 58: 5–176.

Leary, R. L., and H. W. Pfefferkorn. 1977. An Early Pennsylvanian flora with Megalopteris and noeggerathiales from west-central Illinois. *Illinois State Geological Survey Circular* 500: 1–77.

Lehtonen, S. 2011. Towards resolving the complete fern tree of life. *PLoS One* 6: e24851.

Liu, H., and G. Shen. 1978. Carboniferous and Permian floras of the Longshou Mountains in Gansu. Lanzhou University, Lanzhou, China [in Chinese].

Mamay, S. H. 1954. A Permian Discinites cone. *Journal of the Washington Academy of Sciences* 44: 7–11.

Mamay, S. H. 1968. *Russellites*, new genus, a problematical plant from the Lower Permian of Texas. *U.S. Geological Survey Professional Paper* 593-I: 1–15.

Mei, M., Q. C. Huang, M. Du, and D. L. Dilcher. 1996. The Xu-Huai-Yu Subprovince of the Cathaysian Floral Province. *Review of Palaeobotany and Palynology* 90: 63–77.

Meyen, S. V. 1987. Fundamentals of palaeobotany. Chapman & Hall, London, UK.

Němejc, F. 1928. A revision of the Carboniferous and Permian flora of the coal-districts in central Bohemia. *Palaeontographica Bohemiae* 12: 1–82 [in Czech with English summary].

Němejc, F. 1931. The morphology and the systematic relations of the Carboniferous Noeggerathiae with regard to the "genera" *Tingia* and *Plagiozamites* of eastern Asia. *Preslia* 10: 111–114.

Němejc, F. 1937. On Discinites K. Feistm. *Bulletin International de l'Academie des Sciences de Boheme* 38: 3–10.

Němejc, F. 1941. Weitere Fructifikationem vom Typus *Discinites* nebst einigen Bemerkungen über die Archaeopteriden der Mittelböhmischen Kohlenbecken. *Mitteilungen der Tschechischen Akademie der Wissenschaften* 19: 1–13.

Němejc, F. 1963. Subclass Noeggerathiidae. *Paleobotanika* 2: 242–250, plates XXI–XXV.

Neregato, R., C. D'Apolito, I. J. Glasspool, S.-J. Wang, L. Feng, P. Windslow, J. Lu, et al. 2016. Palynological constraints on the provenance and stratigraphic range of a Lopingian (Late Permian) inter-extinction floral lagerstätte from the Xuanwei Formation, Guizhou Province, China. *International Journal of Coal Geology* 162: 139–150.

Ouyang, S. 1962. The microspore assemblage from the Lungtan Series of Changhsing, Chekiang. *Acta Palaeontologica Sinica* 10: 76–119 [Chinese with English summary].

Ouyang, S. 1986. Palynology of Upper Permian and Lower Triassic Strata of Fuyuan District, Eastern Yunnan. Science Press, Beijing, China [Chinese with English abstract].

Potonié, R. 1965. Fossile Sporae in situ: Vergleich mit der Sporae dispersae Nachtrag zur Synopsis der Sporae in situ. *Forschungsberichte des Landes Nordrhein-Westfalen* 1483: 1–71

Pryer, K. M., E. Schuettpelz, P. G. Wolf, H. Schneider, A. R. Smith, and R. Cranfill. 2004. Phylogeny and evolution of ferns (Monilophytes) with a focus on early leptosporangiate divergences. *American Journal of Botany* 91: 1582–1598.

Rai, H. S., and S. W. Graham. 2010. Utility of a large, multigene plastid dataset in inferring higher-order relationships in ferns and relatives (Monilophytes). *American Journal of Botany* 97: 1444–1456.

Read, C. B. 1946. A Pennsylvanian florule from the Forkston Coal in the Dutch Mountain outlier, northeastern Pennsylvania, U.S.A. *U.S. Geological Survey Professional Paper* 210-B: 17–27.

Remy, W., and R. Remy. 1956. *Noeggerathiostrobus vicinalis* E. Weiss und Bemerkungen zu ähnlichen Fruktifikationen. *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie* 2: 1–11.

Remy, W., and R. Remy. 1977. Die Floren des Erdaltertums. Verlag Glückauf GMBH, Essen, Germany.

Remy, W., and R. Remy. 1986. *Archaeonoeggerathia gothani* nov. gen., nov. spec., eine Noeggerathiale aus dem Namur A. *Argumenta Palaeobotanica* 7: 109–121 [in German].

