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A LYCOPSID WITH NOVEL REPRODUCTIVE STRUCTURES FROM THE UPPER DEVONIAN OF JIANGSU, CHINA

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A new lycopsid is described from the Upper Devonian (Famennian) of Wuxi, Jiangsu Province, China. It has isodichotomous branches and long leaves with spiny margins. Two types of fertile structures are present. Megasporangia-bearing conelike structures are found at dichotomies of the branches, having large, densely inserted leaves with enlarged bases, bearing adaxial sporangia containing large megaspores. The other type are terminal cones, having slender, closely inserted leaves, and dark carbonaceous areas adjacent to the axis are interpreted as the remains of microsporangia. The new plant closely resembles lycopsids previously reported from the Middle and lower Upper Devonian of China, but the reproductive characters are more advanced. It demonstrates that the early history of large lycopsids is more complex than has been recognized. We name the new plant *Wuxia bistrobilata* gen. et sp. nov.

Keywords: Lycopsida, cone, Upper Devonian, China, Jiangsu.

Introduction

The Lycopsida is probably the longest-lived group of extant vascular land plants. Today there are many herbaceous and epiphytic species known, but the acme of lycopsid diversity and abundance was in the Carboniferous when large arborescent forms dominated many swamp ecosystems. These highly successful plants had their herbaceous origins in the Late Silurian and Early Devonian (Rickards 2000), and the earliest small tree-shaped pseudobipolar forms, growing both upward to form a trunk and crown of branches and downward to form a dichotomously branching rooting system, have recently been discovered in the Middle and lowermost Upper Devonian of China (Cai and Chen 1996; Schweitzer and Li 1996). Such early treelike forms had terminal cones of closely arranged sporophylls on their aerial branches but otherwise seem quite primitive in their reproductive characters.

We report here the earliest known lycopsid with two distinct types of fertile structures, interpreted as micro- and mega-sporangiate. The fossils demonstrate a novel combination of reproductive characters, the sum of which, combined with the probable age of the specimens, demonstrates that there is much to learn about the early evolution of reproduction in lycopsids when specimens from beyond the Laurussian landmass are taken into account.

Material and Methods

The specimens were collected near Wuxi, Jiangsu Province, People's Republic of China. They derive from Xiaohuoshan quarry, on the north slope of Jilong Mountain, 6 km west of Wuxi City (fig. 1).

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The strata belong to the Wutung Formation, clastic sediments of Late Devonian and Early Carboniferous age. This formation outcrops widely in the Lower Yangtze Valley (Cai et al. 1988). It is composed mainly of sandstones interbedded with siltstones or mudstones in the lower part (Guanshan Member) and of siltstones and mudstones interbedded with sandstones in the upper part (Leigutai Member).

The fossils were preserved in the lower part of the Leigutai Member, composed of medium to thick-bedded grayish white quartz sandstones intercalated with lenticular white mudstones. Other fossils recorded include *Lepidodendropsis* sp., *Sublepidodendron* sp., *Lepidostrobus grabaui*, *Stigmara ficoides*, *Sphenophyllum* sp., and *Hamatophyton verticillum*. This stratum is assigned a Late Devonian age based on the fossil plant assemblage (Cai et al. 1988). The specimens were found mainly in lenticular white silty mudstones that have since been worked out by the quarry operators.

Ca. 40 specimens were collected, including branches, leaves, and cones, predominantly preserved as compressions but also as brown-stained impressions. Some branch material was partly permineralized. Compressions/impressions were uncovered using the dégagement technique of Leclercq (Fairon-Demaret et al. 1999) to expose details of external morphology. Permineralized specimens were embedded in plastic, sectioned, ground smooth, etched in hydrochloric acid, washed, dried, mounted, and examined by scanning electron microscopy (SEM).

The following description is based largely on two remarkable slabs. The smaller measures 35 cm × 40 cm and is ca. 10 cm thick. On one side can be found quite wide branches and fertile structures containing megaspores (fig. 3a), and on the reverse is preserved slightly narrower branches bearing what are interpreted to be microsporangiate cones (fig. 5a) pointing in the same direction. The largest slab (fig. 2g) measures some 80 cm × 60 cm and shows long axes and some

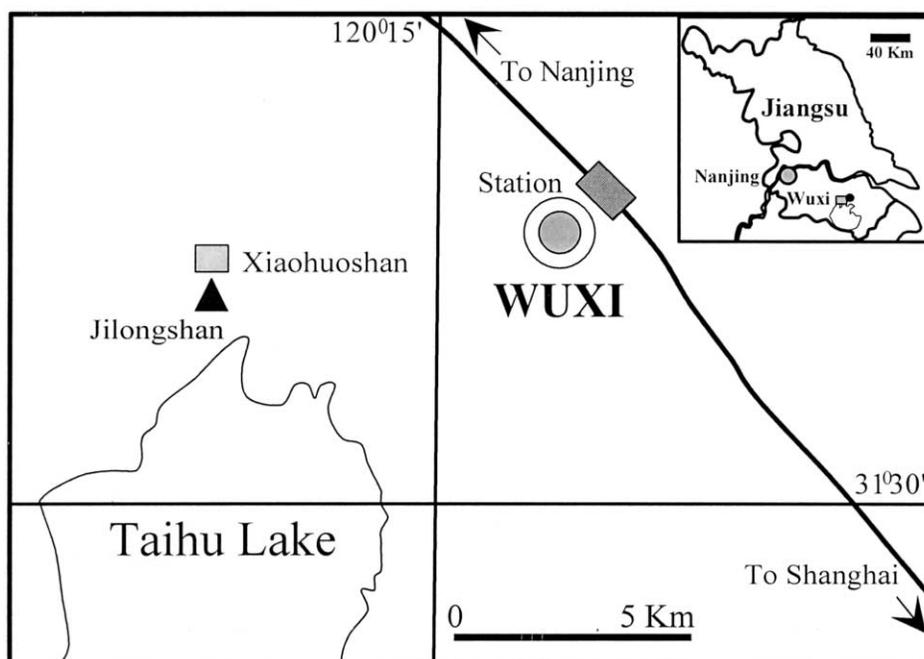


Fig. 1 Map of the fossil locality in Xiaohuoshan, Wuxi City, Jiangsu Province, People's Republic of China

megasporangiate fertile structures and a fragmentary microsporangiate cone (fig. 2g, arrow). A number of smaller pieces make up the remainder of the collection.

