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Source: *International Journal of Plant Sciences*, Vol. 167, No. 3 (May 2006), pp. 551-566
Published by: The University of Chicago Press
Stable URL: http://www.jstor.org/stable/10.1086/501234
Accessed: 21/02/2014 09:00

Int. J. Plant Sci. 167(3):551–566. 2006.

1058-5893/2006/16703-0016$15.00

EOCLADOXYLON (*PROTOPTERIDIUM*) *MINUTUM* (HALLE) KOIDZUMI FROM THE MIDDLE DEVONIAN OF YUNNAN, CHINA: AN EARLY *RHACOPHYTON*-LIKE PLANT?

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New specimens of *Eocladoxylon* (*Protopteridium*) *minutum* (Halle) Koidzumi collected from the Middle Devonian Xichong Formation, Yunnan province, China, demonstrate three orders of branching. Sterile branching systems have a pinnate two-dimensional branching pattern with alternate insertion of lower orders. Up to several times deeply dissected, overall wedge-shaped, flattened appendages are inserted alternately on the third order of branching. Second and third orders of branching have an opposite pair of similar appendages inserted at the base, perpendicular to the plane of the remaining branching system. Fertile appendages, consisting of a dichotomous axial system and terminal pairs of sporangia attached closely in groups of eight, replace the sterile appendages in fertile branches. Anatomy of a probable second-order axis demonstrates a bipolar clepsydroid vascular system. The sterile branching system and anatomy bear some similarity to the Late Devonian fernlike plant *Rhacophyton*. *Eocladoxylon* is neither a cladoxylopsid nor a progymnosperm, as was previously believed. The potential for an ancestor/descendant relationship between Iridopteridales and *Rhacophyton* via *Eocladoxylon* is briefly discussed in the context of the geographical isolation of the Middle Devonian flora of South China.

Keywords: Devonian, plant fossils, Iridopteridales, *Rhacophyton,* Xichong Formation.

Introduction

Halle (1936) described three plants from the Lower and Middle Devonian of Yunnan, South China. One of these was attributed to the genus *Protopteridium* Krejci (1881) as the new species *Protopteridium minutum* Halle. The locality was in a light-gray shale just above a bed containing *Drepanophycus* in the Longhuashan (Longhua Mountain) section, ca. 2 km west of Zhanyi (fig. 1). His specimens are very small coalified compressions that fragment easily, and little is now left of the original fossils. He recognized two orders of branching that bore dichotomous planated appendages that looked like primitive leaves. He also found ovoid to fusiform sporangia attached to dichotomous unplanated appendages. He produced a small partial reconstruction of the branching system (fig. 2*b*). A single large appendage was illustrated close to the base of the second-order axis.

Koidzumi (1943) reiterated Halle's description of the plant but rejected the attribution to the genus *Protopteridium*. He therefore created a new generic name, *Eocladoxylon* Koidzumi.

Hsü (1966) described more specimens from the same locality. It was his opinion that the plant was not small but attained a height of 1 m and had a main axis 18 mm in diameter. However, he did not illustrate any relatively complete large specimens to support this. He considered that some primary and secondary branches divided dichotomously and provided a new reconstruction (fig. 2*a*) as well as detailed descriptions of the various organs of the plant. In his reconstruction, leaves alternate along the second-order axes but are occasionally replaced by what appear to be third-order axes.

Obrhel (1966) made a survey of the then well-known species of *Protopteridium* and decided that the Chinese species was sufficiently distinct to be transferred to a new genus under the name *Cathaiopteridium minutum*, but he was unaware of the name *Eocladoxylon* previously proposed by Koidzumi. *Cathaiopteridium* is therefore invalid.

Schweitzer and Cai (1987) described some new fragmentary material from Panxi, near Huaning (Yunnan province), from the Lower Huaning Formation of Givetian age. They believed the appendages to be three-dimensionally branched. However, they provided a generic diagnosis based on Hsü's material and attributed the plants to the "Progymnospermales." They also illustrated some other fossils, one of which is certainly *Eocladoxylon*, under the name *Pseudosporochnus nodosus* Leclercq and Banks. These last fossils are from Xichong and probably from the same locality as the fossils we describe here.

This study is in the context of a revision of the Yunnan Middle Devonian flora based on large collections we have made over the last 7 yr and building on the already extensive field campaigns of Cai Chongyang. In taking advantage of better transportation of both paleontologists and specimens, together with new road-building activities and exposures, we have been able to improve on the quantity and size of the specimens collected and therefore to make updated reassemblies and reconstructions of many of the Yunnan plants (e.g., Wang and Berry 2003) as well as to describe new ones (e.g., Wang and Berry 2001*a*). Such studies allow us in turn to reassess the taxonomic affinities of the constituents of the flora,

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Manuscript received September 2005; revised manuscript received January 2006.

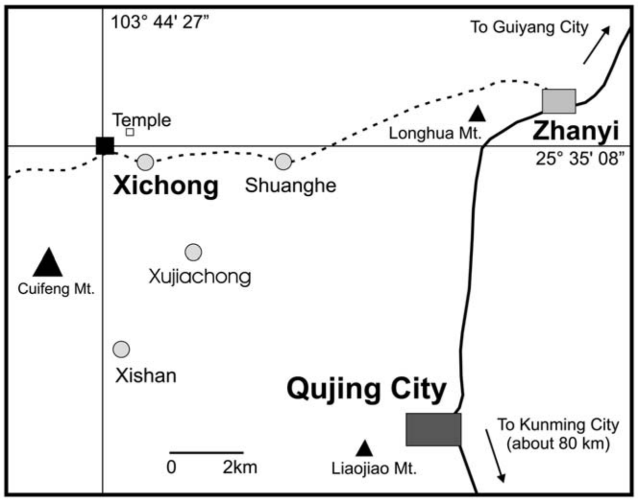

Fig. 1 Map of the fossil locality near Xichong Village, Zhanyi, in Yunnan province, China.

with the eventual aim of assessing its paleogeographic and evolutionary significance.

Material and Methods

The fossils were found in the top part of the Xichong Formation, at an outcrop on the north side of the track leading from the west of Xichong village, near Qujing (Chütsing) City, Yunnan province (fig. 1). In this section there are a number of plant-bearing localities, but the *Eocladoxylon* locality (our locality XCF3) is the westernmost along this road section before a large break in the exposure, ca. 400 m northwest of the main road junction in Xichong. The locality is at lat. 25°35′08″N, long. 103°44′27″E (WGS84 datum). The lithology is a light-gray coarse mudstone that weathers with a yellowish-green tint.

The age of the Xichong Formation is regarded as Givetian based on spores recovered from the upper part of the formation, 7 km southwest of Xichong (Lu and Ouyang 1978; Lu 1980). This age determination is supported by numerous finds of invertebrate and fish fossils found in this formation (see summary in Schweitzer and Cai 1987). However, we are unaware of any dating of the Xichong Formation section at Xichong directly.

The fossils are preserved predominantly as impressions and coalified compressions and were therefore studied using the dégagement method of Leclercq (Fairon-Demaret et al. 1999). Macrophotographs were taken using Nikon 35-mm camera systems and crossed polarized illumination. Microphotographs were taken using a Leica M-12 stereomicroscope and polarized annular ring lighting.

The single anatomical specimen was prepared from a short section of presumed second-order axis that was mostly encased by a matrix, allowing a complete transverse section to be obtained. The preservation of the vascular strand appeared to be in red hydrated iron oxides (limonite), but preparing sections using the method of Stein et al. (1982) did not produce fully cleared sections. The semiprepared sections were therefore examined and photographed using a Vannox reflecting light microscope. Further fragments of the same specimen were mounted on aluminium stubs and examined with a scanning electron microscope (SEM; extra-high tension = 15 kV).

Systematic Paleobotany

Order and Family—Incertae sedis

Genus—Eocladoxylon *Koidzumi (1943) emend.*

Emended generic diagnosis. Sterile and fertile branching systems with three orders of axis known. Second- and third-order axes inserted on first and second orders in an alternate pinnate arrangement in a single plane. Planated, deeply dissected sterile appendages with acute apices inserted alternately on third-order branches also in a single plane; similar sterile appendages attached as opposite pairs at the bases of second- and third-order axes more or less perpendicular to the plane of the principal branching system. Fertile appendages consisting of a dichotomous, three-dimensional axial system and terminal paired sporangia inserted onto third-order axes in an alternate arrangement, with opposite fertile appendages inserted at the base. Protostele clepsydroid with two protoxylem

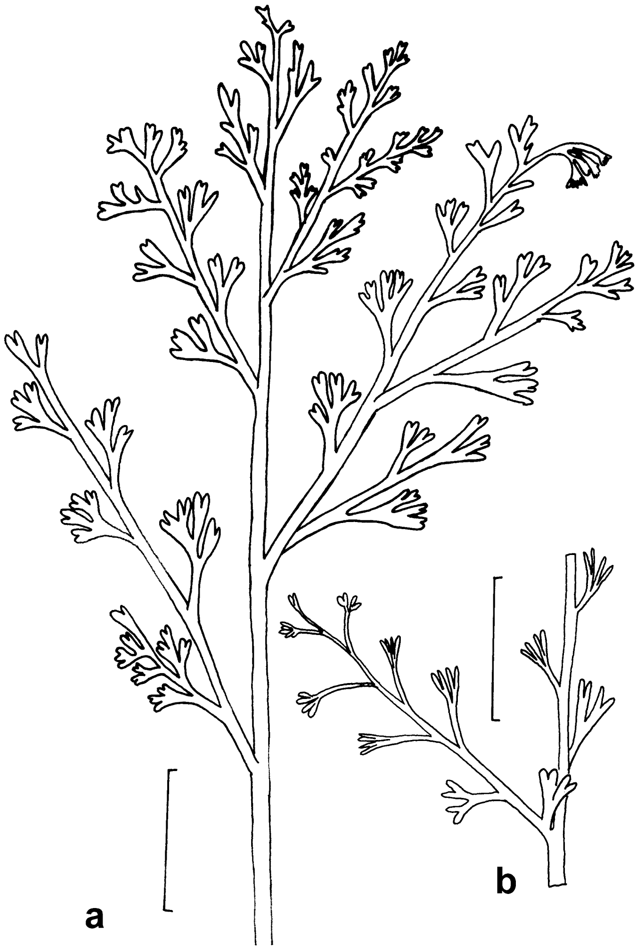

Fig. 2 Previous reconstructions of *Eocladoxylon minutum*. *a*, Redrawn from Hsü (1966). Scale bar = 20 mm. *b*, Redrawn from Halle (1936). Scale bar = 10 mm.

columns positioned toward the middle of each lobe where known (?second order).

