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A NEW IRIDOPTERIDALEAN FROM THE DEVONIAN OF VENEZUELA

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The first permineralized Devonian plant fossil is reported here from the Middle or lowermost Upper Devonian of western Venezuela. Two orders of branching plus dichotomous ultimate appendages are known from compressions. A branch of the first order contains a mesarch actinostele with six primary xylem ribs, each with a protoxylem strand near the rib tip (peripheral edge). Compressions of first-order branches demonstrate three equally spaced lateral organs (higher-order branches and dichotomous ultimate appendages) attached in whorls, with every other whorl displaying laterals placed in identical orientations and intermediate whorls with laterals offset exactly halfway between. The permineralized specimen partly confirms the presence of whorls and indicates that vascular traces are derived from every other primary xylem rib in each whorl, with intervening ribs producing traces in whorls above and below. Second-order branches have only ultimate appendages that are attached in a nonwhorled, three-dimensional, or alternate arrangement. Sterile ultimate appendages dichotomize up to six times and terminate in recurved tips. Fertile ultimate appendages have paired sporangia distally; these sporangia are often upright but are otherwise similar to sterile examples. The stelar anatomy demonstrates an iridopteridalean affinity for these plants, resembling *Arachnoxylon kopfii* Read in arrangement and number of xylem ribs although it is smaller in size. Among iridopteridaleans, the branching pattern and mode of trace departure is unique, and we therefore name the plant *Compsocradus laevigatus* gen. et sp. nov.

Keywords: Devonian, Venezuela, plant fossils, Iridopteridales.

Introduction

Skog and Banks (1973) erected a new order, Ibykales, based on their new genus and species *Ibyka amphikoma*, for which evidence of external morphology and internal anatomy was presented. This plant was subsequently transferred by Stein (1982) to the order Iridopteridales based on the plant's anatomy alone, which was viewed as substantially conforming to the concept of Iridopteridineae, as originally proposed by Arnold (1940). Middle and Upper Devonian Iridopteridales, largely recognized on the basis of anatomical criteria, are characterized by a deeply ribbed mesarch actinostele with two to three centrally united primary xylem segments that dichotomize radially into four to twelve radially directed primary xylem ribs. Single or multiple protoxylem strands are located near the tips (peripheral edges) of each xylem rib and are involved in the production of vascular traces, with a whorled pattern of insertion ("phyllotaxis") and with one trace per rib in each whorl. Traces of two distinct sizes are observed in some whorls, which indicates that the shoot systems bear distinctly different laterals (branches vs. dichotomous ultimate appendages?). Currently included in the Iridopteridales are mostly monotypic Middle Devonian genera from North America, known only from permineralizations, including *Iridopteris* Arnold 1940, *Arachnoxylon* Read 1938 (two species), and *Asteropteris* Dawson 1881. In addition, possible iridopteridaleans have been interpreted from compressions alone, including *Anapaulia* from the Middle or Upper Devonian of Venezuela (Berry and Edwards 1996*a*) and *Hyenia vogtii* from the Middle Devonian of Spitzbergen (Høeg 1942; Berry and Fairon-Demaret, in press). A further possible permineralization/compression *Serripteris* Rowe and Galtier 1989 was described from the Lower Carboniferous of France.

To date, *Ibyka* is the only representative of the Iridopteridales for which both external morphology and internal anatomy are known (to any extent) and for which a reconstruction incorporating both kinds of data has been proposed (Skog and Banks 1973). Based on the original description, the plant has been viewed as having three axis orders, with dichotomous ultimate appendages borne on all three orders, with terminal sporangia in pairs, and with helical "phyllotaxis." As such, *Ibyka* has remained the only iridopteridalean taxon for which a nonwhorled "phyllotaxis" is asserted, although this interpretation has been questioned (Stein 1982), and it has subsequently been shown that three-dimensional, but not necessarily helical, "phyllotaxis" must be considered a possibility in plants of this age (Stein and Hueber 1989). New observations made by our research group (Berry et al. 1997) clearly indicate the presence of a whorled insertion of appendages at most levels in *Ibyka*. The plant is now believed to be very similar in morphology to *Anapaulia* Berry and Edwards (1996*a*) from the Devonian of Venezuela. This latter plant was preserved in the form of compressions only. However, Berry and Edwards were able to infer a relationship between *Anapaulia* and Iridopteridales by comparing the morphology of

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Table 1

Table of Taxa That We Consider (at Present) to Be Members of Iridopteridales based on Anatomical and Morphological Criteria

Anatomy only	Anatomy and morphology	Morphology only
Arachnoxylon Read 1938	*Ibyka* Skog & Banks 1973	*Anapaulia* Berry & Edwards 1996*a*
Iridopteris Arnold 1940	*Compsocradus* gen. nov.	"*Hyenia* " *vogtii* Høeg 1942
Asteropteris Dawson 1881	(*Metacladophyton* Wang and Geng 1997)	"*Hyenia*" *banksii* Arnold 1941

Note. As the current diagnosis of Iridopteridales (Stein 1982) is given in terms of anatomical characteristics only, those preserved in terms of morphology only are included on the basis of inference only. *Metacladophyton* is included (in brackets) because it appears to have Iridopteridalean characters, but it will require some reinvestigation to confirm some characters (see text).

Anapaulia with the morphological features predicted from the characteristic anatomy of Iridopteridales. Berry and Fairon-Demaret (in press) were able to recognize other plants in the literature (e.g., *Hyenia banksii* Arnold, *H. vogtii* Høeg) that also seemed to demonstrate morphological characteristics that indicate an iridopteridalean affinity. In addition, we consider *Metacladophyton* (Wang and Geng 1997), from the Middle Devonian of China, to be a potential iridopteridalean based on xylem configuration and whorled trace departures. In table 1, we list those plants that we consider to be iridopteridaleans (in their various states of preservation).

The Iridopteridales are phylogenetically important because of their morphology and anatomy, which are intermediate between that of the primitive plants of the Lower Devonian and the more complex major groups that are characteristic of the Middle and Upper Devonian, including potential early representatives of extant sphenopsids (horsetails) and ferns (Arnold 1940; Stein et al. 1984; Berry et al. 1997; Kenrick and Crane 1997). Based on shared anatomical features, a case might be made for an especially close relationship between iridopteridaleans and members of Cladoxylopsida (Arnold 1947; Skog and Banks 1973; Stein et al. 1984). However, hampering the interpretation of phylogenetic relationships is the lack of comprehensive biological interpretation of both groups, including a lack of whole-plant reconstructions. Also lacking is a suitable paleogeographic context for the evolution of these groups. Although members of the Cladoxylopsida have been reported from North America, central Europe, Kazakhstan, and Australia (Stein and Hueber 1989), the bulk of our understanding of the Middle Devonian forms is derived from western European compressions. Middle Devonian Iridopteridales, by contrast, are known to date primarily as permineralizations that come only from eastern North America, although we strongly suspect a much wider distribution (Berry and Fairon-Demaret, in press).

The new plant described here, which comes from the northern part of the South American continent, is based on a rare combination of external morphology derived from multiple compressions and internal anatomy from an organically connected permineralized axis fragment. The evidence provides an unusually complete glimpse of iridopteridalean whole-plant external and internal morphology, and in terms of its quality, this evidence exceeds that of any plant yet known for this group. The new plant is also significant because it reveals a whorled nodal architecture that is similar to yet simultaneously distinct from that of previously known iridopteridaleans.

Material and Methods

All fossils described here were found in the Sierra de Perijá (western Venezuela) in sediments of the Campo Chico Formation. They derive from locality 3 of Berry et al. (1993; for an updated map, see fig. 1 from Berry and Edwards 1996*b*). Based on independent evidence, the dating of this locality is not yet secure, but underlying brachiopods indicate a Middle Devonian (probably Givetian) age (Benedetto 1984). Other plant fossils from this horizon include the lycopsids *Haskinsia sagittata* (Edwards and Benedetto 1985; Berry and Edwards 1996*b*), *Colpodexylon cachiriense* (Edwards and Benedetto 1985; Berry and Edwards 1995), the zosterophylls cf. *Sawdonia*, *Serrulacaulis* cf. *furcatus* (Berry and Edwards 1994), the cladoxylopsid *Wattieza* Stockmans, and a progymnosperm. In comparison with the floras of New York State and western Europe, these taxa also indicate a probable Middle Devonian (late Eifelian–Givetian) or earliest Upper Devonian (early Frasnian) age.

The three-dimensional morphological architecture of the fossils was revealed by dégagement (Leclercq 1960; Fairon-Demaret et al. 1999). Each stage of the uncovering of the fossils was recorded by photograph and by camera lucida interpretation. This procedure allowed detailed reconstruction of the plant. Photographs were taken using crossed-polarizing light to increase contrast.

A single specimen (fig. 7) was found to be preserved partly as a compression and partly as a permineralization of hydrated iron oxides (limonite). Both part and counterpart of the permineralized region were embedded in Ward's bioplastic and cut into serial transverse sections using a Gillings-Bronwell thin-section machine. Sections were subsequently reembedded in bioplastic, ground thin, demineralized with hydrochloric acid, and dehydrated in a graded ethanol series following the method of Stein et al. (1982). Following preparation, sections from both part and counterpart series, cut in the same direction from distal to proximal ends of the specimen (see section numbers in fig. 7), were carefully mapped using camera lucida and were analyzed optically to determine the best fit (fig. 11). Additional notes on the preparation methods used are deposited with the specimen.

Figured specimens and the slide series have been deposited in the collections of the Geology Department at the National Galleries and Museums of Wales in Cardiff (United Kingdom) with reference numbers NMW 93.97G.34-38.