Figured specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Academica Sinica), prefix PB.

Description—Morphology

Branches

The widest axis, preserved on a small slab, is 105 mm in preserved length and between 10 and 14 mm wide (fig. 2a). It dichotomizes to yield two smaller branches of 5–8 mm width. The whorls of leaves are closely arranged ca. 1–4 mm apart. On the largest slab (fig. 2g), the widths of nonfertile axes are from 3 to 7 mm, and the branches reach up to 46 cm in preserved length (left upper). The spacing of insertion of leaf whorls varies between ca. 5 and 15 mm and may increase as well as decrease distally. On the other large slab (fig. 3a), the widths of sterile axes are from 3.5–8.5 mm in diameter; up to 350 mm long; and, where branching is observed, dichotomize only once within the preserved length.

A sterile axis that is seen to terminate (fig. 5a, arrowhead) has leaf whorls arranged ca. 2 mm apart and is ca. 1 mm wide at the rounded tip (fig. 2e). Fourteen centimeters proximal to the tip, leaves are 25 mm long, and the axis is 2 mm wide.

Sterile leaves are inserted most usually more or less perpendicularly to the axis. Each whorl is composed of six leaves (fig. 2f). Leaves have slightly decurrent bases (fig. 2a–2c) and are up to at least 63 mm long. Widths range from 0.8 to 3 mm. They have parallel margins for much of their length, and a deeply sunken groove in the position of the midvein (fig.

2d). The margins bear spines up to ca. 1 mm length (fig. 2d). The delicate leaf tips are rarely preserved.

Megasporangiate Conelike Structures

Megasporangiate conelike structures are marked by differences in the density and angle of insertion of leaves, the morphology of the leaves, and branching of the fertile axes. They are found on the largest block (fig. 2g, arrowheads), on one side of the second largest block (fig. 3a), and on several smaller pieces (fig. 3c, 3e, 3f). The width of the axes carrying the cones varies between 2.5 and 5 mm.

At the base of the fertile zone, the density of leaf insertion increases noticeably (figs. 2b, 3e), although nowhere is it possible to actually quantify this change. The angle of insertion of the leaves changes from almost perpendicular to the axes to much more acute (fig. 2b; fig. 3b, 3e). In an example, an area of 30 mm × 22 mm in the center of the conelike structure is represented only by compressed megaspores (fig. 3b). The basal axis measures 5 mm in width, while from the center of the spore mass emerge two axes each of 4 mm diameter (long arrow). These bear only the bases of probably broken sterile leaves, distantly spaced. Some 35 mm from this first dichotomy, the daughter branches divide again (fig. 3b, arrowheads), this time to yield four branches of 2 mm diameter. Here, whorls of leaves are separated by smooth distances of stem up to 14 mm long. The presence of two other isolated axes apparently emerging from the same area of the fertile zone indicates at least one extra dichotomy of the axes. In two other megasporangiate conelike structures, narrower axes are seen to emerge from them (fig. 2g, left-hand arrowheads; fig. 2i, arrowheads). In one example (fig. 2i), part of the upper emerging axis was uncovered by déagament into the middle of the area