Type species. *Eocladoxylon minutum* (Halle) Koidzumi emend.

Eocladoxylon minutum *(Halle) Koidzumi emend.*

1936 *Protopteridium minutum* Halle: Halle, pp. 16–22; pls. 4, 5; fig. 2.
1943 *Eocladoxylon minutum* (Halle) Koidzumi: Koidzumi, p. 64; fig. 13.
1966 *Protopteridium minutum* Halle: Hsü, pp. 56–62; pl. III, 2–4; pl. IV, 2–7; pl. V, 2–9; pl. VI, 5–8; figs. 6–12.
1966 *Cathaiopteridium minutum* (Halle) Obrhel: Obrhel, p. 442.
1974 *Protopteridium minutum*: Gu and Zhi, p. 16; pls. 2, 8–14; pl. 3, 1; fig. 20.
1987 *Pseudosporochnus nodosus* Leclercq and Banks: Schweitzer and Cai, fig. 17*a*.

Emended specific diagnosis. Plants as generic diagnosis. First-order axes 4–6 mm in diameter, second-order axes 1.5–2.5 mm in diameter, third-order axes 0.5–1 mm in diameter. Paired appendages at base of second-order branches up to 16 mm and divided isotomously (deeply dissected) up to four times. Appendages on third-order branches up to 12 mm in total length with three isotomies. Fertile units made up of terete axial system isotomously divided two or three times, with terminal sporangia arranged in clusters of two closely inserted pairs terminating at approximately the same level; sporangia $1.3–3 \times 0.3–0.6$ mm, approximately ellipsoidal with one slightly straighter inner margin and slightly pointed to slightly rounded apices. Second-order axis with primary xylem column ca. 2.0 mm wide, with largest xylem cells 30–40 μm in diameter, protoxylem cells ca. 10 μm in diameter.

Description

The description is based on a collection of ca. 100 new specimens. Most are quite small, fragmentary, and poorly preserved. Only two are large enough and well enough preserved to demonstrate the attachment and nature of three orders of branching when extensively dégaged. In the most complete of these specimens (fig. 3*a*, 3*f*; fig. 4), the first-order axis is 5 mm in width and is preserved over a length of 120 mm. The best-preserved second-order axis is 2 mm in width and preserved over a length of 75 mm. The third-order axis is ca. 21 mm in length and 1 mm in width and has conspicuous lateral, deeply dissected, planated appendages on either side of it.

*First-Order Axes (Fig. 3*a*, 3*b*, 3*d*, 3*f*; Figs. 4, 5)*

The largest order of axes has preserved diameters of 4–6 mm. They flex slightly at the attachments of second-order branches, giving a slight zigzag to their appearance (fig. 3*a*, 3*b*). The surface of the axis is essentially smooth, lacking spines or emergences, but is characterized by the presence of one or two longitudinal ridges or folds on the surface of the impression fossils (fig. 3*b*, 3*d*). The longest first-order axis in our collection is 23 cm long and 4 mm wide.

The second-order branches are inserted alternately in two opposite ranks in most specimens. In the largest illustrated specimen (fig. 3*a*), the distance between successive second-order branches is ca. 20 mm. In figure 3*b*, it varies between 15 and 18 mm. In figure 3*d* (see also fig. 5), it varies from 11 to 12 mm. In most specimens the insertion of the second-order branches is on the surface of the bedding plane. No appendages are inserted directly onto the first-order axes.

In the largest illustrated specimen (fig. 3*a*, 3*f*; fig. 4), the two most proximal second-order branches are preserved flat on the plane of the specimen surface, but the third and fourth are inserted approximately perpendicular, the third projecting above the matrix and the fourth down into the matrix, slightly to the left of the first-order branch (see fig. 4). The most distal is inserted to the right of the first-order axis on the plane of the surface of the slab. These orientations are consistent with an alternate arrangement that has been twisted a quarter of a turn clockwise (looking from proximal to distal) at nodes 3 and 4 and another quarter turn at node 5, a hypothesis consistent with the fact that this part of the branch appears distorted and twisted. Proximally, until node 2, the axis impression is 3.8 mm wide, and the surface is parallel to the surface of the slab. Above node 2, the apparent axis width narrows, and the axis surface angles down to the right. Then, after a short section is missing on the right-hand margin, the stem surface slopes down to the left. The apparent stem width widens as the surface flattens out between nodes 4 and 5. This specimen therefore does not contradict our observation from other specimens, both illustrated and unillustrated, that the arrangement of the second-order branches is alternate and essentially two-dimensional on the first-order branch.

A second example, with three orders in connection (figs. 3*d*, 5), has six alternating second-order axes attached in two ranks of three. The compressed surface of the axis is flat.

A third well-preserved first-order axis, 4 mm in width, has five attached laterals, the first and last being preserved only at their bases but the middle three having the stature of second-order axes (fig. 3*b*). The surface of the stem impression is more or less flat, except at the second node, where the surface of the impression and the second-order axis slopes a little down into the matrix. The specimen strongly suggests that the first-order axis had second-order axes arranged in two ranks in an alternate pattern. Alternate insertion of second-order axes is also illustrated in figure 3*c*.

*Second-Order Axes (Fig. 3*a*–3*f*, 3*h*)*

At the base of the second-order branches, two prominent appendages are inserted, one above and one below the second-order branch, looking down onto the specimen spread out on the matrix. In the most complete branch system, only the upper of these appendages are visible (fig. 3*a*, large arrow). In this specimen, the appendage is 11 mm long and dichotomizes twice, ending in four terminal segments, although these are probably incomplete distally. The base is broad (3 mm) and the terminal segments quite narrow (>1 mm), and the overall appearance is of a structure that is flattened rather than terete in cross section. The position of the second appendage is marked by a deep depression going downward underneath the branch (fig. 4*a*, arrow). In a second specimen, the basal appendage (fig. 3*b*, arrow) is 13 mm in total length and dichotomizes at least three times. In other examples attached to branches of similar size, which, however, do not have more orders of branching attached to them (i.e., determination of branch order based on anything other than size is impossible),