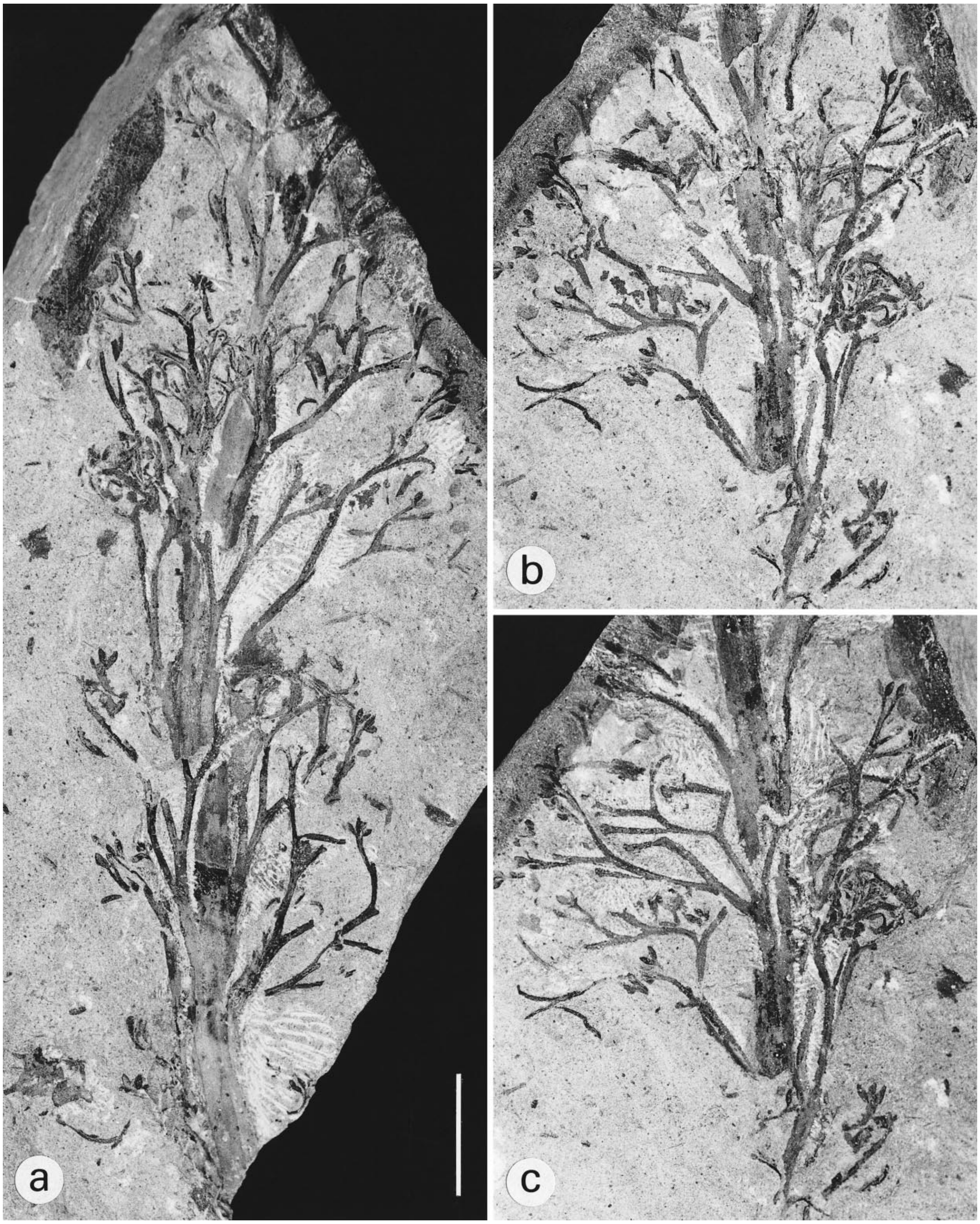

Fig. 1 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. Dégagement of part and counterpart of specimen NMW 93.97G.34a&b. See fig. 2 for interpretation. *a*, Part—second stage of dégagement (see fig. 2*f*). *b*, Counterpart (only upper region preserved)—second stage of dégagement (see fig. 2*b*). *c*, Part—fourth stage of dégagement (see fig. 2*d*). Scale bar = 10 mm.

Systematic Paleobotany

Order—Iridopteridales Stein 1982

Genus—Compsocradus *Berry et Stein gen. nov.*

Generic diagnosis. Plants pseudomonopodial. First-order axes upright, with smooth surface. Second-order axes narrower and shorter, inserted acutely. Ultimate appendages consisting of narrow axes branched predominantly isotomously, successive dichotomies being approximately perpendicular; fertile ultimate appendages terminate in erect paired sporangia; sterile ultimate appendages terminate with oppositely recurved tips. Both ultimate appendages and second-order axes are arranged inserted in loose whorls on first-order axes, with attachments alternating in successive whorls. Protostele ribbed, mesarch, with six primary xylem ribs; traces arising from every other rib at each whorl, successive whorls alternating. Protoxylem strands located permanently peripherally, one in each primary xylem rib. Tracheids with uniseriate circular to oval bordered pits.

Derivation of name. From the Greek *κομπσοσ*—elegant, pretty, and *κραδοσ*—branch, spray, twig.

Type. *Compsocradus laevigatus* sp. nov.

Compsocradus laevigatus *Berry and Stein sp. nov.* (*figs. 1–12*)

Derivation of name. From the Latin *laevigatus*—smooth, referring to the stem surface.

Holotype. NMW 93.97G.34a and b. Figures 1, 2, and 3*c* and *d*.

Syntypes. Morphology NMW 93.97G.35-37, anatomy NMW 93.97G.38 sections 1A–13A, 1B–60B.

Repository. National Museum and Galleries of Wales (Cardiff, United Kingdom).

Locality. Locality 3 of Berry et al. 1993. Caño Colorado, Sierra de Perijá, Zulia State, western Venezuela.

Horizon. Green mudstones and shales close to the base of the Campo Chico Formation, Devonian, probably Givetian (?upper Eifelian/?lowest Frasnian).

Diagnosis. Plants as generic diagnosis. First-order axes are 2–6 mm in width ($\bar{x} = 3.6$ mm; $n = 26$), at least 135 mm long. Second-order branches are 0.7–2.2 mm in diameter, up to at least 45 mm long. Ultimate appendages are up to 1.4 mm in diameter at base and up to 25 mm long, branched isotomously up to six times, inserted predominantly acutely. Sporangia are 1.3–1.7 mm long and 0.4–0.7 mm wide, with a maximum of ca. 64 per truss. Ultimate appendages are partly or completely fertile.

Comments. The type specimen shows most unambiguously the typical branching pattern of the plant as well as some fertile segments. The anatomically preserved specimen is incompletely preserved, does not clearly demonstrate the branching pattern, and might be confused with *Arachnoxylon kopfii* Read or *Ibyka* Skog and Banks based on anatomical features alone (see comparisons below).

Description

Morphology

The description is based on ca. 30 specimens from 12 slabs. Two branch (axis) orders are observed. To both are attached ultimate appendages consisting of small and multiply dichotomous branch systems. We do not know the possible attachment of the first-order axes to larger stems or to roots.

First-order axes. These are the largest axis order known (fig. 1; fig. 3*a*, 3*b*, 3*e*, and 3*f*; fig. 5*a*–5*c*) and are either straight or gently curved. They range from 2 to 6 mm in diameter, with the longest known example displaying a 135-mm length, but all available specimens are clearly incomplete. The surface of the impressions is generally smooth (fig. 3*a*, 3*b*) but broken by longitudinal folds that are usually associated with the bases of second-order axes and ultimate appendages. The bases of both organs are marked by inverted U's that measure 1–2 mm across (fig. 5*e*, large arrow), the proximal margins of which may continue longitudinally down the stem for a distance of >10 mm. This extension of the base partly reflects the acute angle of insertion of the subtending organs (figs. 1, 3), but it also indicates some degree of decurrence. The overall arrangement of the first-order axis is indicative of a monopodial upright habit (i.e., first-order axis = morphological stem or small trunk), but this is nowhere proven by the material at hand.

Attached to the first-order axes are both second-order axes and ultimate appendages arranged in a three-dimensional manner (see below).

Second-order axes. Second-order axes are attached at an acute angle (fig. 3*c*, 3*d*; fig. 5*c*) on many of the larger (first-order) axes. Where they were hidden beneath the sediment, some have been revealed by dégagement at the base. Second-order axes are from 0.7 to 2.2 mm in diameter. The most complete example (fig. 5*c*, arrow), which is ca. 45 mm in length, is curved downward (i.e., proximally) until the point of the tip, where it is below its level of insertion on the first-order axis. The ultimate appendages are inserted upon this axis at an acute angle.

One short second-order axis (fig. 3*c*, 3*d*, base of second-order axis marked with arrowhead) of ca. 10 mm in length was investigated in detail (see organ 3f in fig. 2). At least two of the lateral organs seen on the part and counterpart are typical ultimate appendages as described below. Distally, four shorter, narrower, dichotomizing organs are preserved, each with up to three isotomies and a total length of less than 5 mm. These structures could represent immature ultimate appendages or small mature examples reduced by distal diminution. The apex of the second-order axis is not clearly preserved.

Ultimate appendages. These are either fertile (fig. 5*d*) or sterile or contain both sterile and fertile terminations (fig. 5*e*). There are up to six dichotomies, and the appendages terminate either in recurved sterile tips (fig. 5*e*, small arrows) or in erect pairs of ovate sporangia (fig. 5*d*, 5*e*, large arrow). The appearance of the preserved dichotomous appendages depends on their orientation relative to the parent axis in the compressions. Those lying above and below the parent axis are easiest to uncover most completely and give the impression of a more or less two-dimensional structure. However, those ul-