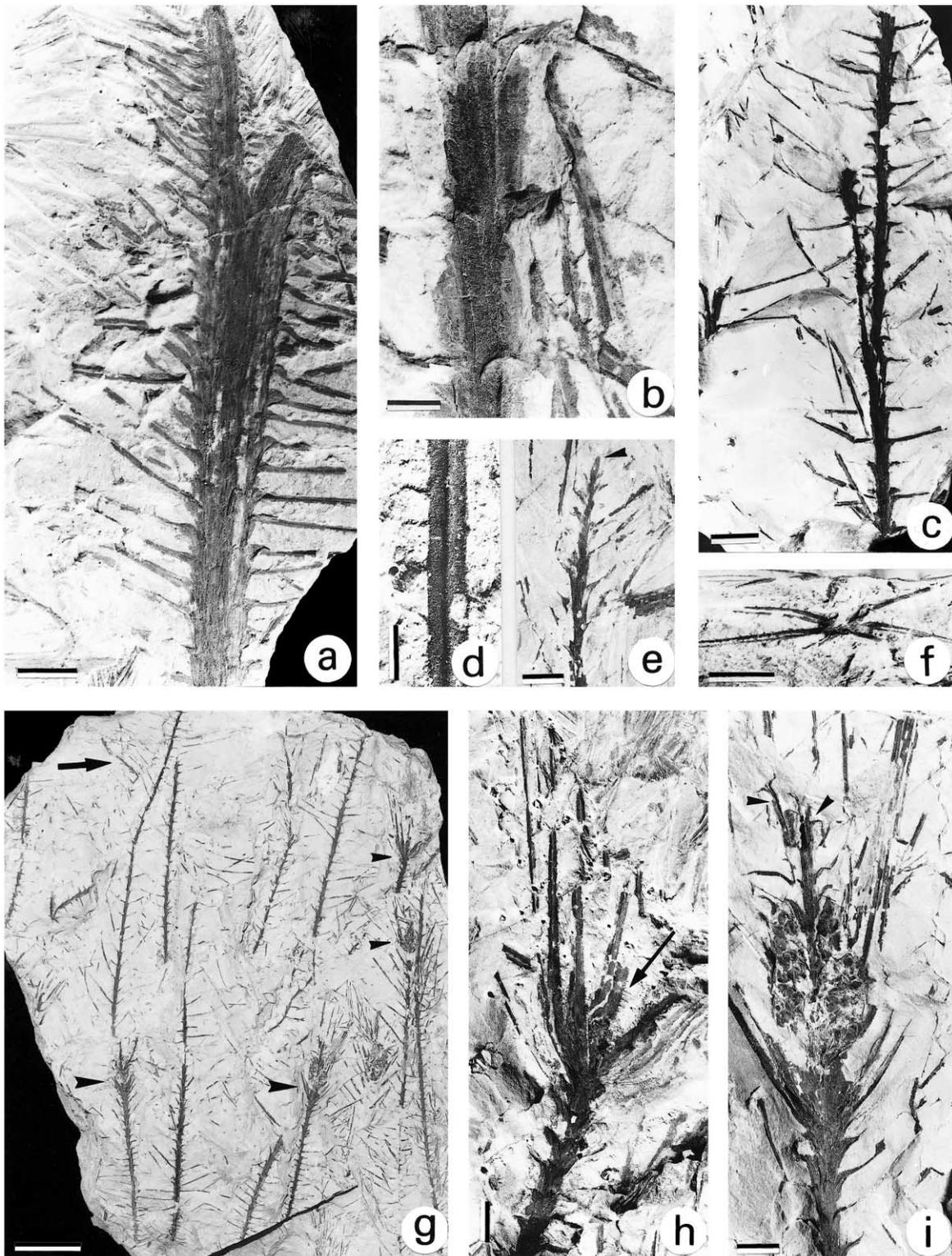


Fig. 2 *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov. *a*, Widest axis; note leaves visible to the side. Specimen PB18860, scale bar = 10 mm. *b*, Close-up of typical axis showing decurrent bases of sterile leaves. Specimen PB18861, scale bar = 3 mm. *c*, Dichotomy of typical axis. Specimen PB18862a, scale bar = 20 mm. *d*, Sterile leaf with spines along parallel margins and deeply sunken medial groove. Specimen PB18863, scale bar = 3 mm. *e*, Termination of sterile axis (arrowhead; see fig. 5a). Specimen PB18864, scale bar = 5 mm. *f*, Six leaves in each whorl, observed on a fracture plane perpendicular to main slab surface (i.e., transverse view). Specimen PB18865, scale bar = 10 mm. *g*, Largest slab, some 80 cm in length. Large arrow pointing to microsporangiate cone; small arrows indicating megasporangiate conelike structures. Paratype, specimen PB18866–68, 79, scale bar = 10 cm. *h*, *i*, Megasporangiate conelike structures. Arrow (*h*) indicates spines on megasporophyll. Arrowheads (*i*) indicate branches emerging distally from conelike structure. Specimens PB18866, 67, scale bar = 10 mm.

covered by megaspores in order to satisfy us of the connection between proximal and distal sterile axes.

Fertile leaves are up to at least 95 mm in length (fig. 3*b*, to the left). They are typically 5 mm wide 20 mm from the base, 2.5 mm wide 45 mm from the base, and 1.4 mm wide 85 mm from the base. The most proximal region of the lamina is slightly more enlarged (fig. 2*b*; fig. 3*d*, 3*e*). The margins bear spines up to 2 mm long that point perpendicular to the margin (fig. 2*b*, arrow; figs. 2*e*, 4). The leaves have a noticeable depressed midrib (fig. 3*d*, right; fig. 3*e*). Our proposed reconstruction of one sporophyll is given in figure 4.

Megaspores are clearly visible in the dark region in the center of the conelike structures (fig. 2*i*; fig. 3*b*, 3*d*). They are 3–4 mm in diameter. Although large, when removed and examined under the SEM, the megaspores prove badly preserved or as merely impressions and show no additional detail. One exceptional specimen (fig. 3*f*, 3*g*) demonstrates an impression of a spore (falsely appearing as a complete spore) that indicates a triangular obtuse convex amb, a prominent trilete mark, and a broad equatorial margin. This specimen is not contained within a sporangium, but the size and position at the base of a leaf may indicate that it indeed belongs with the new lycopsid. One specimen (fig. 3*c*, 3*d*) on a small slab indicates that a megasporangium (fig. 3*d*, arrow) contains the spores in the adaxial position on the fertile leaf, but these are not well preserved.

Probable Microsporangiate Cones

Microsporangia cannot be demonstrated directly on leaves. Rather, their presence is inferred by the presence of a distinctive, terminal, second (presumably microsporangiate) type of cone. Several of these are found on the reverse of the second largest slab (fig. 5*a*), and a single one is found on the surface of the largest (fig. 2*g*, large arrow, top left). These are found on axes bearing the same characteristic leaves (with small marginal spines, e.g., fig. 5*c*, lowest two leaves) with the same whorled appearance as those bearing megasporangiate conelike structures.

Microsporangiate cones have very narrow sporophylls, often only preserved as impressions lacking carbonaceous material (fig. 5*b*, 5*c*). Leaves are up to 55 mm in length and ca. 1 mm wide. They have a prominent midrib (fig. 5*c*). No marginal spines are visible. Leaves are inserted so densely it is impossible to accurately measure their insertion, in contrast to areas of branch below the cones where leaf whorls are separated by a distance of ca. 8 mm along the axis (fig. 5*a*).

The axis entering the cone is 2.5–4 mm in width, and the cone is terminal on the axis. In the center of the cone, a dark oxidized area, which represents the area of the densest remains of organic carbon, is clearly visible in most specimens (fig. 5*a*, 5*b*). This area is up to 105 mm long and 13 mm wide. The dark area is interpreted as representing the area where the sporangia and spores were compressed because of the concentration of preserved organic carbon and associated staining. SEM examination has not revealed the presence of any preserved recognizable spores, and neither has maceration. These cones differ in many ways from the sterile terminations of ordinary axes as described above (fig. 2*e*) and cannot be mistaken for them.

Description—Anatomy

Permineralized tissues were removed from only one length of axis (fig. 2*g*, extreme left; fig. 5*d*) and are partially compressed (fig. 6*a*). Cell lumina were infilled with some limonite (fig. 6*g*), but the cell walls often remain as coal and carbon and can be revealed by etching.