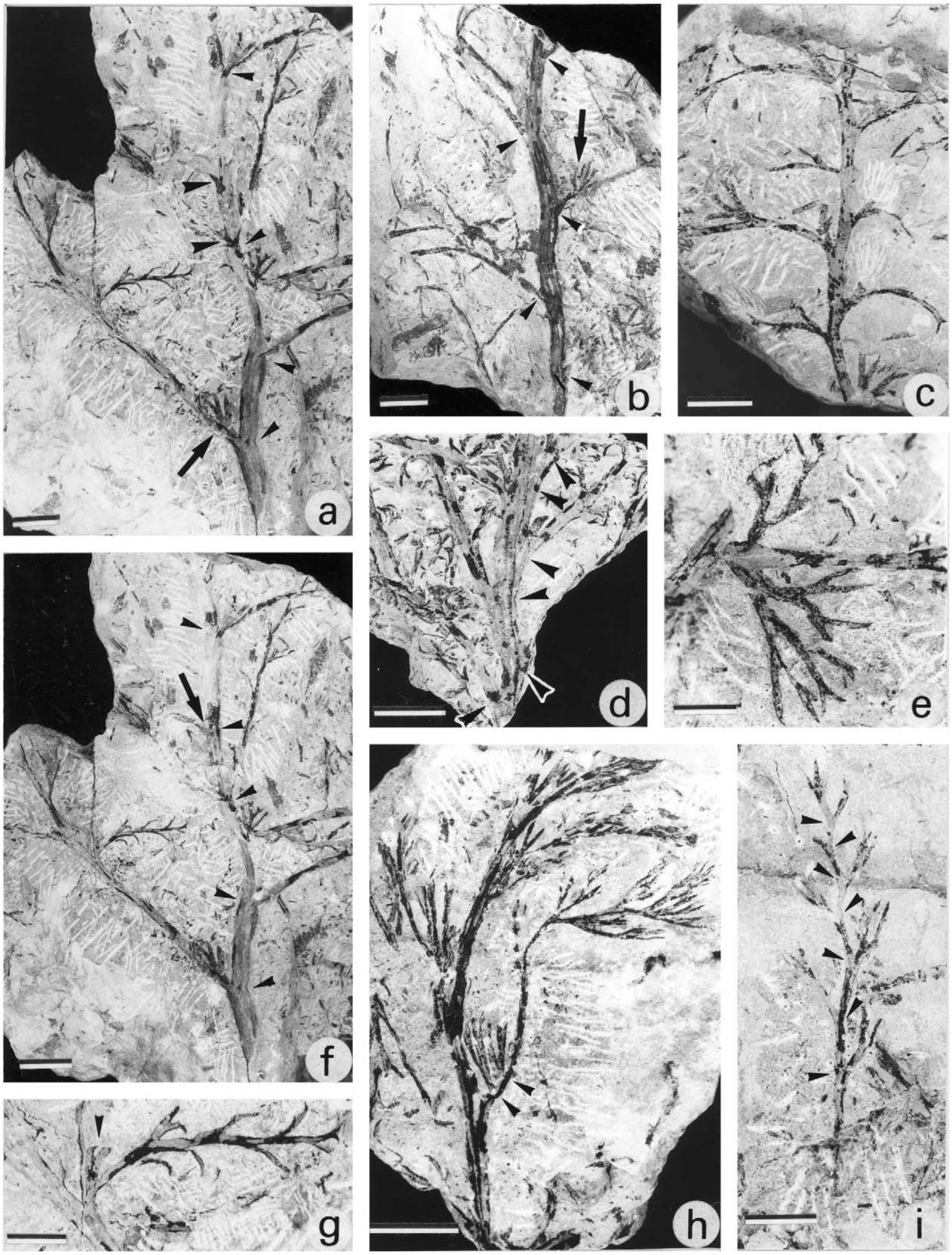

Fig. 3 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. *a*, *f*, First-, second-, and third-order axes in organic connection, showing two stages of dégagement. Arrowheads indicate nodes on first-order axis. Large arrow in *a* shows position of one prominent appendage at base of second-order axis. Large arrow in *f* indicates position of the fourth node on the first-order axis uncovered by dégagement. For line drawing interpretation, see fig.4. PB18917. Scale bar = 10 mm. *b*, First- and second-order axes; arrowheads indicate

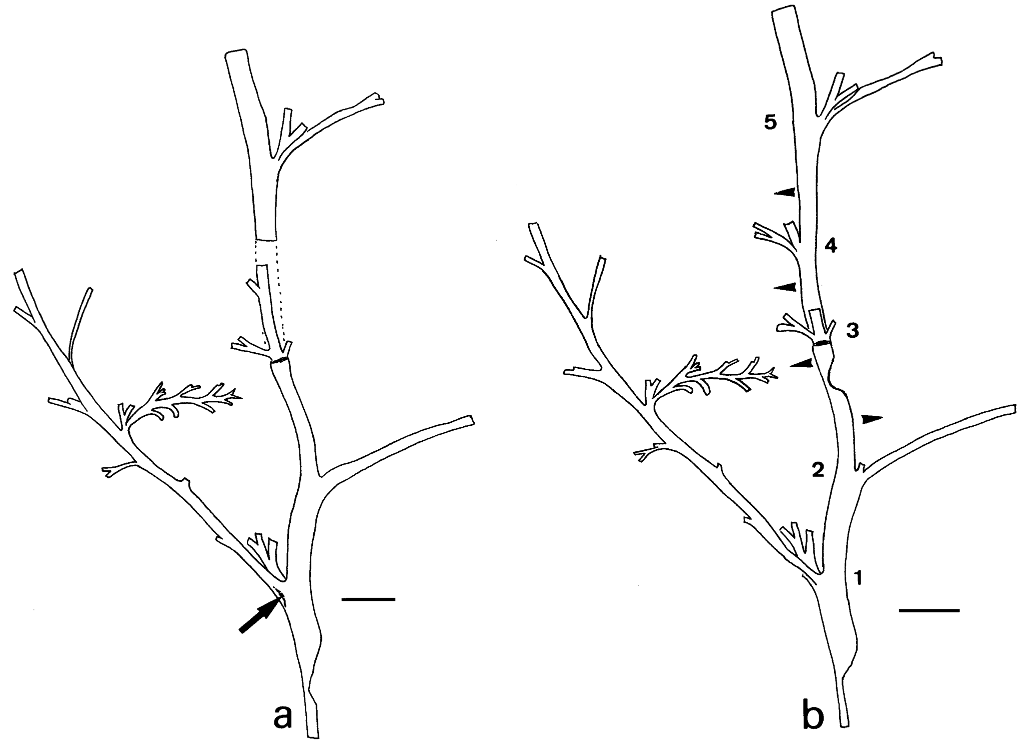

Fig. 4 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretation of two stages of dégagement of specimen showing three orders of branching in organic connection (for photos, see fig. 1*a*, 1*f*, 1*g*). Five nodes on first-order axis demonstrated (numbers). *a*, First stage; node 3 shows a lateral branch with paired basal appendages; arrow marks depression at base of second-order axis indicating presence of a second prominent appendage. *b*, Part of second-order axis at node 3 removed to reveal attached axis at node 4. Note that the first-order axis is twisted a quarter turn between nodes 2 and 3 and between nodes 3 and 4; arrowheads indicate downward slope of stem compression where not flat on surface of slab. PB18917. Scale bar = 10 mm.

the paired appendages may have up to four dichotomies and may be up to 16 mm long (fig. 3*e*).

Second-order axes are 1.5–2.5 mm in diameter when found in attachment to first-order axes. They have one or two longitudinal ridges or furrows visible on the surface of the impressions. The longest preserved in attachment (fig. 3*a*) is 72 mm in preserved length and 2 mm in diameter. In this example, the bases of third-order branches are preserved alternately in the same plane as the other two orders of branching, their separation along the second-order branch being 8 mm (fig. 4*a*, left).

Third-Order Axes (Figs. 3g–3i*, 7*a*, 8)*

The bases of third-order axes are also subtended by a pair of dichotomizing opposite or subopposite appendages that appear more slender than those of the second order, but with up to three bifurcations over a length of 8 mm (fig. 3*g*; fig. 7*a*, 7*b*; fig. 8, arrowheads). They have acute tips and are essentially planated. These basal appendages can occur a short distance along the third-order branch as well as at the intersection of second- and third-order branches.

The only well preserved third-order axis in organic attachment to the second- and first-order axes measures 21 mm long, although it is slightly incomplete distally (fig. 3*a*, 3*g*; fig. 4). This was dégaged entirely from within the matrix. It has at least seven lateral appendages on it, arranged oppositely and alternately, which each dichotomize once. The axis is ca. 0.5 mm in diameter.

Another example (figs. 7*a*, 8) is 25 mm long (although incomplete) and 0.7 mm in diameter, with 4–5-mm-long appendages that dichotomize up to two times. Another (fig. 3*i*) is 30 mm in length and 0.5 mm in diameter, with once-branched opposite and alternate appendages and with an appendage at the apex.

The longest branching system that has potentially the same architecture as those described above is 45 mm in length and

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nodes. Arrow shows one prominent appendage at base of second-order branch. PB18918. Scale bar = 10 mm. *c*, First-order axis. PB18919. Scale bar = 10 mm. *d*, First-, second-, and third-order axes in organic connection. Arrowheads indicate nodes on first-order branch. Note ribbing of first-order axis. For line drawing interpretation, see fig. 5. PB18920. Scale bar = 10 mm. *e*, Paired appendages at base of second-order axis. PB18921. Scale bar = 5 mm. *g*, Third-order axis enlarged from *a* and *f*, with prominent basal appendage (arrowhead). Note that a prominent crack runs through this specimen to the left of the basal appendage (see *f*). Scale bar = 5 mm. *h*, Second- and third-order sterile axes with prominent paired basal appendages (arrowheads). PB18922. Scale bar = 10 mm. *i*, Isolated third-order axis showing alternate insertion of appendages (arrowheads). PB18923. Scale bar = 10 mm.

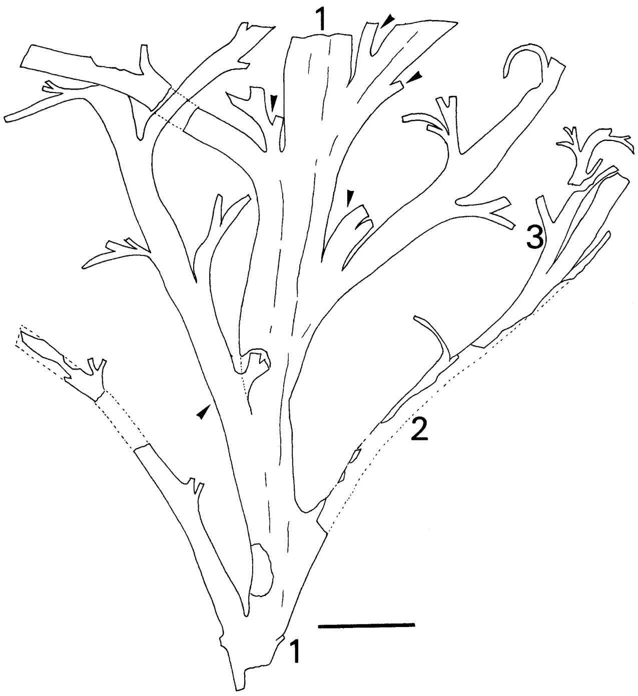

Fig. 5 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretation of fig. 3*d*. Three orders of sterile branching (numbers) in connection. Note prominent appendages well developed at bases of second-order branches. PB18920. Scale bar = 10 mm.

1 mm in basal diameter (fig. 3*h*). However, it is poorly preserved, and the axes and appendages have been distorted by water currents. It has seven or eight visible dichotomous appendages, up to 12 mm in total length, preserved along the margins, mostly crowded together at the apex. The appendages from the proximal parts of this axis are probably missing. It is illustrated here because it can be positively identified as *Eocladoxylon* at this locality on the basis of appendage morphology, but it also bears strong similarity to other specimens previously referred to another taxon (see "Comparisons").