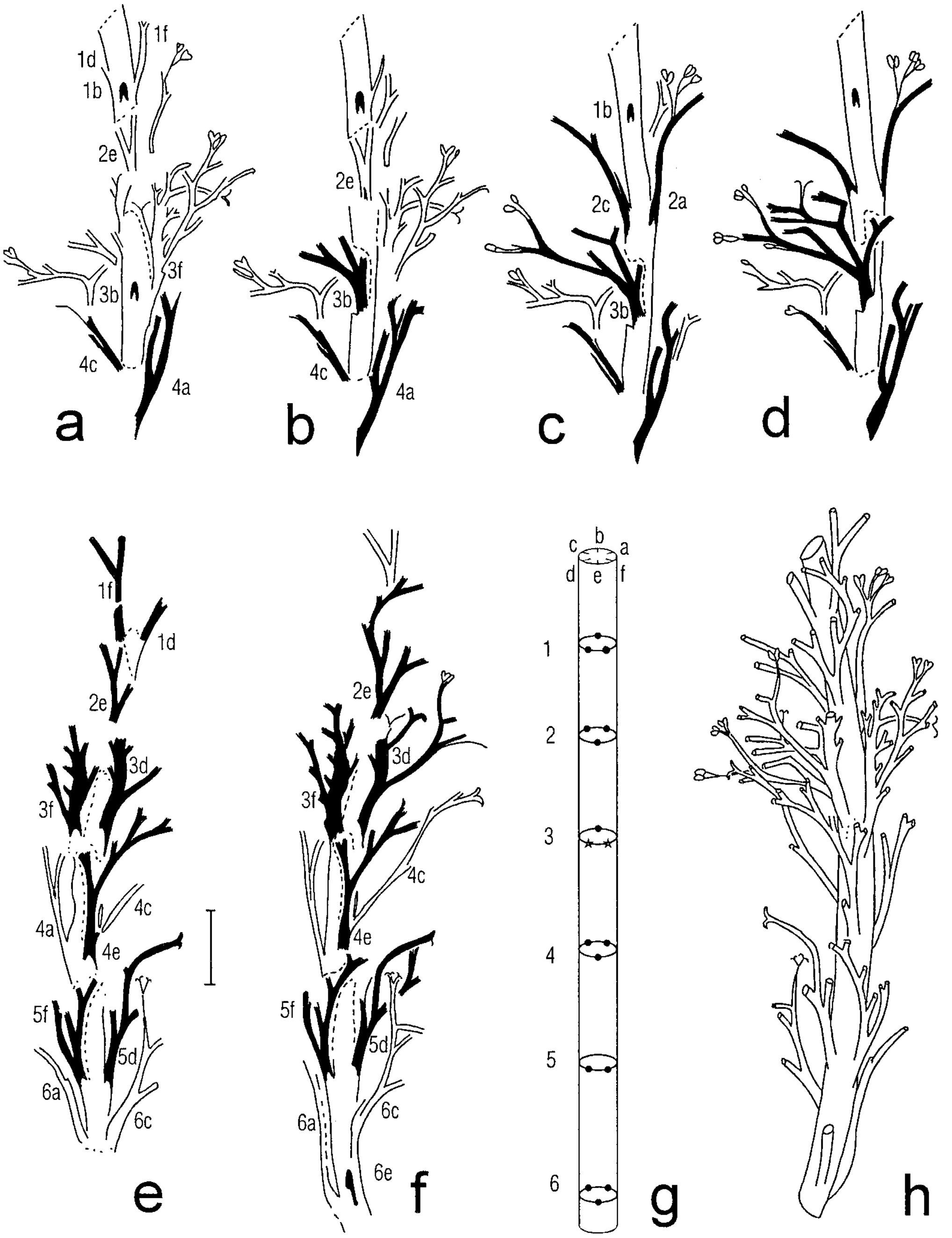

Fig. 2 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. Dégagement of part and counterpart of first-order branch, specimen NMW 93.97G.34a&b. Solid black areas represent ultimate appendages, branches, or bases oriented below the plane of the stem surface. *a–d*, Successive stages of uncovering of counterpart. *e*, *f*, Uncovering of part. *g*, Diagrammatic representation of orientation of insertion of lateral organs. Black circles = ultimate appendages; stars = second-order branches. Cylinder oriented in same aspect as counterpart. *h*, Schematic reconstruction of whole branch oriented as counterpart. Scale bar = 10 mm.

timate appendages preserved beside the parent axis are more crushed but provide more accurate information about their true three-dimensional form.

The first dichotomy of the ultimate appendage is usually in the transverse plane and tangential to the main axis (fig. 5*d*, base). Daughter segments are ascendant, and there is an angle between them of ca. 40°. The second dichotomies, although not exactly coplanar with the first, usually give the impression that they differ by only a few degrees; hence, the entire appendage appears fanlike. Distal branching is more three-dimensional, with successive dichotomies probably nearly perpendicular. Distances between the dichotomies generally decrease distally. Perpendicular orientation of successive dichotomies is clear at some distal branching points (fig. 5*d*,

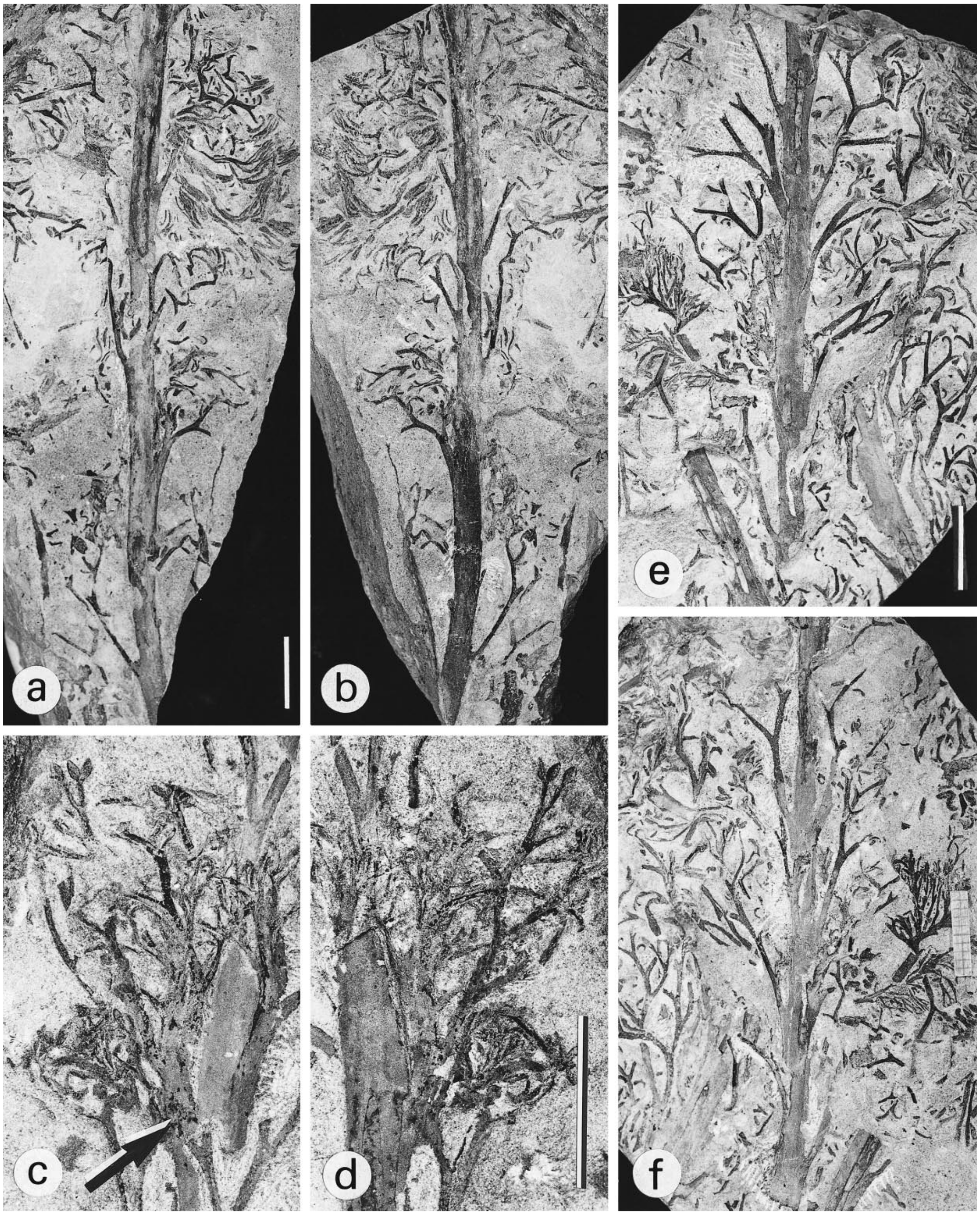

Fig. 3 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. *a, b*, First-order axis part and counterpart. See interpretation in fig. 6. NMW 93.97G.35a&b. Scale bar = 10 mm. *c, d*, Second-order axis part (base indicated with arrow) and counterpart (see fig. 2, organ marked 3f). NMW 93.97G.34a&b. Scale bar = 10 mm. *e, f*, First-order axis, part and counterpart. See interpretation in fig. 4. NMW 93.97G.36a&b. Scale bar = 10 mm.

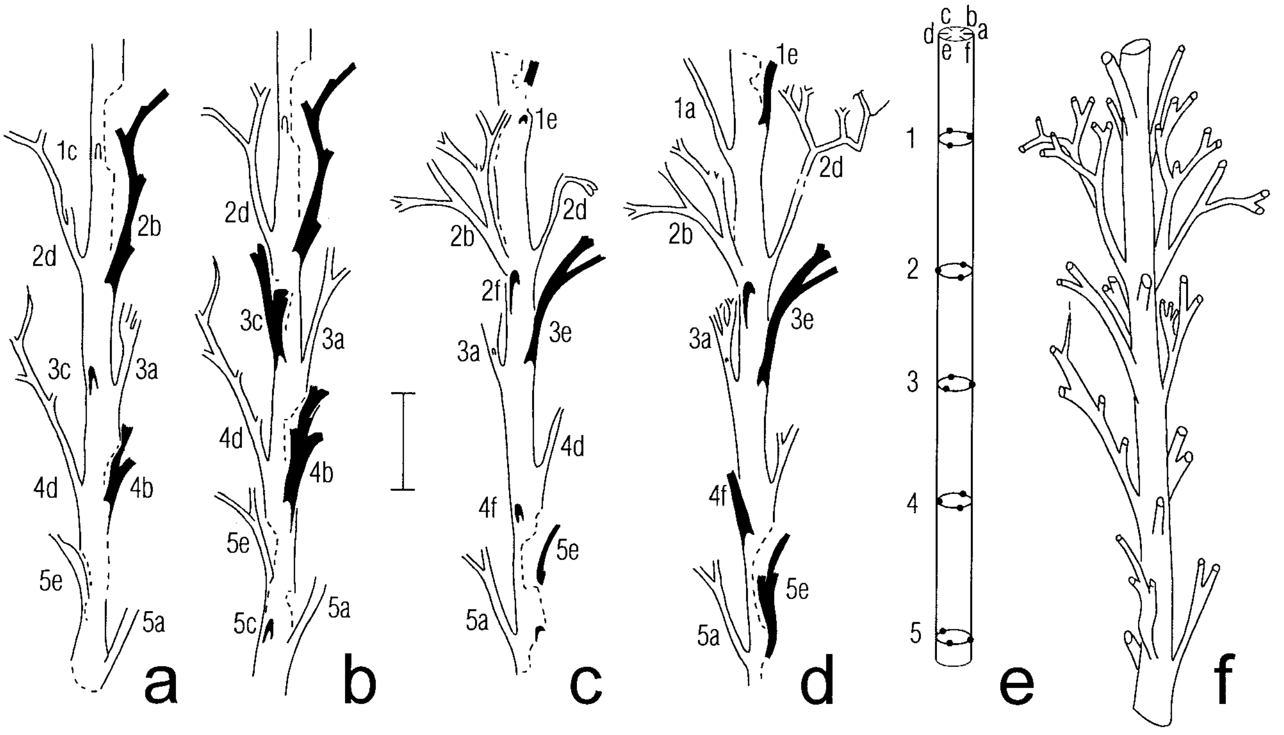

Fig. 4 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. *a–d*, Dégagement of part (*c, d*) and counterpart (*a, b*) of specimen NMW 93.97G.36a&b. Solid black areas represent ultimate appendages, branches, or bases oriented below the plane of the stem surface. *e, f*, Schematic reconstruction oriented as counterpart (as in fig. 2). Scale bar = 10 mm.

arrows). Branching is mostly in the form of isotomous dichotomies, although a number of appendages are observed with anisotomous basal divisions. In the most obvious example (fig. 1*c*), the second dichotomy on the right-hand side of the ultimate appendage (3b in fig. 2) is so close to the basal dichotomy that it indicates a trifurcation. Such branching appears to have little overall effect on the overall morphology of the entire ultimate appendage. Typical sterile ultimate appendages are up to 25 mm long, and completely fertile examples may be up to 20 mm long, both with a maximum diameter of 1.4 mm.