The xylem column has a diameter of ca. 1.8 mm in transverse section. Around the margins of the xylem column are located areas of smaller cells interpreted as protoxylem (fig. 6*a*, arrowheads; fig. 6*b*, indicated by arrow in 6*c*; fig. 6*c*). The cells of protoxylem are circular in outline, ca. 8–10 μm in diameter. The protoxylem forms ridges (fig. 6*a*, arrows; fig. 6*c*) around the metaxylem core. The exact number of the ridges is unclear as they are poorly preserved around the whole xylem column. The protoxylem tracheids have helical thickenings (fig. 6*i*–6*k*, arrowhead).

The metaxylem cells are polygonal in transverse section, ca. 30–60 μm in diameter (fig. 6*a*–6*d*) in transverse view. When the metaxylem tracheids are observed obliquely (fig. 6*b*) or in longitudinal section (fig. 6*f*, 6*l*), scalariform bars can be seen, 3–5 μm thick, 3–4 μm apart (fig. 6*g*, 6*m*). Higher magnification demonstrates the apertures between the bars to be crossed by several longitudinal narrow fibrils (fig. 6*m*), less than 1 μm thick. In lumen and pit casts of metaxylem, the middle lamella can be seen (fig. 6*e*, arrow), as well as rows of holes (circular in outline, less than 1 μm in diameter) on either side of the lamella (fig. 6*e*) representing the former position of the now decayed fibrils across the apertures in transverse view. Lumen casts fractured at the correct level also display longitudinal depressions marking the position of the longitudinal bars or fibrils (fig. 6*g*).

Morphology and Habit

We observed two types of fertile structures in the fossils. Although these are not in organic connection, we infer that they belong to the same plant principally because they are attached to similar axes bearing similar leaves. Further support comes from the observation that the two types occur on the same bedding plane (fig. 2*g*) and because one slab bears examples of each type on opposite sides in similar orientation (figs. 3*a*, 5*a*).

The presumed microsporangiate cones are borne terminally and have closely compacted narrow laminate leaves. Megasporangiate conelike structures occur at branching points of larger axes from which emerge a pair of smaller branches that further dichotomize.

All branching in our specimens is more or less isotomous. We believe that the subparallel arrangement of the axes on the larger slabs indicates that the preserved remains visible on each side are parts of single plants that have fallen over. Such branches in the context of Upper Devonian lycopsids are likely to derive from the dichotomous branching to be found at the top of a small treelike or bushy lycopsid with an unknown trunk length. The upward-projecting, dichotomizing branches would form a conical volume of subparallel axes that would retain this arrangement when the plant fell over. The slightly inward-directed angle of the proximal parts of the axes in figures 3*a* and 5*a* support this hypothesis.