Rothfels, C. J., F.-W. Li, E. M. Sigel, L. Hulet, A. Larsson, D. O. Burge, M. Rusham, et al. 2015. The evolutionary history of ferns inferred from 25 low-copy nuclear genes. *American Journal of Botany* 102: 1089–1107.

Rothwell, G. W., and E. E. Karrfalt. 2008. Growth, development, and systematics of ferns: Does *Botrychium* s.l. (Ophioglossales) really produce secondary xylem? *American Journal of Botany* 95: 414–423.

Rothwell, G. W., and K. C. Nixon. 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences* 167: 737–749.

Rothwell, G. W., and R. Serbet. 1994. Lignophyte phylogeny and the origin of spermatophytes: A numerical cladistic analysis. *Systematic Botany* 19: 443–482.

Rothwell, G. W., and R. A. Stockey. 1989. Fossil Ophioglossales in the early Paleocene of western North America. *American Journal of Botany* 76: 637–644.

Rudall, P. J., J. Hilton, F. Vergara-Silva, and R. M. Bateman. 2011. Recurrent abnormalities in conifer cones and the evolutionary origins of flower-like structures. *Trends in Plant Science* 16: 151–159.

Schenk, A. 1883. Pflanzen aus der steinkohlen formation. *Richthofen F.V. China* 4: 221–244.

Seyfullah, L. J., J. Hilton, M. M. Liang, and S. J. Wang. 2010. Resolving the systematic and phylogenetic position of isolated ovules: A case study from a new genus from the Upper Permian of China. *Botanical Journal of the Linnean Society. Linnean Society of London* 164: 84–108.

Šimůnek, Z., and J. Bek. 2003. Noeggerathiaceae from the Carboniferous basins of the Bohemian Massif. *Review of Palaeobotany and Palynology* 125: 249–284.

Sinnott, E. W. 1935. Botany: Principles and problems. 3rd ed. McGraw-Hill, New York, New York, U.S.A.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider, and P. G. Wolf. 2006. A classification for extant ferns. *Taxon* 55: 705–731.

Smith, D. L. 1962. Three fructifications from the Scottish Lower Carboniferous. *Palaeontology* 5: 225–237.

Sternberg, K. M. 1821. *Noeggerathia. In* Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt [1820-1838], 33, plate 20. F. Fleischer, Leipzig, Germany.

Sterzel, J. T. 1918. Die organischen Reste des Kulms und Rotliegenden der Gegend von Chemnitz. *Abhandlungen der mathematisch-physischen Classe der königlich\Ssächsischen Gesellschaft der Wissenschaften* 35: 205–315.

Stevenson, D. W. 1980. Ontogeny of the vascular system of *Botrychium multifidum* (S. G. Gmelin) Rupr. (Ophioglossaceae) and its bearing on stelar theories. *Botanical Journal of the Linnean Society. Linnean Society of London* 80: 41–52.

Stockmans, F., and F.-F. Mathieu. 1939. La flore Paléozoïque du bassin houiller de Kaiping (Chine), 49-165. Patrimoine du Musée Royal d'Histoire Naturelle de Belgique, Brussels, Belgium.

Stockmans, F., and F.-F. Mathieu. 1957. La flore Paléozoïque du bassin houiller de Kaiping (Chine) (Deuxième partie). Association pour l'Étude de la Paléontologie et de la Stratigraphie Houillères, Bruxelles, Belgium, publication 32, 1-89.

Stubblefield, S. P., and G. W. Rothwell. 1989. *Cecropsis luculentum* gen. et spec. nov.: Evidence for heterosporous progymnosperms in the Upper Pennsylvanian of North America. *American Journal of Botany* 76: 1415–1428.

Sun, G., F. S. Meng, L. J. Qian, and S. Ouyang. 1995. Triassic floras. *In* X. X. Li [ed.], Fossil floras of China through the geological ages, 305–342. Science and Technology Press, Guangdong, China.

Sun, K.-Q., S. Deng, J.-Z. Cui, and P. Shan. 1999. Discovery of *Paratingia* and *Paratingiostachya* from the Shanxi Formation of the Early Permian in the Wuda area of Inner Mongolia, China. *Acta Botanica Sinica* 41: 1024–1026 [largely in Chinese].

Sutton, M. D., R. J. Garwood, D. J. Siveter and D.J. Siveter. 2012. SPIERS and VAXML: a software toolkit for tomographic visualisation and a format for virtual specimen interchange. *Palaeontologia Electronica* 15: 2.4T.

Sze, C. 1953. Notes on some fossil remains from the Shihchienfeng Series in northwestern Shensi. *Acta Palaeontologica Sinica* 1: 11–22.