Sporangia are arranged in pairs as continuations of the distal tips of fertile ultimate appendages (fig. 5*d*). They are 1.3–1.7 mm in length by 0.4–0.7 mm wide, and they taper gradually into subtending axes that possess neither distinct stalks nor abscission zones. Sporangia have an elliptical to fusiform shape, with a rounded or weakly pointed apex. No cellular detail can be observed, and there is no obvious dehiscence line. Despite repeated attempts, spores have not been recovered from *Compsocradus* or any other plant from this locality, nor have they been recovered from the surrounding matrix.

Arrangement of lateral organs on first-order axes. Unprepared specimens show first-order axes that bear numerous overlapping ultimate appendages and second-order axes (fig. 5*a*, 5*b*). It is only by almost complete destruction of the specimens that the true insertion pattern can be established. This situation is best demonstrated by specimen NMW 93.97G.34a/b (figs. 1, 2; fig. 3*c*, 3*d*). Part and counterpart are preserved over a length of 50 mm. Proximally, another 40 mm are preserved on the counterpart only. In the untouched state, a three-dimensional arrangement of the appendages was obvious. Systematic dégagement of the whole specimen reveals an ordered pattern, with second-order axes and appendages attached to the first-order axis at six nodes. Three axes and/or appendages are attached at each node. Their insertion onto the first-order axis within nodes varies by between 1.5 and 6 mm along the axis. The average distance between nodes (i.e., internodal length) ranges between 12 and 18 mm. Thus, the entire system is distinctly whorled.

Dégagement is recorded in photographs (fig. 1) and by line drawings (fig. 2) of part and counterpart. The numbering system for nodes and laterals is demonstrated on the line drawing (fig. 2). At node 1 on the part, three laterals are observed, one (axis or appendage) departing downward in the middle of the compressed first-order axis (1b in fig. 2*a*), visible only as a depression in the surface, and there are two other appendages on each side, rising above the plane of the compressed first-order axis (1d and 1f in fig. 2*a*). The appendages are also visible below the axis surface on the counterpart (fig. 2*e*). At node 2, one dichotomizing ultimate appendage (2e) was preserved on the part directly above the middle of the surface of the axis (fig. 2*b*). This is best preserved as uncovered on the counterpart (fig. 2*f*). Dégagement also reveals two other dichotomous ultimate appendages at node 2 (2a and 2c) that are preserved laterally, one on each side of the axis, and that are seen going down into the matrix.

At node 3, one lateral (3b) was demonstrated to move downward in the center of the part (fig. 2*a*), and when uncovered,

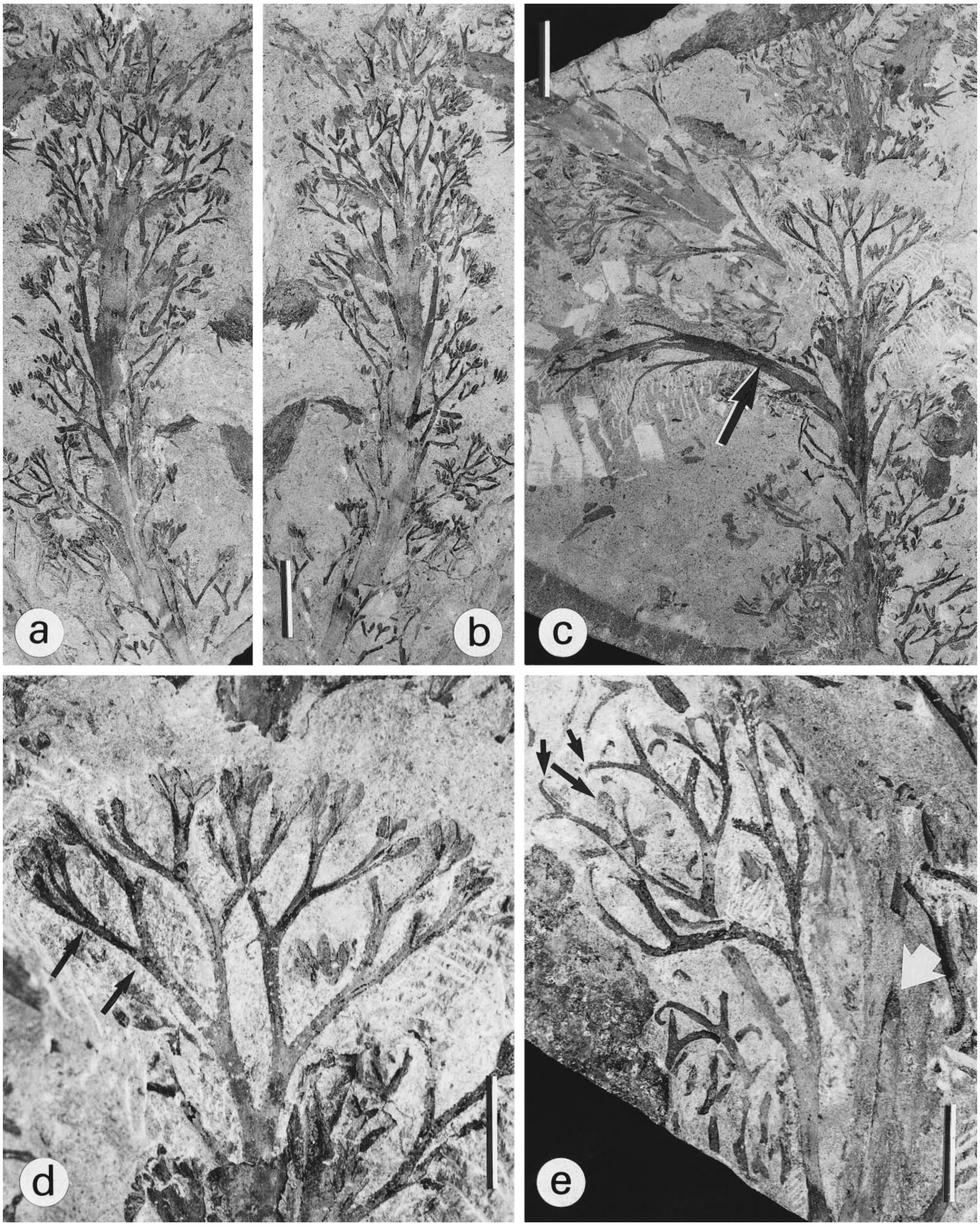

Fig. 5 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. *a, b*, Part and counterpart, first-order axis with densely inserted ultimate appendages. NMW 93.97G.37a&bii. Scale bar = 10 mm. *c*, First-order axis with prominent second-order axis attached (arrow). NMW 93.97G.37ai. Scale bar = 10 mm. *d*, Fertile ultimate appendage. Note successive branching points perpendicular distally (arrow). NMW 93.97G.37ai. Scale bar = 5 mm. *e*, Partly sterile and partly fertile ultimate branching unit. Recurved sterile tips (small arrows) and paired sporangia (large arrow). Large white arrow shows insertion of lateral plunging into the sediment. NMW 93.97G.37bii. Scale bar = 5 mm.

Fig. 6 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. *a*, *b*, Dégagement of part and counterpart of specimen NMW 93.97G.35a&b. Solid black areas represent ultimate appendages, branches, or bases oriented below the plane of the stem surface. *c*, Schematic reconstruction oriented as counterpart. Scale bar = 10 mm.

this lateral was shown to be a dichotomously branched ultimate appendage with two very closely spaced dichotomies proximally (fig. 2*d*). Lateral 3f on the part (fig. 2*a*) is a second-order branch itself, one that bears acutely inserted dichotomized ultimate appendages. This axis occurs on the right-hand side above the surface of the first-order axis. Lateral 3d is only partially preserved on the part, but it is better preserved on the right and below the first-order axis on the counterpart, and it is also a second-order axis.

Node 4 is best preserved on the counterpart, where an ultimate appendage (4e) goes downward into the matrix beneath the axis and where two other ultimate appendages (4a and 4c) are on either side of the stem surface, above the surface (fig. 2*e*).

Node 5 is only preserved on the counterpart, where it demonstrates two ultimate appendages below the stem surface on either side of the axis. Also on the counterpart, at node 6, two more ultimate appendages (6a and 6c) are preserved on each side of the stem, both above the plane of the compressed axis. A third lateral (6e) is indicated by a scar in the center of the stem surface.

In summary, laterals, both second-order axes and ultimate appendages, are preserved in one of six positions around the axis (fig. 2*g*, 2*h*). They are preserved either in the center of the axis (going downward into the matrix), directly above the centre of the axis, or laterally (either above or below the main axis level). Of these six positions at one node, three lateral organs are observed to originate in every other position, with each node above and below alternating in position by occupying the other three (fig. 2*g*, 2*h*). At each whorl the compressions indicate that the three attached organs are inserted at equal divergence angles (i.e., separated by an angle of 120° in the transverse plane at each node). Because of the nature of compression fossils, these angles cannot be established exactly. We describe this pattern as whorled and regularly offset.

The same pattern is repeated over five nodes in specimen NMW 93.97G.33 (figs. 3*e*, 3*f*; fig. 4) and is observed again in the upper four nodes in specimen NMW 93.97G.32 (figs. 3*a*, 3*b*; fig. 6). However, in the latter specimen there are minor differences in spatial arrangement. In the middle (node 3), the three ultimate appendages are inserted over a longitudinal distance of 15 mm along the stem. In the other four nodes, insertion of ultimate appendages occurs over distances if between 4.5 and 8 mm. This compares with the internode length (based on an average location of insertion within nodes) between nodes 1 and 2 of 17 mm. The length of the other three internodes is between 21 and 23 mm. Thus, there is a considerable variation in the distinctness of whorls in this specimen. In addition to the above differences, four ultimate appendages are found at the lowest node on this axis.

Arrangement of ultimate appendages on second-order axes. No second-order axes show clearly the pattern of insertion of ultimate appendages. On the largest second-order axis (fig. 5*c*), ultimate appendages can be seen at the margins of the axis, apparently not in groups, which indicates an alternate pattern. However, at one level, one lateral is visible on the distal margin of the axis, and a second is inserted at the same level, superimposed on the lower margin. This indicates the possibility of opposite or whorled insertion of laterals in second-order axes. Unfortunately, the bases of other laterals are not well enough preserved on the axis surface to provide definitive evidence of a pattern. In another smaller example of a second-order axis (fig. 3*c*, 3*d*), ultimate appendages are crowded together in such a manner that it is impossible to work out their exact pattern.