*Sterile Appendages (Fig. 3*e*, 3*g*–3*i*; Fig. 7*a*–7*c*)*

Sterile appendages, whether they occur as opposite or subopposite pairs at the base of second- or third-order axes or opposite and alternate along third-order axes, have essentially the same morphological characters. In such compressed specimens, lacking anatomical preservation of the appendages, it is impossible to demonstrate conclusively that these appendages are flattened. However, they are much wider than normal for axial, terete, dichotomous structures in coeval vascular plants and are similar to structures found in some compressions of early Archaeopteridales. Furthermore, where compressed obliquely to a final angle of about 45°, they maintain a flat overall surface; no slivers of sediment are found in between the most basal parts of the axes distal to each dichotomy, as would be found if the axes were terete (because of the vertical overlap of terete axes when turned obliquely vs. no overlap when a planate, deeply dissected surface is turned obliquely). They very much give the appearance of being flattened photosynthetic organs. The width of the appendage segments decreases distally with progressive division. The largest examples are ca. 1.5 mm wide before the first dichotomy. We have observed up to four dichotomies in the largest examples and as few as one in the smallest. The tips are acute, and often the inner margins of the final pair of segments curve slightly outward (fig. 7*c*). The total length of these organs is from 15 mm to as little as 3 or 4 mm.

*Fertile Third-Order Axes (Figs. 7*d*–7*n*, 9–12)*

We have no definitive evidence of fertile branches attached to characteristic sterile ones or of partially fertile and partially sterile third-order axes, although a possible example is illustrated by Halle (1936; his pl. IV and fig. 6) and another by Schweitzer and Cai (1987; see "Comparisons"). Certainly, these are rare; none exist in our large collection. We base the determination of order of axis on their size because we have no fertile material with more than two orders of branching preserved.

The largest fertile specimen consists of a second-order axis bearing laterally two third-order axes (fig. 7*f*, 7*k*; fig. 9). The second-order axis (diameter 1.2 mm) is subtended by two third-order axes spaced about 8 mm apart. The most completely preserved of these axes is over 35 mm long and 0.7 mm in diameter. It overlies the second-order axis, but the basal few millimeters are preserved as impression only and are not obvious in the photographs (however, see fig. 9). It bears several dichotomous fertile appendages. Just above the base of this third-order branch, two fertile appendages are

Fig. 6 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Partial reconstruction of branching system. Scale bar = 10 mm.

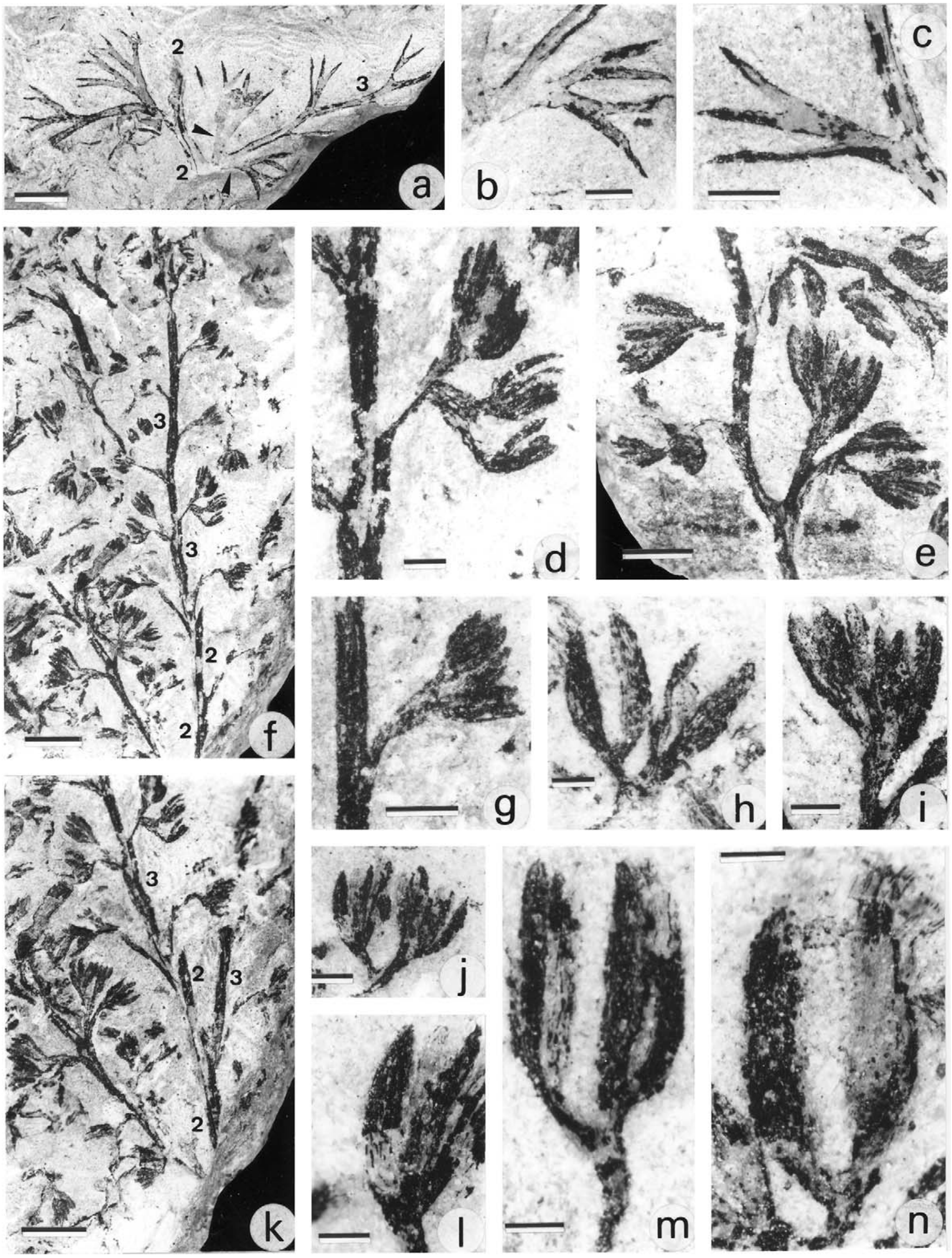

Fig. 7 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. *a*, More or less complete third-order axis demonstrating two basal appendages (arrowheads); for line drawing interpretation, see fig. 8. PB18924. Scale bar = 5 mm. *b*, Enlargement of lower basal appendage in *a*. Scale bar = 2 mm. *c*, Enlargement of lateral appendage midway along third-order branch in *a*. Scale bar = 2 mm. *d*, *e*, *g*–*j*, *l*, *m*, Close-up views of fertile appendages and sporangia, demonstrating sporangial pairs clustered into groups of four and eight on dichotomous terete axes. *d*, PB18925. Scale bar = 1 mm. *e*, PB18926. Scale bar = 2 mm. *g*, Scale bar = 1 mm. *h*, PB18927a. *i*, Enlargement of *e*. Scale bar =1 mm. *j*, PB18928. Scale bar = 1 mm. *l*, Enlargement of *j*. Scale bar = 0.5 mm. *m*, PB18929. Scale bar = 0.5 mm. *n*, PB18927b. Scale bar = 0.5 mm. *f*, *k*, Fertile branching system showing presumed second- and third-order branches in connection (numbers) in two stages of dégagement. *f*, View before uncovering. *k*, Lower third-order axis revealed. For line drawing interpretation, see fig. 9. PB18925. Scale bar = 5 mm.

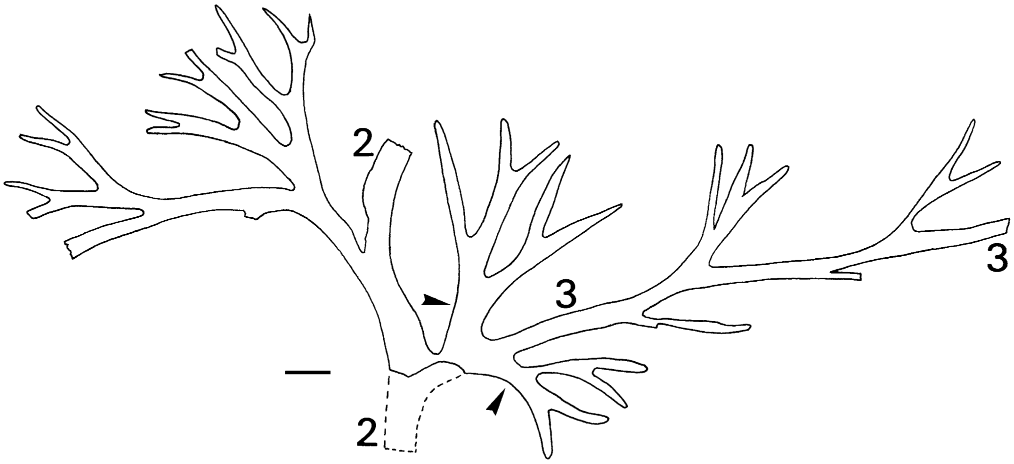

Fig. 8 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretation of fig. 7*a*. Sterile third-order axes attached to a second-order axis. Prominent basal appendages indicated (arrowheads). PB18924. Scale bar = 5 mm.

inserted suboppositely. Distal to this pair, fertile units are inserted in an increasingly alternate manner. The continuing second-order axis is largely covered by sediment (fig. 7*k*). The less well preserved, more proximal third-order axis (fig. 7*k*, right), lying at a level lower than the second-order axis, has been uncovered for only 10 mm so as not to destroy the overlying sporangia, but at the base two opposite appendages are inserted (fig. 9, bottom right). The basal pairs are inserted in the plane perpendicular to the plane of the second and third order of branching. The oblique fertile axis at the lower left in figure 7*k* is not organically attached to the second-order axis, perhaps because of the proximity of the margin of the slab; it may be a more proximal third-order axis of the same branching system.

A reconstruction of a second- and third-order fertile branching system is given in figure 12.