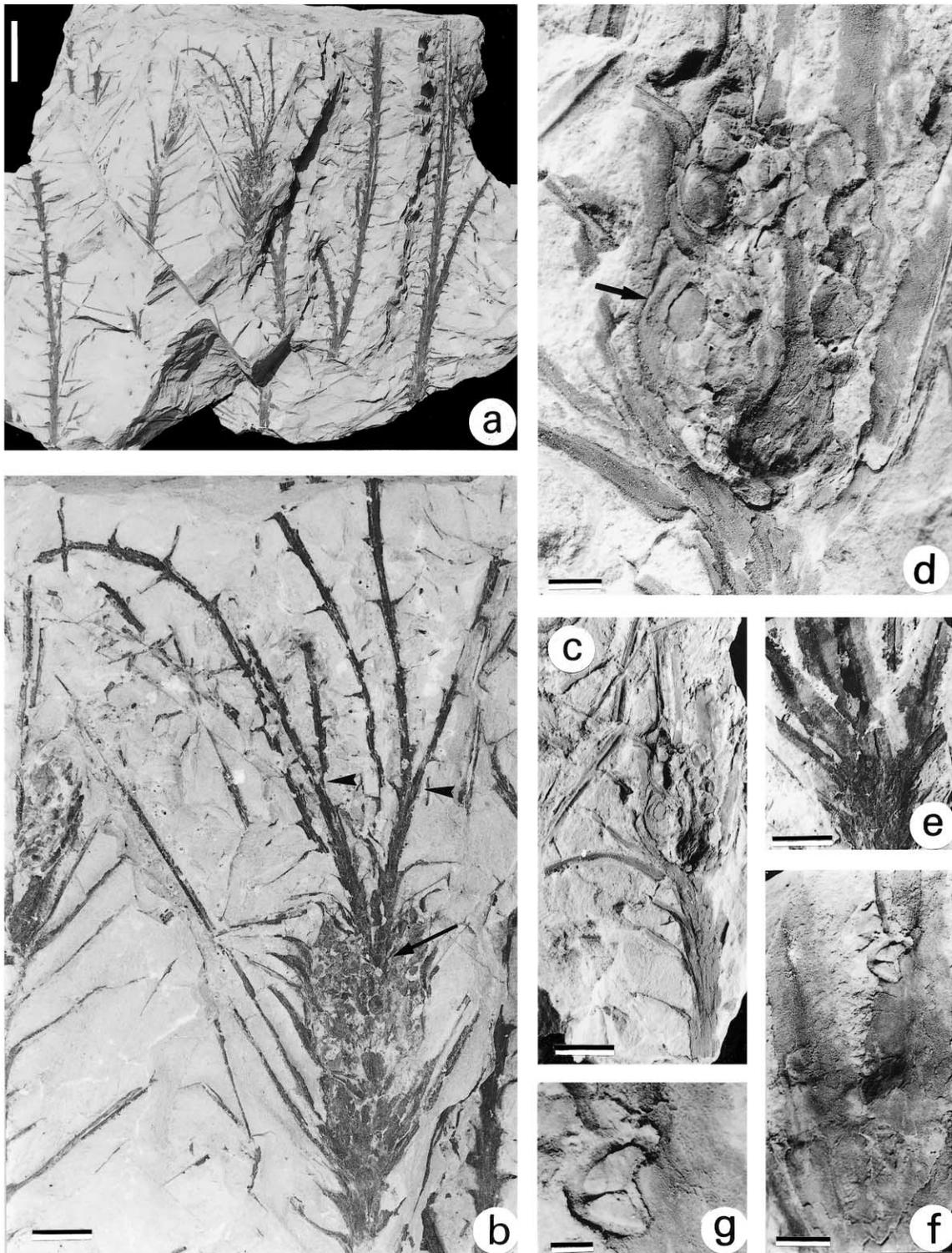


Fig. 3 *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov. *a*, Second largest slab (see fig. 5*a* for reverse), some 40 cm wide, showing megasporangiate conelike structure (holotype—PB 18870) and sterile axes. Specimens PB18862*b*, 69, 71, scale bar = 5 cm. *b*, Holotype. Enlargement of *a*, showing the megasporangiate conelike structures. Long arrow indicating dichotomy of axis within conelike structure; smaller arrowheads showing dichotomies of daughter axes. Specimen PB18870, scale bar = 10 mm. *c*, Megasporangiate conelike structure. Specimen PB18872, scale bar = 10 mm. *d*, Detail of *c*, showing megaspores; arrow indicating possible sporangium wall. Scale bar = 3 mm. *e*, Conelike structure with megasporophylls. Specimen PB18873, scale bar = 10 mm. *f*, Megasporophylls, with an external cast of a dispersed megaspore. Specimen PB18874, scale bar = 3 mm. *g*, Detail of *f*, megaspore, lighting from bottom (invert for true view), scale bar = 1 mm.

Systematic Descriptions

Division—*Lycopsida*

Family—*Incertae sedis*

Genus—*Wuxia* Berry, Wang et Cai gen. nov.

Diagnosis. Lycopodiaceous plant with isodichotomous division of aerial axes. Sterile leaves long, acute with deep-sunken midvein and spiny margins. Megasporangiate conelike structures with long megasporophylls with enlarged proximal region protecting megasporangium; deep-sunken midvein and spiny margins situated at dichotomies of axes. Microsporangiatic cones with closely packed narrow simple microsporophylls positioned terminally on aerial axes. Xylem column arch with several protoxylem ridges on margin.

Derivation of name. Wuxi: the type locality.

Type species. *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov.

Species—*Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov.

Diagnosis. As stated in generic diagnosis. Aerial axes known up to 14 mm diameter. Sterile leaves inserted in whorls of six, spaced between 2 and 15 mm longitudinally along axes; up to 63 mm in length, 3 mm in width, with deep midvein, bearing spines along both straight margins up to 1 mm in length. Megasporangiate conelike structures positioned at dichotomies of the axes; central axis width 2.5–5 mm; megasporophylls up to 96 mm length with prominent midrib, inverted spoon shaped with spines up to 2 mm along margins, closely and acutely inserted to form compact conelike fertile zone, bearing megaspores up to 4 mm diameter with prominent trilete mark. Probable microsporangiatic cones up to 105 mm in length, terminal on supporting axes up to 4 mm in width; microsporophylls densely and acutely inserted, up to 1 mm width; microsporangia and spores not observed.

Holotype. Specimen PB 18870 (fig. 3b).

Paratypes. Specimens PB 18862b, 64, 66–69, 71, 75–77, 79 (fig. 2; fig. 3a, 3c–3f; figs. 5, 6).

Type locality. Xiaohuoshan quarry, 6 km west of Wuxi city, Jiangsu Province, People's Republic of China.

Horizon. Wutung Formation, Upper Devonian (Famennian).

Derivation of name. *Bi*: Latin, meaning two; *strobilus*: Latin, meaning cone; referring to the two different fertile structures of this plant.

Discussion

Terminology of Fertile Compound Structures

Most definitions of “cones” or “strobili” state or imply that they occupy a terminal position on the supporting axis. The new megasporangiate fertile structures are not terminal. However, many other features of these megasporangiate fertile zones are conelike in nature. Sporophylls are modified with a strongly widened base protecting the sporangium. The sporophylls are inserted in a compact arrangement, with the basal

areas tightly abutting, and are bent upward at an acute angle. We therefore refer to these as conelike structures.

Comparisons with Other Devonian Lycopsid Taxa

The new genus and species described above bears most similarity to two small tree-shaped lycopsids from the Middle and Upper Devonian of China. *Longostachys latisporophyllus* Zhu, Hu et Feng, emend. Cai et Chen, was described from the Middle Devonian (Givetian) of Hunan Province by Cai and Chen (1996). The concept of this plant forms a good model for discussion of the habit and gross morphology of *Wuxia* because it is one of the most complete examples of knowledge of Devonian lycopsid anatomy and morphology. *Longostachys* has a pseudobipolar growth habit, with a downward-directed dichotomizing rooting system (lacking rootlets) and an upward-directed trunk with a crown of upward-pointing isodichotomous branches with terminal cones. It reached an estimated height of ca. 1.5 m. *Chamaedendron multisporangiata*

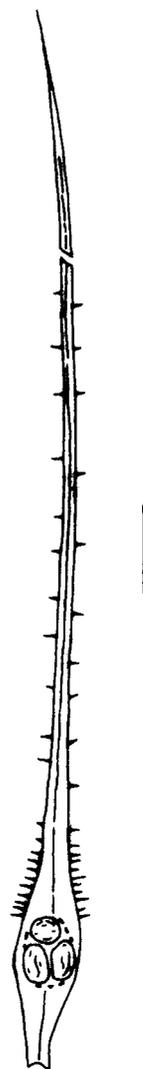


Fig. 4 *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov. Reconstruction of one megasporophyll. Scale bar represents 10 mm.