Taylor, T. N., E. L. Taylor, and M. Krings. 2009. The biology and evolution of fossil plants (2nd ed.). Elsevier, Amsterdam, Netherlands.

Walton, J. 1958. XV.-On Protopitys(Göppert): Wwith a description of a fertile specimen Protopitys scotica sp. nov. from the Calciferous Sandstone Series of Dunbartonshire. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 63: 333–340.

Wang, H., L. Shao, L. M. Hao, P. F. Zhang, I. J. Glasspool, J. R. Wheeley, P. B. Wignall, et al. 2011. Sedimentology and sequence stratigraphy of the Lopingian (Late Permian) coal measures in southwestern China. *International Journal of Coal Geology* 85: 168–183.

Wang, J. 2000. Discovery of a petrified noeggerathialean strobilus, *Discinites sinensis* sp. nov. from the Permian of Shizuishan, Ningxia, China. *Chinese Science Bulletin* 45: 560–566.

Wang, J. 2006. *Tinga unita* sp. nov. (Noeggerathiales) with strobilus from the Lower Permian of Wuda, Inner Mongolia, China. *Chinese Science Bulletin* 51: 2624–2633.

Wang, J. 2008. A note on fructification of *Plagiozamites* Zeiller (Noeggerathiales) based on association. *Global Geology* 11: 115–124.

Wang, J., and D. Chaney. 2010. A re-examination of the type specimens of *Yuania* H.C. Sze 1953 and its junior synonym *Russellites* Mamay 1968 (Noeggerathiales). *Taxon* 59: 517–524.

Wang, J., H. W. Pfefferkorn, and J. Bek. 2009. *Paratingia wudensis* sp. nov., a whole noeggerathialean plant preserved in an earliest Permian air-fall tuff in Inner Mongolia, China. *American Journal of Botany* 96: 1676–1689.

Wang, J., H. W. Pfefferkorn, Z. Feng, and G. L. Shen. 2004. A new species of *Discinites* (Noeggerathiales) associated with a new species of *Yuania* from the Lower Permian of Inner Mongolia, China. *International Journal of Plant Sciences* 165: 1107–1119.

Wang, J., H. W. Pfefferkorn, Z. Zhang, and Z. Feng. 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of China. *Proceedings of the National Academy of Sciences, USA* 109: 4927–4932.

Wang, J., and G. Shen. 2000. A new species of *Discinites* (Noeggerathiales) from the Upper Permian of Weibei Coalfield, North China. *Review of Palaeobotany and Palynology* 110: 175–190.

Wang, S.-J., J. Hilton, M.-M. Liang, and L. G. Stevens. 2006. Permineralized seed plants from the Upper Permian of southern China: A new species of *Cardiocarpus*. *International Journal of Plant Sciences* 167: 1247–1257.

Wang, S.-J., J. Hilton, B. Tian, and J. Galtier. 2003. Cordaitean seed plants from the Early Permian of North China. 1. Delimitation and reconstruction of the *Shanxioxylon sinense* plant. *International Journal of Plant Sciences* 164: 89–112.

Wang, Z.-Q., and L.-X. Wang. 1986. Late Permian fossil plants from the Lower part of the Shihchienfeng Group in North China. *Bulletin of the Tianjin Institute of Geology and Mineral Resources. Chinese Academy of Geological Sciences* 15: 1–80 [Chinese, with English abstract].

Weiss, C. E. 1879. Bemerkungen zur Fructifikation von *Noeggerathia. Zeitschrift der Deutschen Geologischen Gesellschaft* 31: 111–116.

Zeiller, R. 1894. Notes sur le flore des couches permiennes de Trienbach (Alsace). *Bulletin de la Société Géologique de France* 4: 163–182.

Zhang, H. 1987. Palaeobotany. *In* Institute of Geology Exploration, CCMRI Coal Ministry and Provincial Coalfields Exploration Corporation of Shanxi, Sedimentary Environment of the Coal-Bearing Strata in Pinglu-Shuoxian Mining Area, China, 195–204. Shaanxi Peoples Education Publishing House, Xi'an, China.

Zhao, X. H., Z. G. Mo, S. Z. Zhang, and Z. Q. Yao. 1980. Late Permian flora from western Guizhou and eastern Yunnan. *In* Nanjing Institute of Geology and Palaeontology, Academia Sinica [eds.], Stratigraphy and palaentology of the Upper Permian Coal Measures of western Guizhou and eastern Yunnan, 70–122. Science Press, Beijing, China [in Chinese].

Zimmermann, W. 1959. Die Phylogenie der Pflanzen. Fischer, Stuttgart, Germany.