Anatomy

A single first-order axis (fig. 7) shows evidence of compressed ultimate appendages associated with limonite permineralization of the main axis over a length of ca. 60 mm. In transverse section (fig. 8), permineralized tissues are ca. 2.6 mm in diameter along the bedding plane and exhibit significant compression normal to bedding. Preserved tissue regions include the primary xylem (fig. 8; fig. 9*a*, 9*b*; fig. 10*b*, 10*d*), fragments of probable outer cortex (fig. 8*b*, arrow a), vascular traces (figs. 8*b* [arrow b] and 9*a*), and basal portions of ultimate appendages (fig. 10*a*, 10*c*; fig. 11). The vascular system is actinostelic. The primary xylem consists of a solid and deeply six-ribbed column of tracheids, with mesarch order of maturation (figs. 8, 9*a*, 10*b*). A single permanent protoxylem strand occurs near the tip (peripheral edge) of each xylem rib and is the site of origin of vascular traces (figs. 8, 9*a*). Near the level

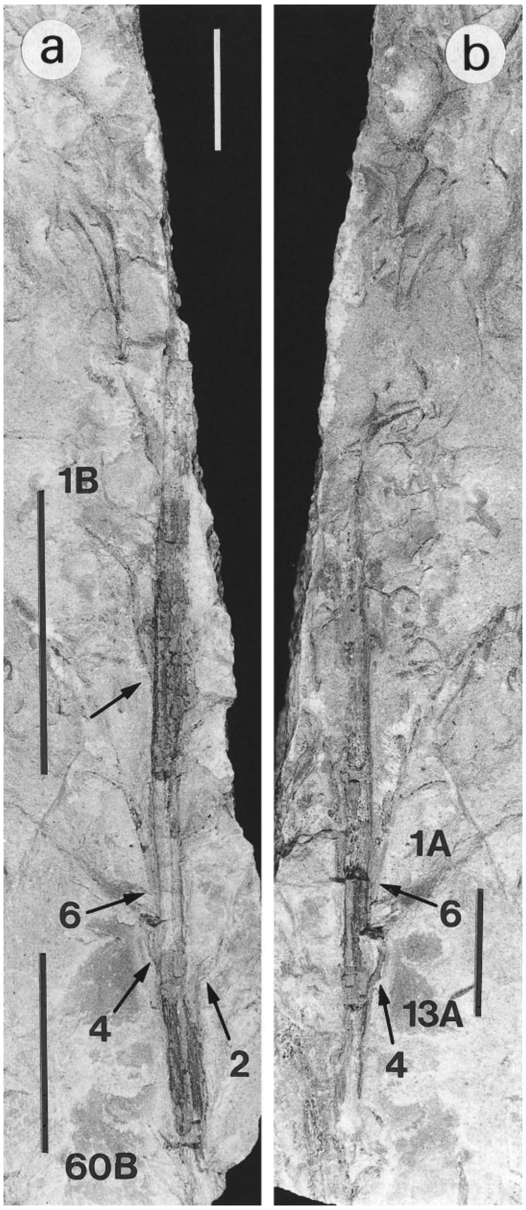

Fig. 7 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. *a*, *b*, Counterpart and part of only permineralized specimen before sectioning. Arrows show attached ultimate appendages and roman numerals refer to probable rib numbers from which laterals were derived at whorl 2 (see text and fig. 11). Black lines show well-preserved permineralized regions, numbers 1B–60B, 1A–13A show approximate position of prepared sections. NMW 93.97G.38a&b. Scale bar = 10 mm.

of their attachment to the axis, ultimate appendages appear to be tangentially bifurcate (figs. 10*c*, 11 [sections 57B and 11A]). Distally, each portion of the ultimate appendage has a circular outline in transverse section (fig. 10*a*) and contains cortex surrounding one or more vascular bundles (figs. 10*a*, 11 [sections 11A and 24B]). Epidermis is not recognizable in the first-order axis but may be present as highly fragmentary tissues in the ultimate appendages (figs. 9*c*, 10*a*).

Primary xylem and traces. Individual ribs of the primary xylem range from ca. 0.7 to 0.9 mm in radial extent and from 0.30 to 0.35 mm in width at the tip, tapering slightly to between 0.20 and 0.25 mm near the center of the stele. At the center, ribs are united singly or in groups of two or three to form a stellate system (figs. 8, 11 [section 51B]). Protoxylem is characterized by a distinct gradient of decreasing cell size and ellipticity toward the center of each protoxylem strand, as observed in transverse section (figs. 9*a*, 10*b*). The center of protoxylem strands consists of tracheids (fig. 9*a*, arrow a) or, more commonly, of limonite-filled lacunae of variable sizes and shapes as a result of mode of preservation or proximity to level of trace departure (figs. 8, 10*b*). The smallest cells in the protoxylem region measure as small as 12 μm in transverse diameter; wall ornamentation confirming cell identity is not observed under the light microscope. However, small-diameter cells with helical thickenings, presumed to be protoxylem (fig. 12*a*, arrows), are observed by scanning electron microscopy (SEM). Metaxylem tracheids are larger, ranging from 60 to 84 μm in transverse diameter, with the largest cells generally occurring along midplanes of xylem ribs and toward the center of the stele (figs. 9*a*, 10*b*). Some cells on the surface of the primary xylem appear to be more thinly walled and may have been immature at the time of preservation.

Although the specimen is fragmentary, wall layers of metaxylem tracheids are in places exceptionally well preserved, albeit in different ways (figs. 9*b*, 10*d*). In some tracheids, presumed organic material that originally comprised cell walls is mostly opaque (fig. 10*b*, 10*d*) and provides striking views of pitting in slightly oblique section under the light microscope (fig. 10*d*). Bordered pits are uniseriate with respect to individual wall facets and variably elongate in the transverse plane, with corresponding elliptical apertures. In other well-preserved tracheids of the metaxylem, organic materials in cell walls have been cleared (probably oxidized), revealing considerable detail in light microscopy of secondary wall, compound middle lamella, and small intercellular spaces (fig. 9*a*, 9*b*). In transverse section, extensive pit cavities spanning an entire wall face are again observed (fig. 9*b*, arrow a), and distinctive secondary wall thickenings marking the boundaries of pit borders are found in adjacent corners of neighboring cells (fig. 9*b*, arrow b). Casts of pit apertures (fig. 12*a*, left) and casts of pits and pit pairs (fig. 12*b*–12*d*) are readily observed by SEM.

In one thin section (fig. 9*d*), the lumen of a metaxylem tracheid is occupied by a pyriform fungal spore measuring 28 μm in length by 25 μm in width, with an attached hypha of ca. 2.8 μm in diameter. A single septum is observed in the hypha ca. 6.7 μm from its attachment to the spore.

The specimen provides incomplete evidence of probable ultimate appendages borne at several levels on the shoot, although preservation is insufficient to determine their precise arrangement and number (fig. 7; fig. 10*a*, 10*c*; fig. 11). Some ultimate appendages are represented as compressions only (fig. 7), whereas others are represented exclusively by anatomically preserved vascular traces, or more often, as originally attached ultimate appendage bases (figs. 10*a*, 10*c*; fig. 11 [sections 57B, 11A, and 24B]). In no instance is preservation sufficient to allow us to follow traces from their point of origin into the ultimate appendages. Interpretation, therefore, comprises a composite view derived from observations of multiple lateral

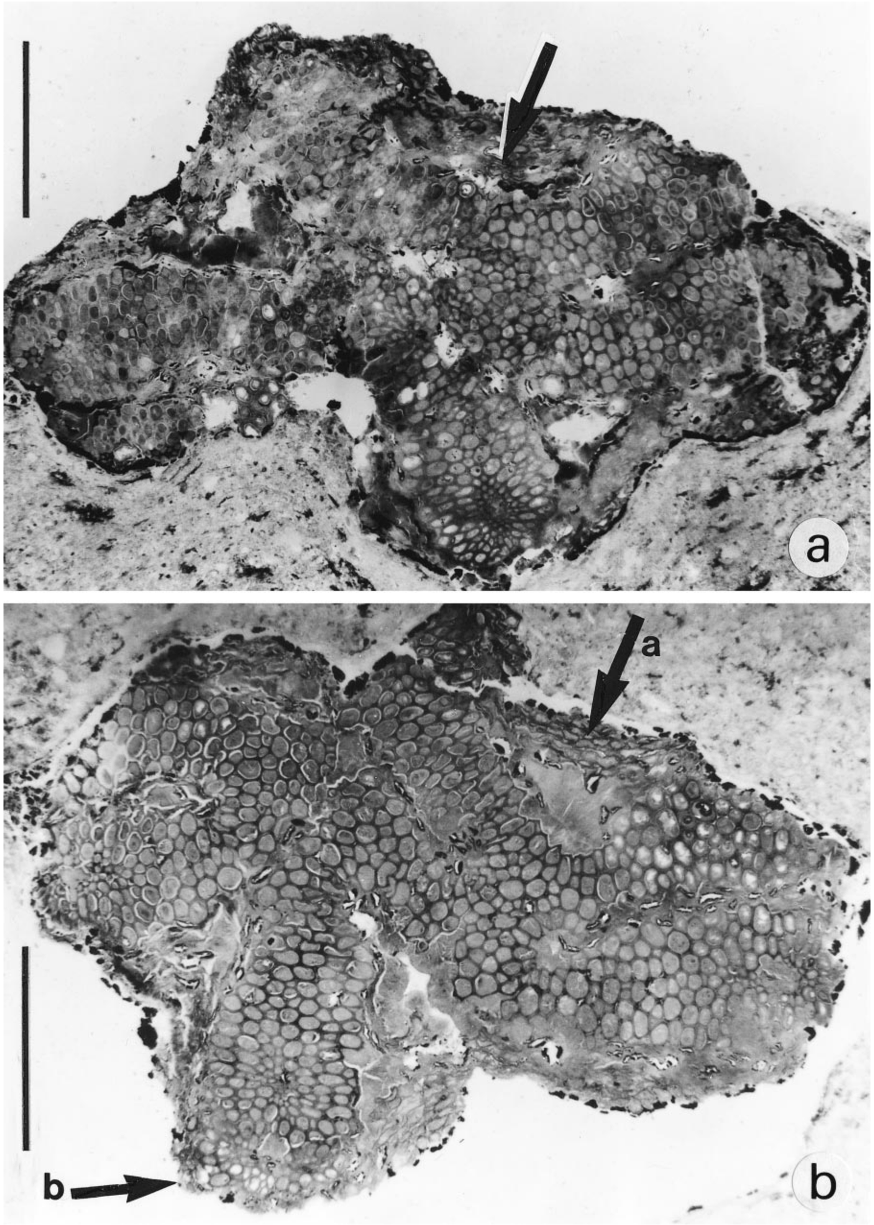

Fig. 8 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. Permineralized transverse sections from specimen NMW 93.97G.38a&b. *a*, Entire preserved axis showing configuration of vascular tissues and outer cortex, thick-walled cells (arrow). Section 48B. Scale bar = 0.5 mm. *b*, Entire preserved axis showing six-ribbed primary xylem column in the center embedded in an amorphous region interpreted as primary phloem and inner cortex and fragments of outer cortex at the periphery (arrow a). Section 8A. Scale bar = 0.5 mm.

appendages and traces at different levels in the specimen. Incipient traces are recognized proximally at the tips of the primary xylem ribs as a radial bifurcation of the permanent protoxylem strand (fig. 11, section 51B, rib 2). Distally, in incipient traces, the outer protoxylem divides in a tangential direction, resulting in a primary xylem rib containing three more or less triangularly arranged protoxylem strands (figs. 8*b* [arrow b]; 9*a* [arrows a and b]; 11 [section 42B]). One incipient trace (figs. 8*b* [arrow b], 9*a*) measures ca. 0.4 mm in tangential dimension. Near the level of separation from the primary xylem of the axis (fig. 11, 51B, rib 4), a nearly free but fragmentary trace measures ca. 0.25 mm in the tangential direction and 0.15 mm in the radial direction. Other free traces within the tissues of the axis have not been observed. At the level of the node (fig. 11, section 57B), one attached ultimate appendage base appears nearly bifurcate and most likely contains two separate vascular bundles. At what may be nearly an equivalent level (figs. 10*c*, 11 [section 11A, right]), another ultimate appendage appears, single but elliptical, measuring ca. 0.6 by 1.0 mm, in transverse section. Above this level, the specimen exhibits ample evidence that appendages are at least once bifurcate (fig. 11, sections 57B, 11A, and 24B, paired arrows).