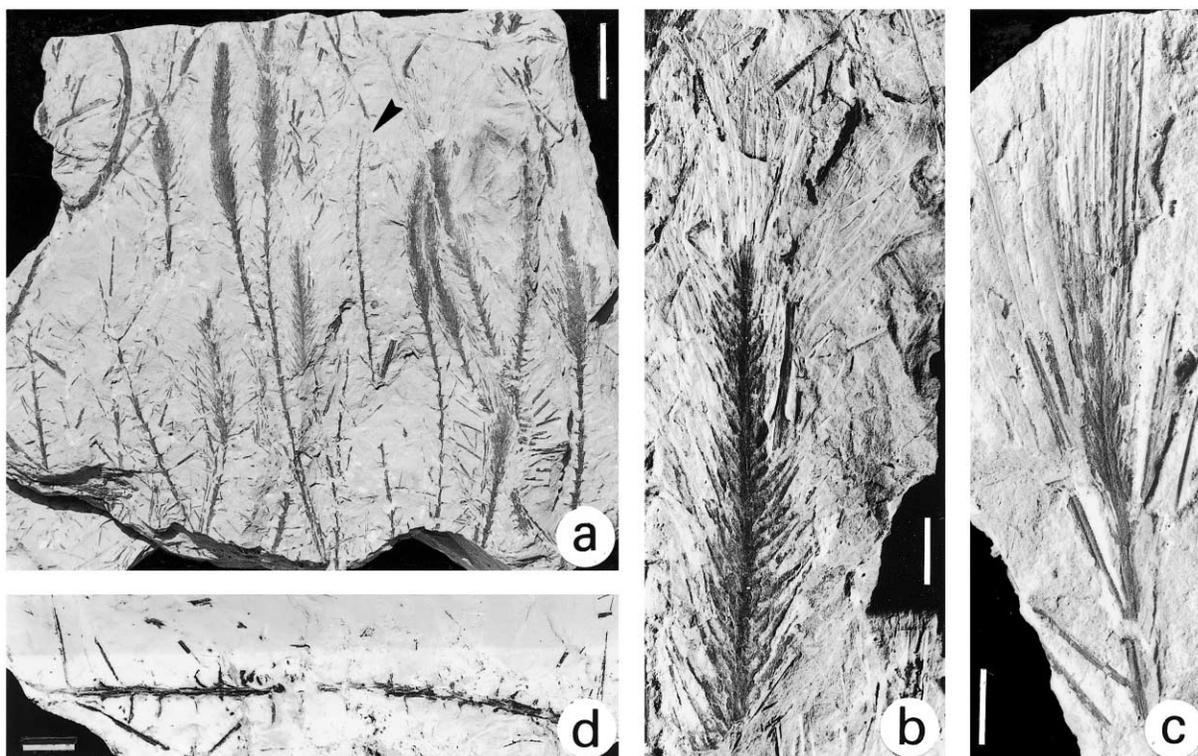


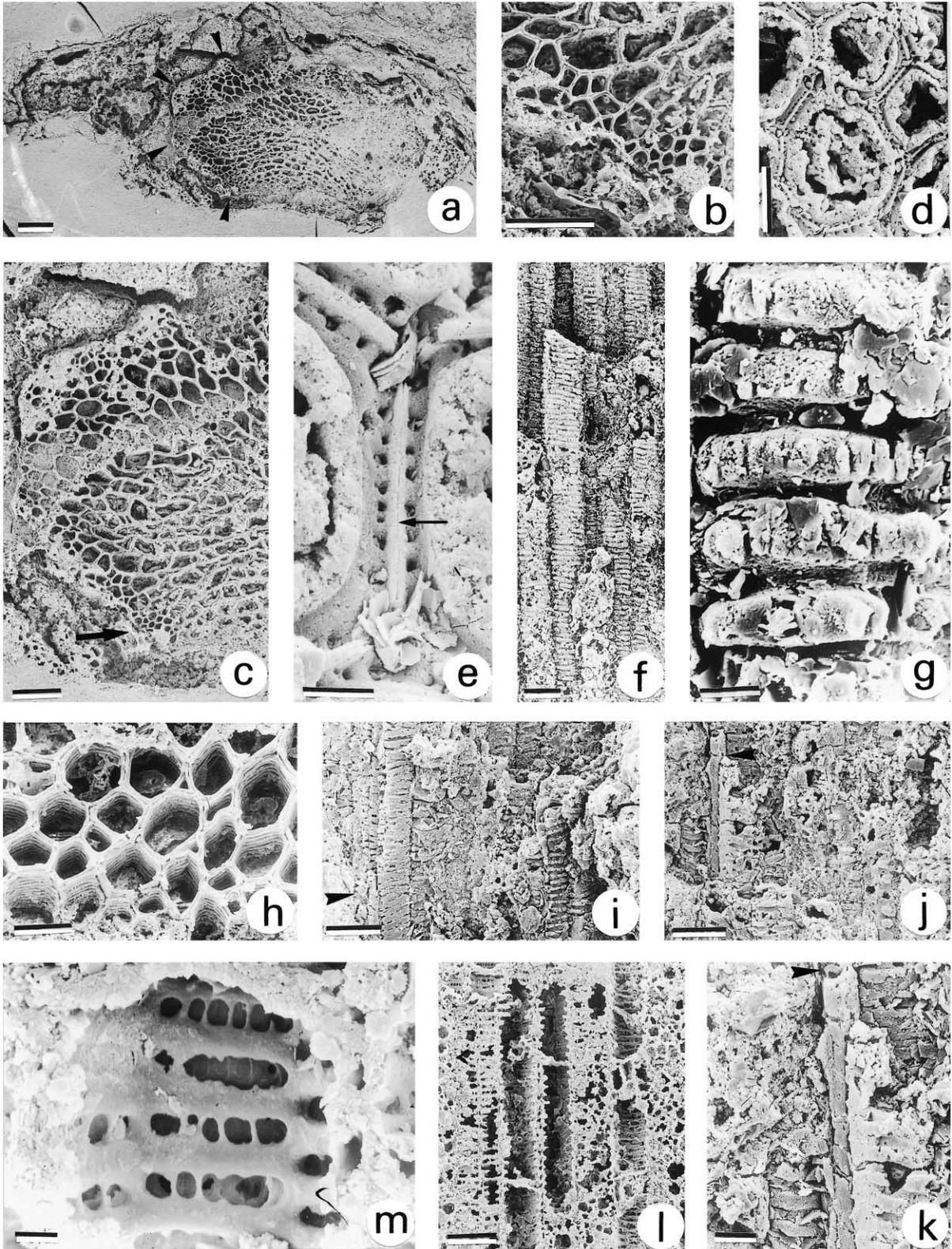
Fig. 5 *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov. *a*, Second largest slab (reverse of fig. 3*a*), showing the presumed microsporangiate cones. Arrowhead indicates termination of sterile axis (see fig. 2*e*). Specimens PB18864, 75–77, scale bar = 50 mm. *b*, *c*, Presumed microsporangiate cones demonstrating difference in preservation between narrow leaf laminae and area around the central axis suggestive of poorly preserved sporangia. Specimens PB18875, 78, scale bar = 10 mm. *d*, Axis from which permineralized tissues were removed (see fig. 2*g*, extreme left; fig. 6). Specimen PB18868, scale bar = 20 mm.