*Ultimate Fertile Units (Figs. 7*d*–7*m*, 10)*

Ultimate fertile units are made up of paired sporangia inserted erect and terminal on dichotomous axial systems. In most examples observed, the unit is inserted just above the perpendicular to the third-order axis and branches isotomously two or three times. The final dichotomy is just below the level of insertion of the pairs of sporangia (fig. 7*h*, 7*m*; fig. 10). Sporangia are therefore arranged in two close pairs. Throughout the fertile units, daughter axes after dichotomies are often seen to be overlying (unlike the sterile appendages), and successive dichotomies are observed to be perpendicular, suggestive of the fact that the overall branching pattern is three-dimensional rather than planate. Whether the sporangia appear more bunched or more open depends on the orientation of the first dichotomy relative to the surface of the slab.

*Sporangia (Figs. 7*d*–7*n*, 11)*

Sporangia range from 1.5 to 3 mm in length and from 0.3 to 0.6 mm in width. They are inserted in pairs. When preserved spread out on the matrix (e.g., fig. 7*h*, 7*n*; fig. 11), they can be seen to arise from a slightly widened subtending segment and to have a slightly straighter inner margin than outer margin. Most often, however, they are adpressed closely either in their pair (fig. 7*m*) or into tighter groups of four or eight (fig. 7*e*, 7*g*, 7*i*, 7*j*, 7*l*; fig. 10). They have apices that vary from slightly pointed to slightly rounded. Within a complete fertile unit, all sporangia terminate at approximately the same level. No clear dehiscence line has been observed in our specimens. Halle (1936; his pl. V, 9) illustrated a probable indistinct longitudinal dehiscence line in isolated sporangia from the type locality.

Anatomy (Figs. 13, 14)

Thirteen sections were prepared spaced exactly 1 mm apart, of which four sections proved most well preserved and useful. Only the primary xylem column is preserved, and there is no evidence of secondary growth. Around the outside of the xylem column, a thin layer of darker material demonstrates the compressed remains of the cortical and epidermal tissues (fig. 13*c*, 13*e*), tapering outward to give a diameter for the complete stem of 2.5 mm, as was visible on the specimen before preparation. Therefore, this probably represents the anatomy of a second-order axis.

The primary xylem column has a flattened-oval to hourglass shape (clepsydroid) in cross section (fig. 13*a*, 13*c*–13*e*), with a total width of ca. 1.7–2.0 mm. The bulk of the cells in the xylem strand measure 30–40 μm in diameter, with the largest found in the middle of the column (fig. 13*a*). At each end of the section, there is a prominent area of smaller cells surrounding an area where no cells are preserved (fig. 13*a*, arrows; fig. 13*b*, 13*f*, 13*h*, 13*i*). The smallest cells in these regions measure 10 μm in diameter (fig. 13*b*). From their position and distribution of cell sizes, these areas of smaller cells are interpreted as protoxylem poles. In reflected light, little detail can be discerned from the cell boundaries (fig. 13*d*) on polished sections. Where there is little lumen infill, polygonal cell boundaries are visible, marking the position of the middle lamella (fig. 13*b*, 13*g*). SEM examination demonstrates poor preservation of the cell walls (fig. 14). In oblique (fig. 14*a*) and longitudinal sections (fig. 14*b*–14*h*), scalariform bars with tangentially elongate elliptical apertures are observed (fig.

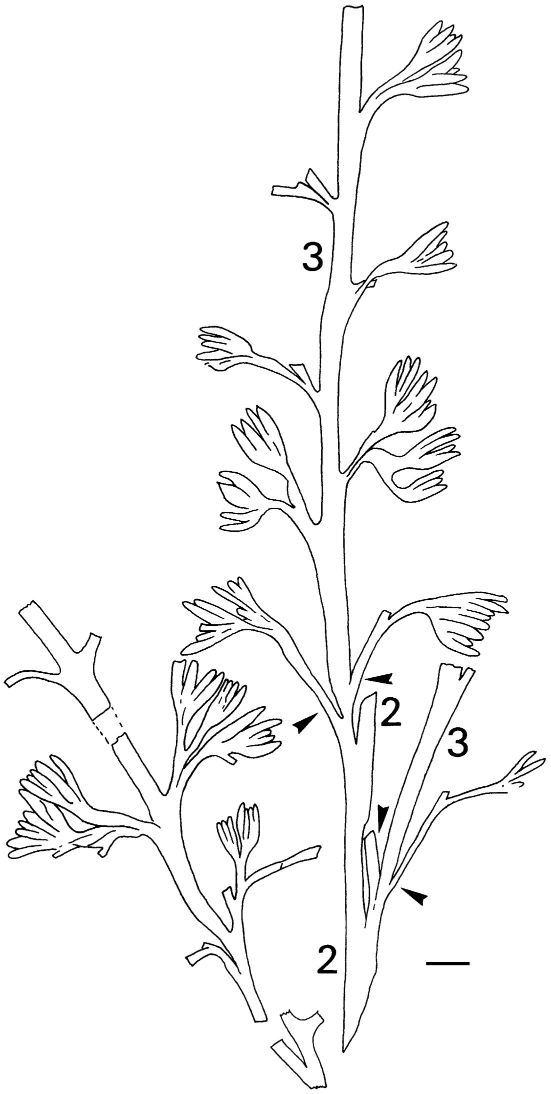

Fig. 9 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretation of fertile second- and third-order axes (compare with fig. 7*f*, 7*k*). Fertile appendages inserted in pairs at base of third-order axis (arrowheads) and alternately distally. Numbers refer to orders of axes. PB18925. Scale bar = 2 mm.

14*b*, 14*c*). Below these are situated elliptical to circular bordered pits (fig. 14*d*–14*h*), which are normally uniseriate (fig. 14*d*, 14*e*, 14*h*), covering the full width of each facet, but are sometimes biseriate (fig. 14*f*, 14*h*). Further detail of cell structure could not be determined from the specimens.

Reconstruction of Branch Systems

Sterile

Our observations above give us a good idea of the morphology of three orders of sterile branching. The first order of branching is more or less straight, with a slight zigzag between the nodes. Second-order branches are emitted in an alternate, two-dimensional pattern, subtended at the base by a pair of deeply dissected appendages that are not in the same plane as the rest of the branching but are arranged tangentially around the first-order stem. Second-order branches are slightly more straight than those of the first order and have third-order branches inserted upon them in the same plane as the first- and second-order branches. The bases of these third-order branches are again subtended at the base by dichotomizing appendages perpendicular to the plane of the rest of the branching system, and they have laterally inserted alternating, sparsely dichotomized, deeply dissected appendages of decreasing length attached to them.

The overall impression is of a very nearly planate branching system, bearing at the nodes and on the final order of branching dichotomizing leaflike appendages perpendicular to the plane of the rest of the branching. Although the appendages have not been proved to be laminate, their flattened, more or less planate nature is evident because there is very little overlap of successive segments, as found in the fertile organs. Even obliquely preserved appendages maintain this appearance. We provide a reconstruction of this part of the plant (fig. 6).

Hsü (1966) indicated the presence of a larger main stem, 18 mm in diameter, to which his branching systems might have been attached. We believe it is likely that such a stem might have existed but can add no further proof of its existence with the material at hand.

Fertile

Fertile parts of the plant are fewer in our collection, and we have not found any such material with three orders of branching in connection. We reconstruct the ultimate two orders of branching, together with the fertile units, in figure 12.

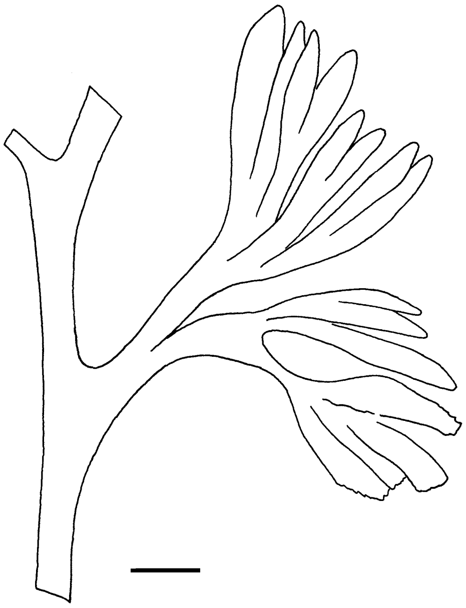

Fig. 10 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretation of a single fertile appendage (fig. 7*e*), showing dichotomous axial system with eight pairs of terminal sporangia. PB18926. Scale bar = 1 mm.

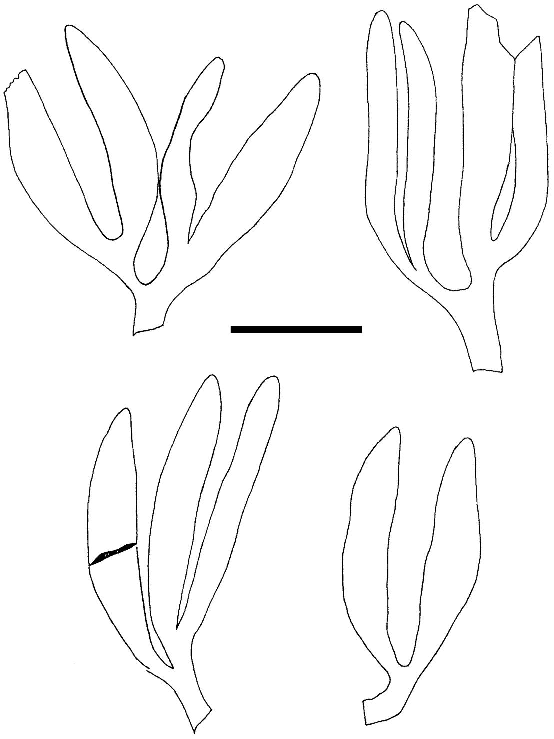

Fig. 11 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Line drawing interpretations of terminal sporangial pairs (see fig. 7*b*, 7*l*–7*n*). Scale bar = 1 mm.