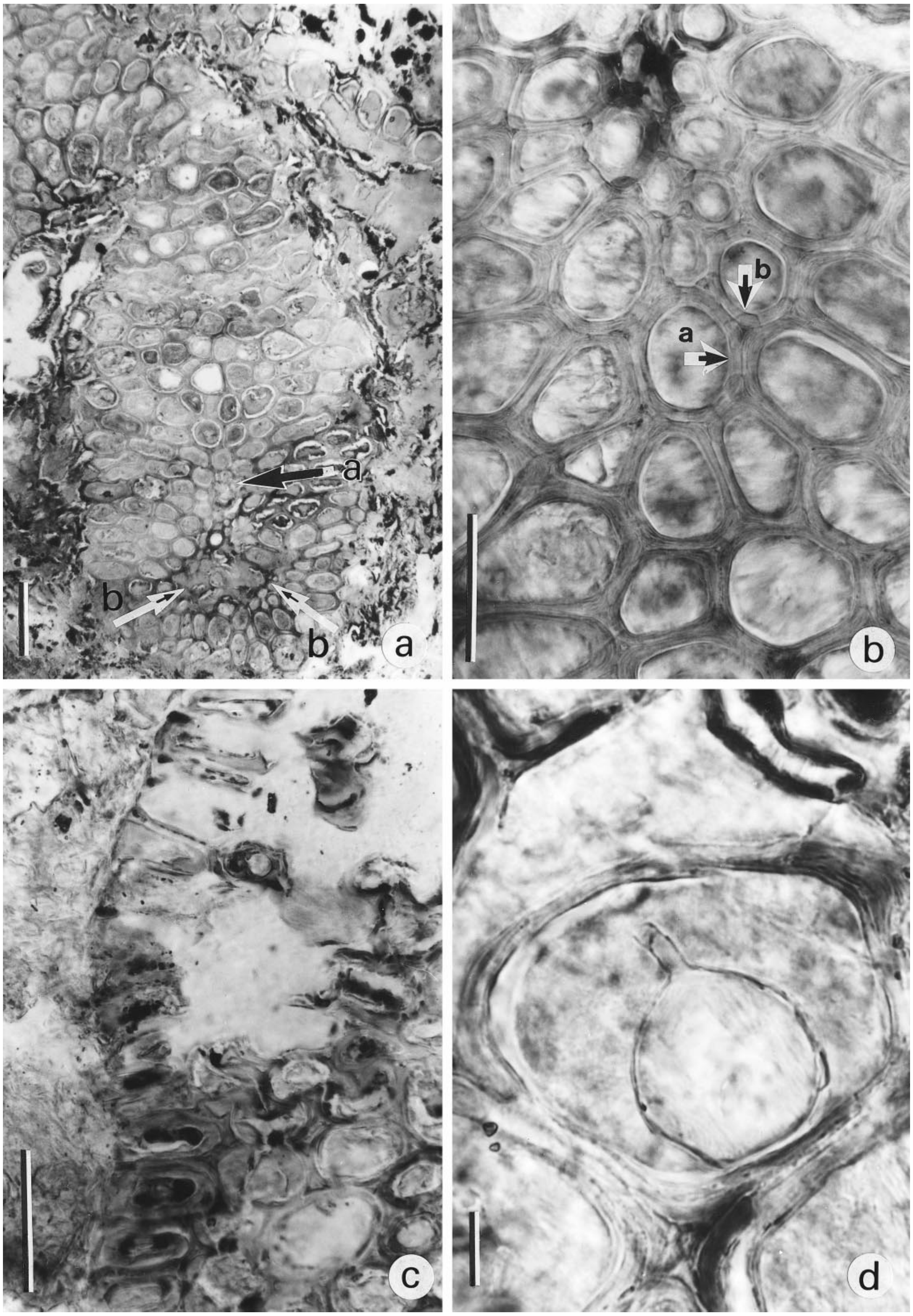

Fig. 9 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. Permineralized transverse sections from specimen NMW 93.97G.38a&b. *a*, Primary xylem rib with incipient vascular trace, protoxylem strands (arrows). Arrow a represents the permanent peripheral protoxylem strand, arrows b represent protoxylem locations within the incipient trace. Section 43B. Scale bar = 100 μm. *b*, Higher magnification of tracheids of the primary xylem showing some cells with dark walls (right) and cells with lighter walls (left), providing evidence of primary and secondary wall layers and pit borders. Section 48B. Scale bar = 50 μm. *c*, Boundary layer of cells in a lateral appendage interpreted as epidermis, exterior to the left. Section 13A. Scale bar = 50 μm. *d*, Fungal spore with attached hypha within a metaxylem tracheid, septa visible at top of neck. Section 21B. Scale bar = 10 μm.

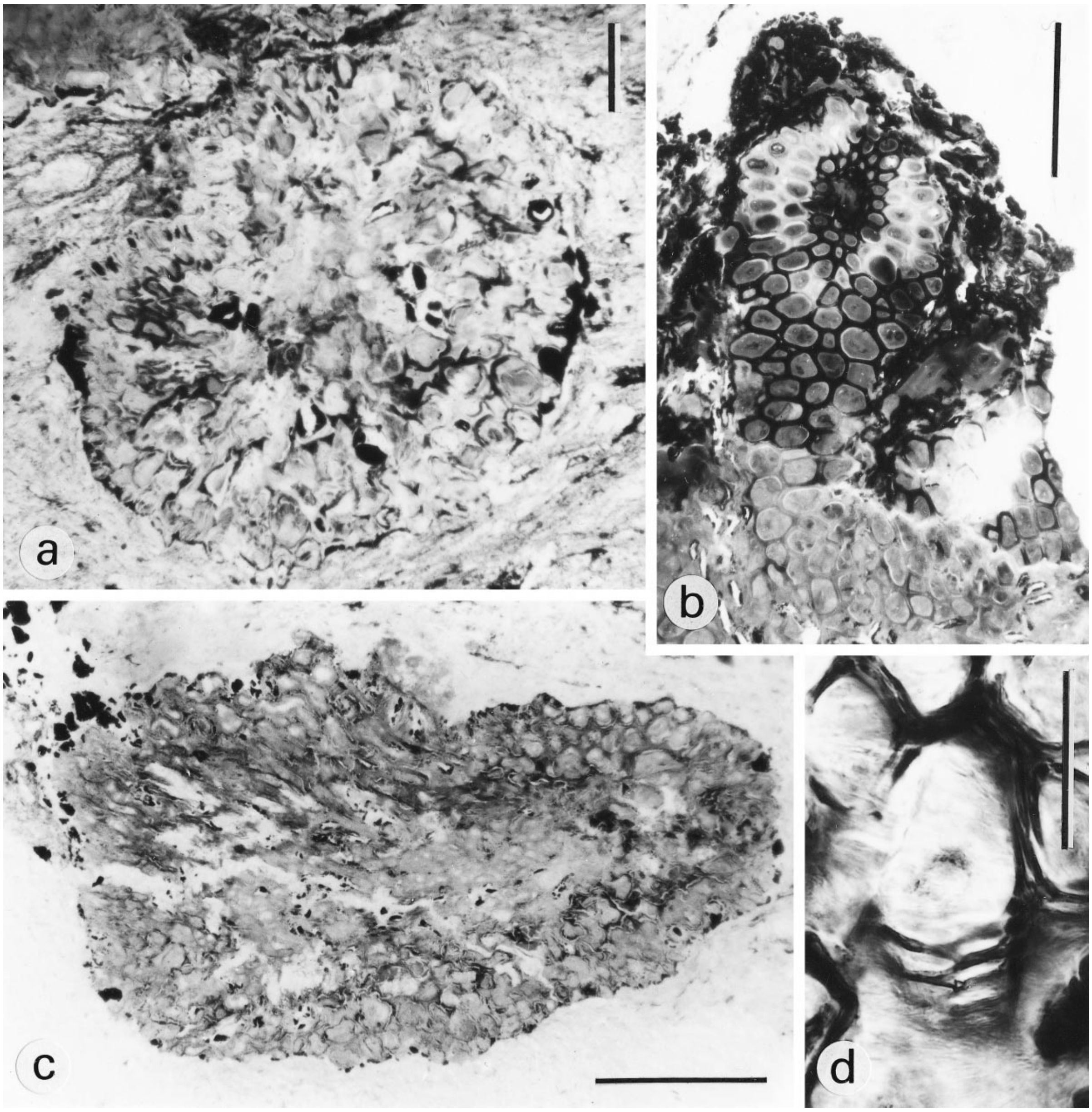

Fig. 10 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. Permineralized transverse sections from specimen NMW 93.97G.38a&b. *a*, Lateral appendage probably at level below initial bifurcation, cells comprising possible epidermis around periphery. Section 24B. Scale bar = 100 μm. *b*, A single primary xylem rib showing regions of differential preservation of tracheid walls and a lacuna in the region of the peripheral protoxylem strand. Section 5B. Scale bar = 250 μm. *c*, Lateral appendage, probably at level below initial bifurcation; compare with drawing in fig. 11 (11A, right). Section 11A. Scale bar = 250 μm. *d*, Oblique view of metaxylem tracheids showing large elliptical bordered pits with elliptical apertures. Section 10B. Scale bar = 50 μm.

Where well preserved (figs. 10*a*, 11 [sections 24B and 11A]), derivative ultimate appendage axes are more or less circular, ca. 0.6 mm in diameter in transverse section, and contain either a single elongate vascular bundle or two closely spaced terete bundles. In no instance is protoxylem of these bundles sufficiently preserved to be measured. Metaxylem tracheids near the base of one ultimate appendage (fig. 10*c*) range up to ca. 30 μm in transverse diameter.