tum Schweitzer and Li (1996) from the Upper Devonian (Frasnian) of Hubei province has a similar growth habit and morphology but is of smaller size and lacks secondary tissues. The new plant reported here is represented by aerial branches and fertile units only, as we lack details of roots and trunk. Points of morphological similarity include the long sterile leaves with marginal spines, sporophylls with an enlarged proximal region crudely protecting the sporangium, and isodichotomous branching of axes. In terms of anatomy, the cylindrical exarch protostele with many ridges of protoxylem is common to many Devonian lycopsids, and the scalariform tracheids are common to *Chamaedendron*, *Longostachys*, and *Wuxia*. Between the bars of the tracheids of *Wuxia* are well-developed longitudinal fibril structures, and these have been observed in *Longostachys* but not *Chamaedendron*. The main observed point of dissimilarity in *Wuxia* is the fact that the megasporangiate conelike structures are not terminal but occur at branching points. In *Chamaedendron*, there are no well-developed cones, but rather the sporophylls are spread along parts of the branching systems including across dichotomies. According to the illustrations, the proximal part of the sporophyll is only slightly enlarged as compared with the sterile leaf. Only megaspores were illustrated by Schweitzer and Li (1996). Although it was claimed that microsporangiate sporophylls were present with multiple sporangia, no spores were illustrated and it is unclear if the multiple “microspangia”

they illustrated, rather, represent megaspores. In *Longostachys*, cones are distinct from sterile axes because they have a denser insertion of leaves as in *Wuxia*. However, the cones of *Longostachys* are found on the distal branches only, and only megasporophylls were found—microspores remain unknown. *Wuxia* remains unique among Chinese Devonian lycopsids because it is the only one in which two distinct “cone” types have been recognized. However, there must remain some doubt about this character, since microspores and microsporophylls are unknown in *Longostachys* and *Chamaedendron*, and male cones only are inferred in *Wuxia*.

Outside of China, spoon-shaped sporophylls with spiny margins are known in the cones of *Barsostrobus famennensis* (Fairon-Demaret 1977, 1991) from the Upper Devonian (Famennian) of Belgium. Little is known of the remainder of the plant; it has a typical exarch protostele like the Chinese plants but differs in the marked terete pedicel at the base of the leaf and the more emphasized folding of the proximal margins of the megasporophyll about the sporangium. Cones are terminal. Isolated spoon-shaped sporophylls with spiny margins are also known from the Upper Devonian of South Africa (Gess and Hiller 1995), although the parent plant remains unknown.

The Middle Devonian (Givetian) lycopsid cone *Mixostrobus* (Senkevitch et al. 1993) from Kazakhstan represents a grade of organization in which the cone contains a mixture of mega- and microsporangia. *Bisporangiostrobus* (Chitaley and



McGregor 1988), from the Upper Devonian of Pennsylvania, has microsporangia distally and megasporangia proximally in the cone, with a transition zone between. *Wuxia* is distinct from both these taxa on the basis of its apparently distinct microsporangiate and megasporangiate cones.

Cyclostigma kiltorkense Haughton from Ireland (Chaloner 1968) has a cone with sporophylls that abscise to form a leaf scar with parichnos. Such abscission and scar is not known in *Wuxia*. The sporophylls have a narrow proximal region (pedicel) on top of which the sporangium sat and a long tapered lamina with a fimbriate margin.

In comparison to members of Protolpidodendrales, *Wuxia* has a leaf that is essentially long and undivided, unlike the divided leaves of such taxa as *Colpodexylon* Banks (1944), *Leclercqia* Banks et al. (1972), and the broad deltoid laminae of *Haskinsia* Grierson and Banks (1983). Protolpidodendrales have sporophylls that are undifferentiated from the sterile microphylls and are not distinctly arranged into cones. Distinctive scalariform tracheids (as found in *Wuxia*) with prominent longitudinal structures connecting the bars are observed in one member of Protolpidodendrales, *Minarodendron* Li from the Middle Devonian (Givetian) of Yunnan Province, China. Li (1990, text; figs. 5, 6) summarized the structure of this type of cell and its various stages of preservation. He described the tracheids of *Minarodendron* as having “multiperforate bordered pits.” That is to say he interpreted the chambers between the scalariform bars to be covered with a “pitlet sheet” into which are sunk a number of holes (pitlets) connecting the chamber to the cell lumen. In *Wuxia*, scalariform bars and the fibril structures between them compare in almost every way in all states of preservation (cf. Li 1990, pl. 6, fig. 3 with our fig. 5e) except that we place more emphasis on the individual fibrils between the scalariform bars than we do on recognizing them as amalgamated and extended to form a “pitlet sheet.” In *Leclercqia* (Grierson 1976) and *Haskinsia* (Grierson and Banks 1983), bordered pits only are illustrated that have no form of longitudinal subdivision of the chamber aperture. Among non-protolpidodendralean lycopsids, some holes are observed within the sheets between scalariform bars in the Famennian *Barsostrobus* (Fairon-Demaret 1977), longitudinal bars were observed across the chamber apertures of Lower Carboniferous (Visean) *Eskdalia* from England (Rowe 1988b), and a more complex network of interconnecting structures was observed in *Selaginellites* from the same locality (Rowe 1988a). These structures taken together indicate a continuum of forms from those with distinct longitudinal fibrils to those with a sheet of material with a number of oval or circular apertures between the scalariform bars.