At the base of the third-order fertile axes, there are more or less opposite pairs of fertile units that are perpendicular to the plane of the rest of the fertile system. Groups of two to four pairs of sporangia are closely arranged on dichotomized fertile units that are branched in a three-dimensional manner.

Comparisons

Notable morphological features of our plant are the three known orders of sterile branching, each subtended by flattened paired appendages, and the persistent alternate, two-dimensional ramification. Fertile branches have three-dimensional fertile units bearing paired sporangia. The only known anatomy is a figure-eight-shaped (clepsydroid) primary xylem column with two protoxylem columns arranged symmetrically and peripherally. The traces to the next order of branching are assumed to derive from the two protoxylem columns directly into the two ranks of organs on each side of the central axis. Because of the persistence of a single pattern of branching within the three known orders, we are of the opinion that this pattern of anatomy probably exists through the first two orders of branching that we know and perhaps goes into the third.

Protopteridium *and Other Plants from Yunnan*

Our specimens compare well with the initial fragmentary reports of *Protopteridium* by Halle (1936) and Hsü (1966) from the Longhuashan type locality, apart from the fact that we have revealed the acute nature of the apices of the sterile appendages by dégagement. We have also demonstrated the presence of paired basal appendages by the same method.

Of the fossils from Xichong described by Schweitzer and Cai (1987), one illustrated as *Pseudosporochnus nodosus* Leclercq and Banks (their fig. 17*a*) is more or less identical to the specimen of *Eocladoxylon* in our figure 3*h*. Interestingly, it appears to have sporangia on an appendage attached to the third-order branch near the base, supporting our association of the sterile and fertile portions of the plant. The second specimen illustrated by Schweitzer and Cai (their fig. 17*b* and pl. 12, 4) bears less resemblance to fertile *Eocladoxylon* but also lacks any defining characters of *P. nodosus*. We have yet to find any material similar to this last specimen in our own collecting in Yunnan.

Of the badly preserved plant remains from Panxi, named *Eocladoxylon minutum* by Schweitzer and Cai (1987) (their figs. 22–25 and pl. 15, 2–6), we can see none of the characteristic features of *Eocladoxylon* as defined by Halle (1936) and Hsü (1966) and elaborated by us. Because we are aware of other plants from the Middle Devonian of Yunnan that are more similar to their specimens than is *Eocladoxylon*, we are unable to accept their identification. The specimen illustrated in their plate 15 and figure 7 is more similar to the fertile organs of *Eocladoxylon*, but the presence of erect elongate sporangia alone is not enough to allow confidence of generic assignment.

Wang and Berry (2001*b*) described some small fossils from a locality near Xichong village as *Psilophyton striatum*. The sporangia of this plant are borne in clusters of eight, recurved toward the stem. The sporangia in particular bear a strong similarity of form to those of *Eocladoxylon*. However, the sterile axes associated with the material do not. Neither did we find any of the characteristic sterile appendages of *Eocladoxylon*. We are therefore mindful of the potential for *P. striatum* in part to be *Eocladoxylon*, but we wish to revisit the locality before making any final judgment.

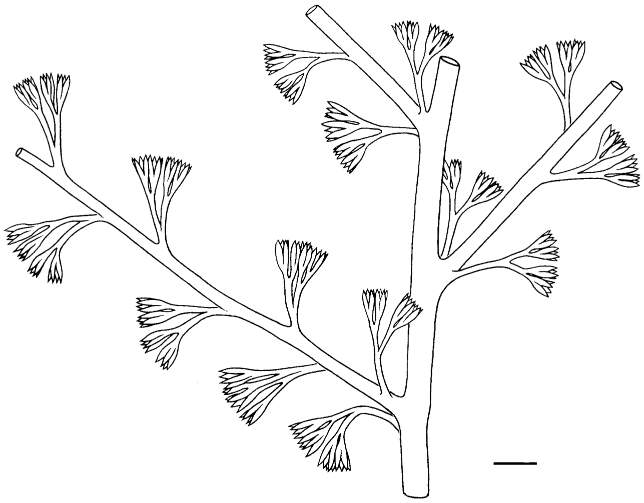

Fig. 12 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Schematic reconstruction of fertile second- and third-order branch system. Scale bar = 2 mm.

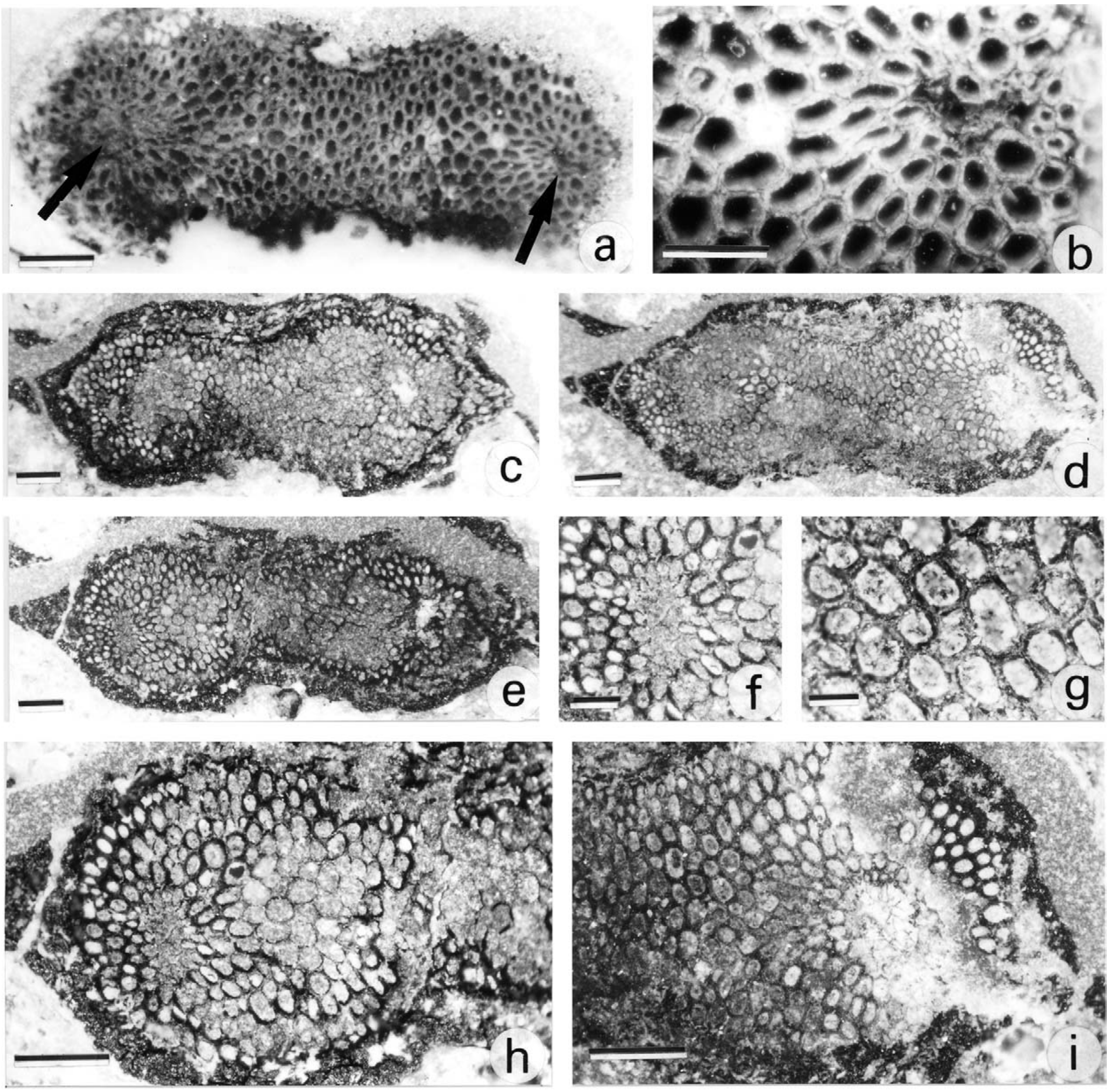

Fig. 13 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Limonite thin sections prepared using the method of Stein et al. (1982) and photographed under incident light. *a*, General view of transverse section, showing clepsydroid shape and two prominent protoxylem poles (arrows), section etched. Scale bar = 0.2 mm. PB19830-13. *b*, Protoxylem pole; enlargement of *a*. Scale bar = 0.1 mm. *c–e*, General views of sections. Scale bars = 0.2 mm. PB18930-7, PB18930-8, PB18930-3. *f*, Protoxylem pole. Scale bar = 0.1 mm. PB18930-8. *g*, Close-up of metaxylem. Scale bar = 0.05 mm. PB18930-8. *h*, Enlargement of left-hand protoxylem pole in *d*. Scale bar = 0.2 mm. *i*, Enlargement of right-hand protoxylem pole in *d*. Scale bar = 0.2 mm. PB18930.

Rhacophyton, Ellesmeris, *and* Chlidanophyton

The characters described above show some obvious similarities to the genus *Rhacophyton* Crépin (1874–1875). Three species are known: *R. condrusorum* Crépin, *R. zygopteroides* Leclercq (1951), and *R. ceratangium* Andrews and Phillips (1968). They are known from a variety of Famennian (Upper Devonian) localities in Belgium, Germany, and North America. Similarities between *Rhacophyton* and *Eocladoxylon* include the clepsydroid (figure-eight-shaped, bipolar) primary xylem column in known orders of branching, the general opposite/alternate insertion of the next order of branching and/or appendages, an overall pinnate branching style, and the insertion of paired appendages (aphlebiae) at the base of lateral branches of one or more orders. In *Rhacophyton*, there is debate over whether the complete planate axial systems are modified branching structures or are actually "fronds," and fern frond terminology is often applied to them.