Careful mapping allows us to follow individual primary xylem ribs throughout the entire structurally preserved region of this specimen (fig. 11, Arabic numerals) and provides evidence of at least three nodes. The proximal node (fig. 11, section 57B) includes ultimate appendages that have clearly been produced from rib 3 and possibly rib 5 (arrows). A second node clearly involves ribs 4 and 6 (fig. 11, sections 11A–42B) and may also be identified at the level of incipient traces (fig. 11, section 51B, arrows at ribs 2 and 4), which indicates trace production from rib 2 as well. The distal node (fig. 11, section 24B, arrows, and section 42B at the level of an incipient trace) clearly shows production from rib 3 plus a fragment of tissue

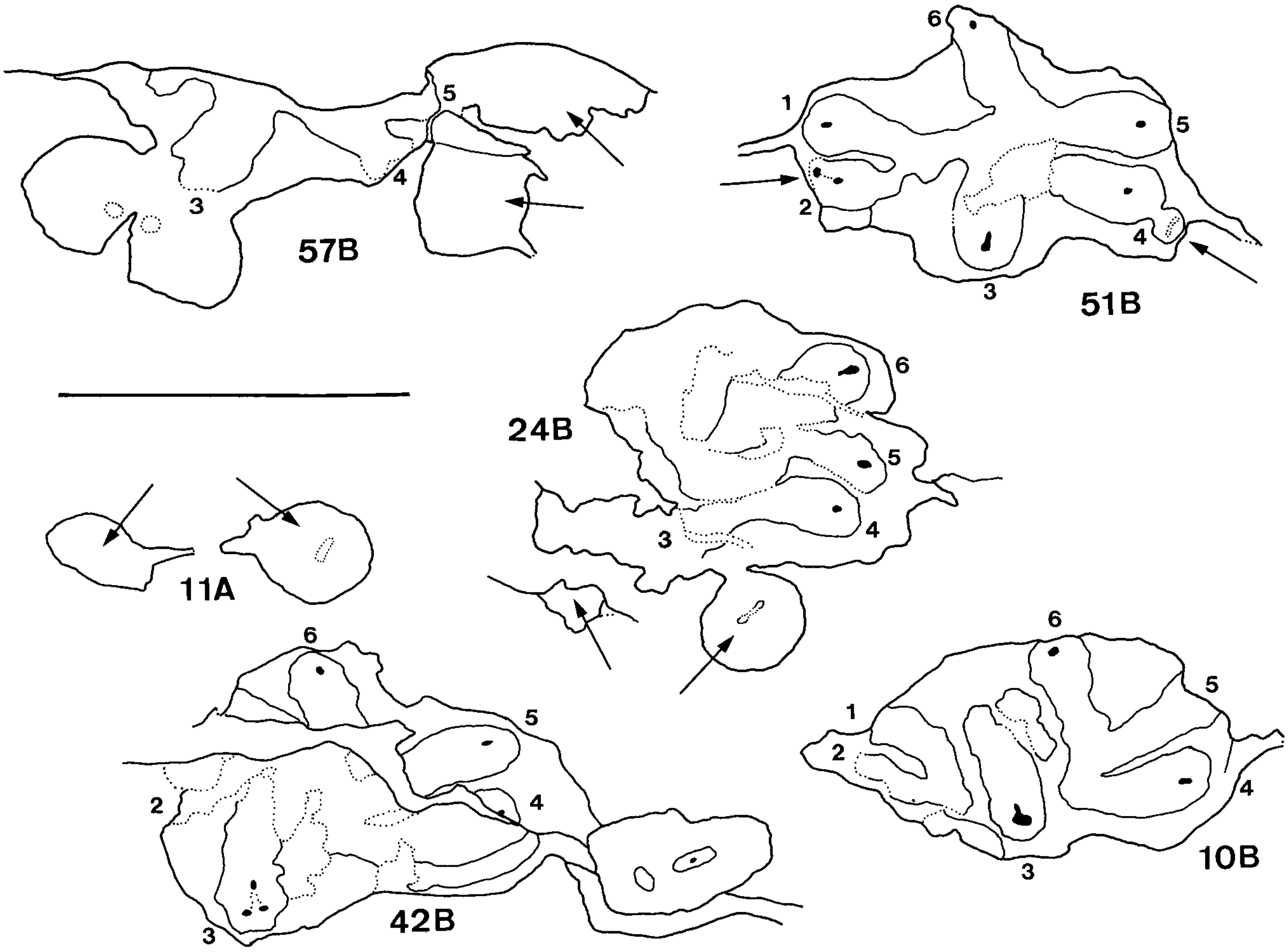

Fig. 11 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. A series of transverse sections showing configuration of the primary xylem, traces, and lateral appendages; proximal end of specimen section 57B, distal end 10B. Part (series A) and counterpart (series B) series of sections are numbered in the same direction from proximal to distal (see fig. 7) and are related to each other at the level of section 11A and 42B. All sections are viewed from the distal surface. Small Arabic numerals identify individual primary xylem ribs mapped throughout the specimen and related to lateral appendages (see text). Sections 24B, 11A, and 57B demonstrate sections through bifurcate appendages (arrows) derived from ribs 3, 6, and 5. Section 51B arrow (left) indicates radial bifurcation of permanent protoxylem strand in rib 2; arrow (right) indicates almost separated trace from rib 4. Specimen NMW 93.97G.38a&b. Scale bar = 2 mm.

in section 30B (not figured), which possibly indicates involvement from rib 4 or 5 as well. Thus, the pattern of lateral appendage departure in the permineralized specimen supports the interpretation (made from compressions) of a whorled lateral appendage arrangement, most likely with three appendages per whorl. Anatomical evidence also indicates that members of each whorl are regularly offset with members of adjacent whorls produced from alternating sets of primary xylem ribs. Within each whorl, only every other primary xylem rib is involved in trace production.

Examination of the photographs of the compression (fig. 7) together with the transverse sections reveals a correspondence in terms of the interpretations of anatomy and morphology. For example, at the second node (ca. sections 11A–42B), three compressed laterals are preserved attached to the axis (numbered arrows). Comparison indicates that the two shorter truncated axes represent the ultimate appendages derived from xylem ribs 4 and 2, whereas the longer preserved segment represents one-half or one-quarter of the ultimate appendage derived from rib 6.

Extraxylary tissues. Tissues immediately surrounding the primary xylem in the axis, probably primary phloem and inner cortex, are represented by a mostly amorphous region comprised of blocks of radiating crystal fabric and occasional organic debris. External to this region are fragments of tissue that we have interpreted to represent outer cortex (fig. 8). The cells toward the inside of this region appear to be somewhat thinner-walled, and they are often compressed or crushed in a radial direction. The tangential dimension of cells in this tissue region ranges from 20 to 50 μm, and occasional cells contain dark (most likely organic) materials within their lumina. Some cells toward the periphery of the preserved tissues appear to have very thickened cell walls (fig. 8*a*, arrow), perhaps indicating remnants of a very robust cortex similar to

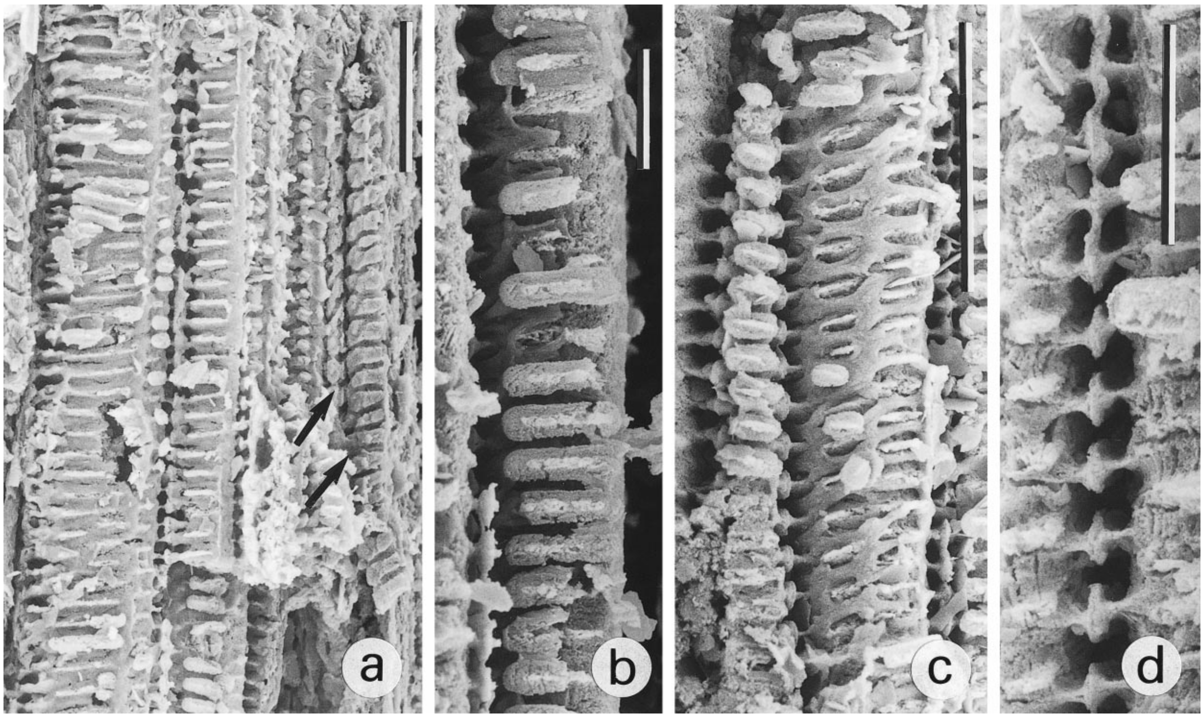

Fig. 12 *Compsocradus laevigatus* Berry et Stein gen. et sp. nov. SEM micrographs of limonite permineralization of a small fragment of xylem strand lifted from specimen NMW 93.97G.38a. *a*, General view of part of xylem column, showing casts of the pit apertures (left) and helically thickened casts of protoxylem cells (arrows). Scale bar = 50 μm. *b*, Limonite cast of cell lumen and oval pits. Scale bar = 20 μm. *c*, Cast of tapering cell end with pit casts rows shown on each facet of cells. Scale bar = 50 μm. *d*, Cast of pit pairs between cells. Scale bar = 20 μm.

that observed in members of the Iridopteridales (for example in *Arachnoxylon kopfii*—Stein [1981], fig. 4). Bounding the preserved tissues at most levels of the axis is a black noncellular organic residue (fig. 8*b*). Commonly encountered in other limonite and pyrite permineralizations (Stein et al. 1983), this material likely represents outer tissues of the axis that were compressed beyond recognition prior to the onset of permineralization.

Cortical tissues occupy most of the volume of preserved ultimate appendages (fig. 10*a*, 10*c*). An outer zone of cortex, ranging from 0.1 to 0.2 mm in thickness, is comprised of cells that range from 100 to 200 μm in diameter. This zone apparently corresponds to the outer cortex of the main axis. Toward the center and immediately surrounding the area where the primary xylem would have been located, probable inner cortex and primary phloem are represented only by cell fragments. The outermost layer of cells in the ultimate appendage appears to form a distinct boundary, which possibly represents epidermis (figs. 9*c*, 10*a*), although stomata are not recognized in this layer. Individual cells of this boundary layer have thickened cell walls and range from 12 to 20 μm in tangential dimension and from 33 to 40 μm radially, as observed in transverse section.