Of Protolpidodendrales, the Chinese *Minarodendron* shares the most characters with *Wuxia*. These include an almost identical construction of primary xylem tracheids incorporating substantial longitudinal fibril structures between scalariform bars and spiny margins to the microphylls. These contrast with the known Laurussian Protolpidodendrales that have tracheids with bordered pits and microphylls with simple margins. Thus, the earliest known examples of bipolar lycopsids (*Longostachys*—Givetian) share the characteristic scalariform tracheids with fibrils or equivalent structures and spiny leaf margins with both *Minarodendron* (Givetian) and *Wuxia* (Famennian). These characters were more geographically widespread by the Famennian. The observed distribution of characters indicates that China may have been an important area of evolutionary innovation in lycopsid morphology and development and points to the possible evolution of *Longostachys*-type bipolar lycopsids from *Minarodendron*, these taxa being known only from China.

Comparison to Carboniferous Lycopsid Taxa

The most well-known Carboniferous lycopsid taxa are rhizomorphic, and without knowing the rooting system of *Wuxia*, the value of comparisons is lessened. However, with regard to fertile characters, many Carboniferous genera had megasporangia in which only a single functional megaspore was retained. These include *Lepidophloios* and *Diaphrodendron*. These are clearly distinguished from *Wuxia* that had large megaspores with large distinctive trilete marks, demonstrating that tetrads were fully developed within the sporangium.

Sigillaria, like *Wuxia*, had two types of monosporangiate cones, the megasporangiate with sporangia containing multiple megaspores and the microsporangiate with sporangia with numerous microspores. However, leaves were abscised, cones were borne on short lateral branches, and the tree was not so profusely branched as inferred for *Wuxia*.

Anabathra, a genus that ranges from the Lower Carboniferous (Visean) into the Upper Carboniferous, bore bisporangiate cones at the ends of the lateral branches (DiMichele 1980). It was therefore “primitive” with respect to fertile characters as compared with *Wuxia*.

Classification

Higher-level classification of *Wuxia* is impossible because of the lack of many diagnostic features, in particular the rooting system and many anatomical details. This is regretful in that the most informative discussions of lycopsid phylogeny are

Fig. 6 *Wuxia bistrobilata* Berry, Wang et Cai gen. et sp. nov. SEM micrographs of permineralized tissues from specimen PB18868 (see fig. 5d). *a*, Transverse view, arrowheads indicating protoxylem ridges. Scale bar = 200 μm . *b*, Detail of *a*, a protoxylem ridge. Scale bar = 100 μm . *c*, Detail of *a*; arrow indicates position of protoxylem area shown in *b*. Scale bar = 100 μm . *d*, Lumen and pit casts of metaxylem tracheids. Scale bar = 20 μm . *e*, Detail of *d*, pit pair cast, arrow indicating the middle lamella. Scale bar = 5 μm . *f*, Metaxylem tracheids, lumen, and pit casts, longitudinal view. Scale bar = 50 μm . *g*, Detail of *f*, pit casts, showing the aperture and position of narrow fibrils. Scale bar = 5 μm . *h*, Metaxylem tracheids in oblique view. Scale bar = 50 μm . *i*, *j*, Longitudinal view of lumen and pit casts, arrowheads indicating probable helically thickened tracheids (protoxylem). Scale bars = 30 μm . *k*, Detail of *j*, arrowhead indicating helical tracheid. Scale bar = 10 μm . *l*, Metaxylem tracheids with some preservation of coalified wall material. Scale bar = 50 μm . *m*, Detail of *l*, showing the narrow longitudinal fibrils across pit apertures. Scale bar = 5 μm .

based on analysis of many characters drawn from detailed knowledge of both anatomy and morphology of whole plants (Bateman et al. 1992), and it is to the Carboniferous rhizomorphic lycopsids that the most fascinating comparisons might be made. The lack of rooting structures does not even allow us to know if it should be included in the rhizomorphic lycopsids or not. Neither can we include *Wuxia* in the Devonian Longostachyaceae of Cai and Chen (1996), as the diagnosis of that family includes terminal cones.

An interesting observation concerning *Wuxia* is that although the inferred reproductive characters (separate male and female monosporangiate “cones”) are relatively advanced, there is no abscission of the leaves, and the leaf base/cushion is relatively poorly developed, the latter character typically found in some of the Carboniferous lycopsids that retained bisporangiate cones (e.g., *Anabathra*, *Chaloneria*; Bateman et al. 1992). We can only suggest at present that *Wuxia* is an early example of the plexus of bistrobilate lycopsids from which the more advanced forms that retained only a single functional megaspore in each fertile female sporangium were to emerge. Therefore, we prefer to leave the new lycopsid *incertae sedis* at present until further characters are established.

Summary

Wuxia is the oldest example of a lycopsid inferred to have two types of cone, one containing microspores and one containing megaspores. Although we cannot see the sporangia in our fossils clearly, we interpret the large trilete marks observable on the spores to infer that megasporangia contained at least one tetrad. In Bateman's (1992) cladistic analysis of lycopsids, the acquisition of fertile characters was mapped onto

a cladogram of Carboniferous rhizomorphic forms. Plants with two types of cones (bistrobilate) form a derived clade within this group.

We cannot be sure that *Wuxia* had a true rhizomorphic rooting system given that the most morphologically similar plants (*Longostachys*, *Chamaedendron*) lack rootlets. This character is among the most important for interpreting the early history of lycopsids. Furthermore, important details of leaf anatomy (presence/absence of parenchyma, etc.) and many other characters remain unknown. Therefore, there are two possibilities: that *Wuxia* is a latest Devonian example of a rhizomorphic lycopsid with a bistrobilate reproductive syndrome, or that the bistrobilate condition arose in more than one lineage of lycopsids.

Despite the advanced status of the reproductive organs, the plant retains “primitive” characteristics such as the relatively unprotected sporangia and the spiny sterile leaves. There remains much to be learned about the early history of pseudobipolar lycopsids.

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