Some orders of branching in *Rhacophyton* species are sometimes quadriseriate; these consist of branches that are inserted in two rows of close pairs. Such structures are probably simply precociously dichotomized branches. The basal appendages in *R. ceratangium* have been particularly well

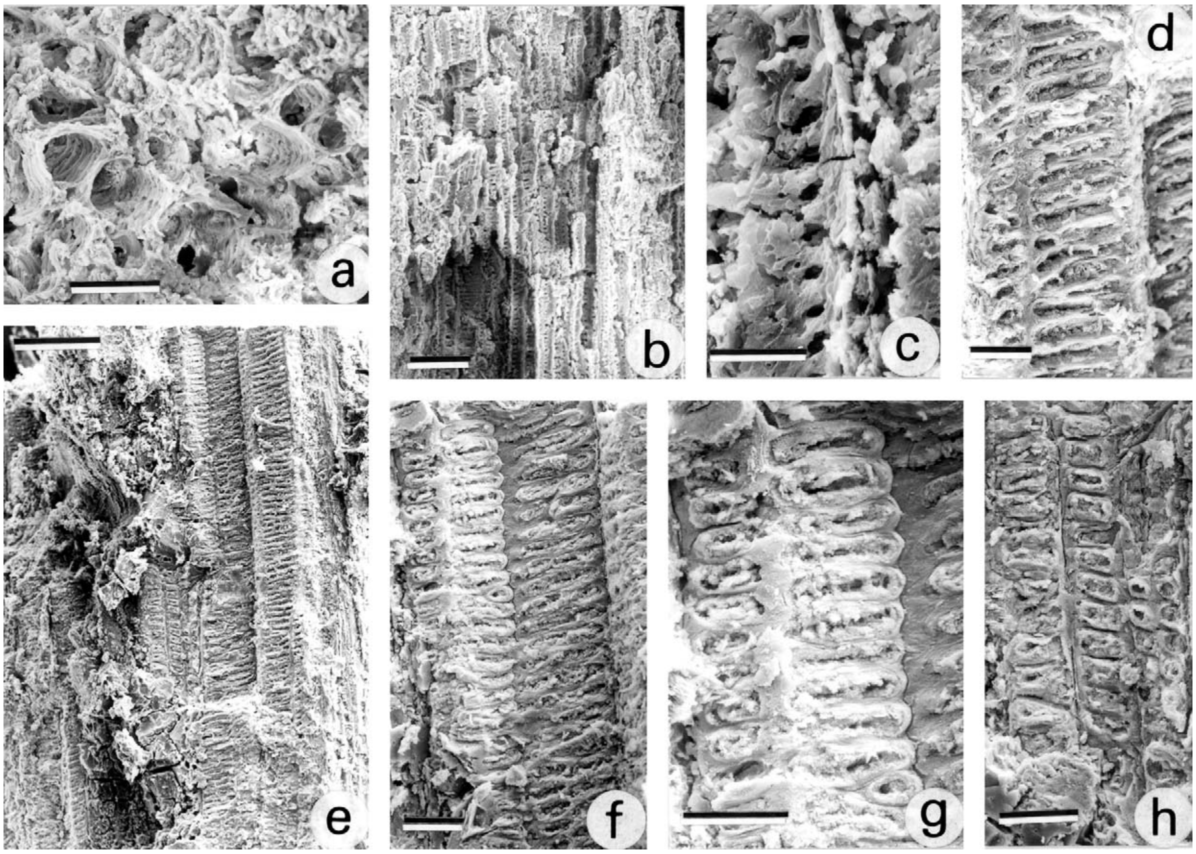

Fig. 14 *Eocladoxylon minutum* (Halle) Koidzumi emend. Berry et Wang from Xichong, Yunnan. Scanning electron micrographs of tracheids preserved as coalified cell walls and as limonite internal casts. PB23078. *a*, Scale bar = 50 μm. *b*, Scale bar = 100 μm. *c*, Scale bar = 20 μm. *d*, Scale bar = 20 μm. *e*, Scale bar = 100 μm. *f*, Scale bar = 25 μm. *g*, Scale bar = 20 μm. *h*, Scale bar = 25 μm.

studied (Cornet et al. 1976), and in some specimens they are not simple dichotomous units but may have overtopping and appear as small monopodial branching systems. In *R. ceratangium*, these appendages can be either three-dimensional or less or more planated (Cornet et al. 1976).

In *R. ceratangium*, the sporangia are found at fertile "nodes" at the base of pairs of sterile axes bearing alternate dichotomous ultimate appendages. At the base of this branch pair are inserted two shorter, profusely dichotomous fertile units. At the ends of the final segments, long curved sporangiophores bear laterally numerous elongate sporangia with a long terminal tip ("beak"). These fertile units appear as tight "balls" of sporangia (Andrews and Phillips 1968). In *Eocladoxylon*, dichotomous fertile appendages with four pairs of sporangia are arranged laterally and alternately in two ranks along the sides of probably the third order of branching, but fertile appendages are also found as the basal pair of appendages on the fertile branch.

A new genus very similar to *Rhacophyton* but with webbed laminated leaves rather than open dichotomizing axes as the final level of branching (often referred to as pinnules) has been described from the Middle Frasnian of Ellesmere, Arctic Canada, by Hill et al. (1997). This plant, named *Ellesmeris sphenopteroides*, is the nearest stratigraphically to our Chinese plant. Unfortunately, fertile morphology is unknown in *Ellesmeris*, so there is no opportunity to study potential morphological trends of reproductive organs over time.

Anatomy of *Eocladoxylon* in second-order axes shows a "clepsydroid" primary xylem strand with a distinct constriction in the width of the primary xylem in the middle and two peripherally placed (mesarch) protoxylem traces. This bilaterally symmetrical arrangement, through trace departures from the tips of the strand, presumably controls the two-dimensional nature of branching. This type of anatomy is therefore also consistent with the morphology of the first- and third-order axes and may potentially extend throughout the branching system. This is the basic pattern of anatomy in the known orders of branching in *Rhacophyton* (e.g., Leclercq 1951, 1954; Schultka 1978). Dittrich et al. (1983) described the anatomy of *R. ceratangium*, showing that the central primary core of the xylem strand was clepsydroid and demonstrating the presence of rays in the surrounding secondary xylem. They demonstrated an etapteroid pattern of trace departure. Transverse sections of other specimens prepared by Andrews and Phillips (1968) showed that the primary xylem had been largely overwhelmed by the production of copious amounts of secondary tissues. *Ellesmeris* has a similarly shaped xylem strand in its main axis (Hill et al. 1997), but secondary tissues have not been reported.

Chlidanophyton Gensel (1973) emend. Hilton (1999), while bearing some similarity to *Rhacophyton* in terms of morphology, lacks anatomy and is difficult to assign to a higher group. It was first described from the Early Carboniferous (Mississippian) of Virginia but has more recently been described from the latest Famennian of southwest England. "Fronds" are inserted singly rather than in pairs, as in *Rhacophyton*; this character is unknown in *Eocladoxylon*. However, in fertile branching systems, sporangia are terminal on dichotomous trusses alternately arranged, and in this character *Chlidanophyton* is more like *Eocladoxylon* than *Rhacophyton*. Aphlebiae are found at the bases of branches.

Iridopteridales

A whole-plant (morphological and anatomical) concept of Iridopteridales has recently emerged (Stein 1982; Berry and Edwards 1996; Berry and Stein 2000; Berry and Fairon-Demaret 2001; Berry 2005). This group of Middle and early Late Devonian plants (see Berry and Stein 2000 for a recent summary) shares many of the morphological characters of trimerophyte-derived plants, including terminal paired sporangia and dichotomous fertile and sterile ultimate appendages. The primary xylem column is deeply ribbed (usually four to six ribs but up to ca. 18), with mesarch protoxylem forming columns permanently located towards the periphery of the lobes of the xylem ribs. In this latter character, *Eocladoxylon* is reminiscent of an iridopteridalean with a xylem column reduced to two united ribs forming a clepsydroid xylem strand.

The branching patterns of Iridopteridales are closely related to the anatomical configuration. In most Iridopteridales (e.g., *Arachnoxylon* Read [1938)], *Ibyka* Skog and Banks [1973]), traces are emitted from each protoxylem strand, one to a rib, at nodal points, and so the branching can be considered whorled (Berry et al. 1997). In *Compsocradus* Berry and Stein (2000), traces are emitted in whorls, but only every other rib is involved in trace production at any given whorl. In the subsequent whorl, the other ribs produce the traces. This is a whorled but alternate arrangement.

Iridopteridaleans have sterile tips that are strongly recurved, whereas only the extreme tips of some *Eocladoxylon* appendages hint at recurvation. Whereas *Anapaulia* has recurved sporangia, *Compsocradus* has erect terminal pairs. Some iridopteridaleans bear spines (e.g., *Ibyka*) whereas others (e.g., *Compsocradus*) do not. No iridopteridaleans are known to have aphlebiae.

Protopteridophyton

Protopteridophyton devonicum was described from the Givetian and Frasnian of Hubei and Hunan provinces, China, by Li and Hsü (1987). The plant has a predominantly alternating insertion of lower-order axes, but the axes are inserted in pairs. Ultimate appendages are axial, dichotomous, and three-dimensional, also inserted in pairs. There are no prominent basal appendages. Attached sporangia are unknown. The anatomy of a single length of main axis was prepared, unfortunately showing only a part of a potentially multiribbed xylem column. The preserved fragment is V shaped, with protoxylem poles permanently located in the extremities of each arm. From these emerge clepsydroid traces to lower-order axes. Tracheids display oval to circular bordered pits. *Protopteridophyton* is therefore much more three-dimensional than *Eocladoxylon*.

Metacladophyton

Metacladophyton tetraxylum was described from the Givetian of Hubei province, China, by Wang and Geng (1997). The plant was described with whorled insertion of first-order branches on the main axes but with subopposite pairs of second-order branches. Subsequent examination of some specimens from the type locality kept in the Paleobotanical Collection of the Beijing Botanical Garden, Academica Sinica, by C. M. Berry suggests that the second order of branches may also be whorled. Wang and Geng (1997) also described the axes as devoid of hairs/spines, but these were observed on the same material. Wang and Geng (1997) made a list of comparisons with the iridopteridalean *Ibyka* Skog and Banks (1973), recently restudied (Berry et al. 1997). The plants can now be seen to share many characteristics, including whorled departure of traces on stems (?and first-order branches), presence of spines, ribbed xylem tissues, and protoxylem points permanently located toward extremities of xylem ribs. The main differences between the two genera are the dissection of the stele into four V-shaped strands between the nodes (apparently, at nodes they may be centrally joined) and the presence of secondary tissues all around these V-shaped ribs in *Metacladophyton*. It may well be the case that the dissection of the stele in this manner is to allow secondary growth to occur around the margin of each of the V-shaped xylem segments. However, the manner of trace departure, by the formation of a lacuna within the protoxylem, and the subsequent detachment of a crescentic xylem trace first on one side, then on the other, is quite unlike the more simple division of the protoxylem observed in *Ibyka* and other Iridopteridales. It is more similar to that observed in *Rhacophyton* by Dittrich et al. (1983).

Pseudosporochnales and Cladoxylopsida

Devonian and Carboniferous Cladoxylopsida are generally recognized from their highly dissected xylem systems. Known Middle Devonian members of the Pseudosporochnales from Europe and North and South America, including the genera *Pseudosporochnus*, *Calamophyton*, *Wattieza*, and *Lorophyton*, appear to have similar body plans (Berry and Fairon-Demaret 2002). This consists of an upright trunk with lateral branches inserted densely around it. The branches are divided in a digitate manner, and on them are borne smaller appendages in a three-dimensional fashion with no regular geometrical arrangement. A principal difference between the genera of Middle Devonian Pseudosporochnales is the nature of branching of these sterile and fertile ultimate appendages. Neither branches nor appendages of these plants can be confused with the regular, pinnate branching of *Eocladoxylon*. Traces to appendages are generally fed by one to three or more traces emerging from adjacent xylem ribs in the highly dissected vascular system of the pseudosporochnalean branch. However, there is evidence to suggest that at the dichotomy of a branch of *Pseudosporochnus*, two clepsydroid traces were formed perpendicular to the dichotomy (Stein and Hueber

1989), which fed stout dichotomous appendages. Although homology has been suggested between these clepsydroid traces and those of *Rhacophyton* (Kenrick and Crane 1997), this has been disputed (Berry and Stein 2000).

Recently, a new genus of cladoxylopsid from the Late Devonian of Hubei province has been described by Hilton et al. (2003). Significantly, it differs from Pseudosporochnales in having lateral branching systems that are more or less pinnately organized. In this respect, it is more similar to *Eocladoxylon*. However, the branches retain a highly dissected vascular system unlike the simple bipolar xylem column of *Eocladoxylon*.

Protocephalopteris *(Høeg) Ananiev*

Protocephalopteris, from Spitzbergen (Høeg 1942; Schweitzer 1999) and Siberia (Ananiev 1960), is represented by axes that give off closely inserted pairs of lower-order axes at nodes, each branch being subtended by a pair of highly dichotomous aphlebiae. Successive pairs are inserted on opposite sides of the main axis. Appendages attached to the lower-order axes are dichotomized only once or twice and may bear terminal pairs of sporangia. The compressed axes have many longitudinal ribs, and this may reflect an actinostele, although the anatomy of the branches is unknown. Apart from the basal aphlebiae, there is little similarity between *Protocephalopteris* and *Eocladoxylon*.

Progymnosperms

Plants belonging to the Middle and Late Devonian Aneurophytales have a primary xylem column with three or more ribs, development of secondary wood, and multiple sporangia inserted laterally on a well-defined specialized, often pinnate, fertile appendage. Furthermore, traces to branches and appendages originate from a single protoxylem pole that is located in the middle of the xylem column (radiate protoxylem group of Beck and Stein 1993). *Eocladoxylon* apparently has two permanent protoxylem poles (permanent protoxylem group) and has paired or clustered terminal sporangia borne on simple dichotomizing truss.

In terms of Archaeopteridales, the similarity of the sterile appendages of *Eocladoxylon* to leaves of late Givetian *Svalbardia* (Høeg 1942; Schweitzer 1999) and some early *Archaeopteris* is notable, but the leaves of such progymnosperms were carried in an ontogenetic spiral and not in two ranks, and the anatomy of the branches included a stellate vascular system with a clearly defined pith (Carluccio et al. 1966). Fertile characters are also more complex than in *Eocladoxylon*. Schweitzer and Cai's (1987) assertion that *Eocladoxylon* belongs to "Progymnospermales" is not sustained by this study.

Discussion

Eocladoxylon can in some ways be most closely compared to *Rhacophyton*. The main points of similarity with *Rhacophyton* are the pinnate branching pattern, the predominantly alternating pattern of insertion of laterals, the highly dichotomous prominent appendages/aphlebiae positioned at the base of known orders of lateral branching, and the clepsydroid, bipolar nature of the xylem strand. These details yield a sterile branching pattern that is strikingly *Rhacophyton*-like in appearance. Noticeable differences include the position of the sporangia (replacing sterile appendages rather than on a specialized basal appendage), the nature of branching of the sporangial complex, and the lack of secondary tissues.

The planate branching pattern of *Eocladoxylon* is apparently controlled by the bipolar, clepsydroid anatomy that we think may extend throughout the known parts of the plant. In *Rhacophyton*, quadriseriate branching is also known (Leclercq 1951; Andrews and Phillips 1968; Cornet et al. 1976) in some parts of the plant, which nonetheless retains a clepsydroid anatomy, the traces simply dividing in two immediately after departure.

In very simplistic terms, therefore, *Eocladoxylon* appears to have a derived branching pattern comparable with the biseriate form of sterile *Rhacophyton* (and matching anatomy), specialized semiplanated appendages (?leaves/?pinnules), yet it has comparatively underived reproductive organs based on a simple dichotomizing branch system, which are found in positions similar to those of the sterile appendages. The reproductive characters are therefore comparable at the broadest level with the trimerophyte-derived Middle Devonian plant groups Iridopteridales and some members of Pseudosporochnales.

The anatomical configuration of the branching system, a bipolar, clepsydroid xylem column, is most directly comparable to *Rhacophyton*, but important characteristics of the trace departures are not yet known. These might demonstrate whether the traces depart in a manner similar to either of those observed in Iridopteridales (e.g., Stein 1981) and *Rhacophyton* (Dittrich et al. 1983).

It is tempting to suggest that previous indications of a relationship between Iridopteridales and *Rhacophyton* (Berry and Stein 2000, p. 825; Berry and Fairon-Demaret 2001, p. 133) are fulfilled in *Eocladoxylon*. Putative points of relationship between Iridopteridales and *Rhacophyton* include membership of the "permanent protoxylem group" (perhaps a fundamental character) and alternating branching patterns (*Compsocradus*). The bipolar anatomy of *Rhacophyton* might be regarded as a reduced (two-rib) version of the typical multiribbed iridopteridalean xylem column. *Eocladoxylon* clearly has the potential to straddle the gap between the sterile and anatomical characteristics of *Rhacophyton* and the fertile and anatomical characteristics of Iridopteridales. However, the discovery and description of the anatomy of the principal axis (stem) of both *Rhacophyton* and *Eocladoxylon* and their comparison would clearly be a significant test of such a hypothesis of phylogenetic relationship.

A point of caution is necessary, however. The Middle Devonian flora of South China has many unique elements. During our current study of the Xichong Formation, we have found no cosmopolitan elements. Extremely obvious to us is the lack of recognizable members of Aneurophytales and Pseudosporochnales and typical iridopteridalean plants that make up the bulk of the nonlycopsid flora at other Middle Devonian localities across Laurussia and into Gondwana (Berry and Fairon-Demaret 2001). We do not yet fully understand the extent or duration of the floristic isolation of the South China continent. However, the first records of *Rhacophyton*-like plants (*Ellesmeris*) are in the Middle Frasnian of Arctic Canada (Hill et al. 1997). Any proposal of an ancestral relationship between the Givetian *Eocladoxylon* from Yunnan and the Frasnian

Ellesmeris from Canada must take account of the problems of dispersal to and from the South China continent during this time.

Eocladoxylon is the most fascinating plant we have studied from Yunnan. It remains *incertae sedis* because we do not yet have sufficient material to understand its morphology and anatomy, particularly of the basal parts of the plant. Alignment with *Rhacophtyon* is tempting; however, at the moment we are aware that the small number of characters concerned may be convergent. We are hopeful that during further exploration of the area we will find new material that will help us understand its systematic position. This may potentially include stem and root material, *in situ* spores and wall ultrastructure, and more extensive permineralization of axial systems, allowing observation of trace departures.

Acknowledgments

We would like to thank the Royal Society of London and the National Natural Science Foundation of China for supporting scientific exchanges between Cardiff and Nanjing and fieldwork in Yunnan. Further financial support was provided by the Chinese Academy of Sciences (KZCX2-SW-130), the National Natural Science Foundation of China (40232019, 40472005), and the Cardiff China Studies Centre, Cardiff University.

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