Comparisons

Anatomical Comparisons

Beck and Stein (1993) recognized two types of stelar configuration in basal trimerophyte–derived land plants. The "radiate protoxylem group" is characterized by those forms in which the vascular supply to laterals on an axis is ultimately derived from a single, centrally located, continuous, and evidently cauline protoxylem strand in the stele. In such plants, one observes a multiribbed primary xylem in transverse section; a number of protoxylem strands distributed along the midplane of each rib are "caught in the act" of supplying vascular traces at the rib tip. Plants placed in this group include "advanced trimerophytes" (Beck and Stein 1993) such as *Gothanophyton*, aneurophytalean progymnosperms, members of Stenokoleales, and some early seed plants. These plants contrast strongly with members of the "permanent protoxylem" group, in which the central protoxylem strand is missing and in which several longitudinally continuous protoxylem strands occur toward the periphery of the metaxylem, from which traces to laterals are derived. Beck and Stein recognized Iridopteridales, some cladoxylopsids, and possibly sphenopsids as belonging to this group. It is within the permanent protoxylem group that the anatomy of *Compsocradus* should be placed. In addition to the above list, we recognize the similar anatomy in reported "pre-ferns" *Protopteridophyton* Li and Hsü (1987) and *Metacladophyton* Wang and Geng (1997).

Of the permineralized genera assigned to Iridopteridales (table 1), *Compsocradus* bears the closest anatomical resemblance to the genus *Arachnoxylon* Read. The latter has a similarly ribbed stele with peripheral protoxylem strands. Of the three specimens of *Arachnoxylon kopfii* reported by Stein (1981), the single permineralization of *Compsocradus* bears closest resemblance in primary xylem form to Arnold's specimen (*Asteropteris kopfii* of Arnold 1935), which is the type of the genus. However, this specimen shows no evidence of traces to appendages, and the vascular system is much larger overall. Two specimens assigned to *Arachnoxylon kopfii* by Stein (1981), from other western New York localities, demonstrate whorled insertion of lateral traces, with one trace per rib per node. They also demonstrate the existence of larger four-ribbed "major" traces and of smaller terete "minor" traces, which likely represent the vascular supply to branches and to dichotomous ultimate appendages, respectively. *Compsocradus* does not demonstrate the existence of major traces in the specimen that was available to us, although their presence is reasonably inferred from the presence of attached second-order axes observed in compressions.

The only major difference between *Arachnoxylon* and the permineralizations of the smaller axes of the compression fossil *Ibyka amphikoma* Skog and Banks (1973), according to Stein (1981), was the reported helical trace departure in *Ibyka*. However, our reexamination (with J. Cordi) of the type specimens of *Ibyka amphikoma* has demonstrated that whorled insertion of lateral organs is prevalent in most parts of the plant. In the smaller distal axes of *Ibyka*, less regularity in insertion might superficially resemble a helix. Thus, the anatomy of permineralized *Arachnoxylon* can no longer be distinguished from the permineralizations of *Ibyka*. However, the anatomies of *Arachnoxylon*/*Ibyka* and *Compsocradus* can be readily distinguished from each other by the whorled trace departure in *Arachnoxylon*/*Ibyka* and by the whorled, every-other-rib departure of traces in *Compsocradus*.

In terms of the tracheid wall structure, the large uniseriate pit cavities with a single slitlike opening (as evidenced by the ridges on the pit cavity casts observed by SEM) of *Compsocradus* were recognized. Similar (but not so regularly patterned) pits are found in iridopteridales such as *Arachnoxylon kopfii* (Stein 1981), the cladoxylopsid *Pseudosporochnus hueberi* (Stein and Hueber 1989), and *Rhacophyton ceratangium* (Dittrich et al. 1983).

Morphological Comparisons

Comparison with Ibyka *and other Iridopteridales.* The new plant bears essentially similar dichotomous sterile and fertile ultimate appendages on more than one axis level, which is a known characteristic of *Ibyka amphikoma* (Skog and Banks 1973), which Stein (1982) included in the Iridopteridales on the basis of its anatomy and which was the only member of the order that Stein recognized as having preserved morphology (see table 1). In *Ibyka*, the ultimate appendages are very similar to those of the new plant and are arranged on all three known orders of branching. The anatomy of higher-order axes suggested to Skog and Banks (1973) a helical arrangement of laterals. Restudy of *Ibyka* demonstrated that the branching is in fact distinctly whorled in larger low-order axes (Berry et al. 1997).

Anapaulia moodyi (Berry and Edwards 1996*a*) was included in the order on the basis of comparison of its morphology to *Ibyka* and to the morphology predicted from anatomically preserved Iridopteridales. *Anapaulia moodyi* is very similar in morphology to the new concept of *Ibyka*, except that no ultimate appendages are observed on second-order axes; appendages are observed only on axes of the first, third, and fourth orders. In addition, both *Ibyka* and *Anapaulia* have similar spines on all orders of axes except the very distal dichotomies of the ultimate appendages. Sporangia have been previously reported from *Ibyka* and *Anapaulia*. Those of *Ibyka* were poorly preserved but were believed to be obovoid to pyriform, arranged terminally distal to the last dichotomy of the ultimate appendage, and slightly recurved (Skog and Banks 1973). In the case of *Anapaulia*, the sporangia were of a similar shape and position, with pairs of sporangia perhaps being slightly closer together but often markedly recurved (Berry and Edwards 1996*a*). Those sporangia of *Compsocradus* are more or less erect but are otherwise similar to the sporangia of *Ibyka* and *Anapaulia*.

Other possible members of Iridopteridales are "*Hyenia*" *vogtii* Høeg 1942 and "*Hyenia*" *banksii* Arnold 1941. A hypothesized relationship is based on published descriptions and photographs of dichotomous ultimate appendages and higher-order axes inserted on larger axes in whorls (Berry and Fairon-Demaret, in press). "*Hyenia*" *vogtii* has spines similar to those of *Ibyka* and *Anapaulia*. No spines were reported on "*Hyenia*" *banksii*. However, the dichotomous lateral branching systems are inserted so densely on this plant that spines might be difficult to see. Both taxa appear to bear little resemblance to the classic image of *Hyenia* (e.g., Kräusel and Weyland 1932).

In conclusion, the most obvious differences between *Compsocradus* and established members of Iridopteridales are the unique whorled yet alternate branching pattern in *Compsocradus* and the definite lack of spines.

Comparison to Protopteridophyton *and* Metacladophyton. *Protopteridophyton devonicum* (Li and Hsü 1987), reported from Givetian and Frasnian sediments in South China, is recognized based on its two branch orders and its dichotomizing sterile or fertile ultimate appendages. Close pairs of second-order axes were reported to be arranged on the first-order axes in a decussate fashion, and the ultimate appendages were similarly arranged on the second-order axes, thereby resulting in a three-dimensional pinnate branching pattern. Ultimate sterile and fertile appendages are essentially identical, 1.5–5.0 cm long, and have usually six isotomous dichotomies. In fertile examples, pairs of sterile terminations are replaced by pairs of spheroid to ellipsoid sporangia. Some ultimate appendages may be only partly fertile. Differences between *Protopteridophyton* and the new plant therefore relate to the pinnate arrangement of the branching, the lack of second-order axes that are borne together with ultimate appendages on the main stems, and the characteristic paired arrangement of lateral branches.

The xylem column of *Protopteridophyton* is ribbed, with the two known ribs arranged in a V, although preservation of the stem is incomplete and although more ribs may possibly have been present in the living plant. *Metacladophyton tetraxylum* (Wang and Geng 1997) has a more complete preserved anatomy, demonstrating four separate V-shaped double ribs, which join centrally only at the nodes. The lowest order of branching was shown to be whorled, although higher orders were believed to be opposite or decussate pinnate in two dimensions. Examination of some specimens of *Metacladophyton* from the type locality (by C. M. Berry) indicated that whorled insertion of laterals also occurs in some higher orders of branching.

We place *Metacladophyton* tentatively in the Iridopteridales, whereas Kenrick and Crane (1997) place it in the Equisetopsida stem group. The systematic position of *Protopteridophyton* is more problematic as a result of the incomplete preservation of the vascular system.

Comparison to Belgian Middle Devonian plants. Stockmans (1968) described diverse assemblages of plants from Middle Devonian localities in Belgium, some of the taxa of which superficially resembled *Compsocradus*. *Niayssoidea belgica* Stockmans from Sart-Dames-Avelines has dichotomous laterals inserted in whorls on very narrow axes and terminal pairs of sporangia on the fertile ultimate appendages. The material is very fragmentary, with type specimens being only 6 mm in length. Compare *Niassoidea belgica*, from Ronquières, is larger (1–1.5 mm in diameter) and has nodes with both dichotomizing appendages and larger lateral organs (possibly second-order axes) inserted upon them. *Hoegia filiformis* Stockmans, also from Ronquières, has axes of 1–2 mm in diameter that are marked with longitudinal ridges, which run along the axes (indicating a ribbed vascular system). The dichotomous laterals are possibly inserted in whorls. At least two types of sporangia are associated with the fragments, including paired-sporangia terminating dichotomous ultimate appendages. None of the above plants is well or completely enough preserved to show definitive patterns of insertion of lateral organs, as demonstrated in *Compsocradus*, or to demonstrate enough characters for comparison. However, they all show characters that indicate an affinity with Iridopteridales based on the concept of the group presented here, but the specimens are presently too fragmentary to be included in the order.

Leclercq (1940) described a sterile axis under the name *Hyenia elegans* (EH.9, Leclercq's fig. 7). This specimen is preserved in a grey matrix that is very different from the yellowish matrix containing the famous fertile specimens from the same Middle Devonian locality of Oe. The specimen demonstrates dichotomous appendages that are attached to the stem in the same whorled but alternate manner that has been observed in *Compsocradus*. Unfortunately, Leclercq's specimen is very poorly preserved, so no further information is available.

Comparison to Cladoxylopsida. Morphologically preserved specimens of Devonian Cladoxylopsida often show a superficial similarity to *Compsocradus* and other Iridopteridaleans. The taxonomy of Devonian cladoxylopsids is currently in a state of flux (Fairon-Demaret and Berry 2000). *Calamophyton* and *Hyenia* in particular have sterile dichotomous lateral branching systems (Leclercq and Andrews 1960; Fairon-Demaret and Berry 2000) that might be confused with the ultimate appendages of Iridopteridales. However, reconstructions of more complete branching systems and, in some cases, whole plants will reveal very obvious differences from *Compsocradus* and other iridopteridaleans. Lateral branching systems of cladoxylopsids (superficially similar to the ultimate appendages of iridopteridaleans) where investigated in detail (Stein and Hueber 1989; Berry and Fairon-Demaret 1997) usually showed an insertion pattern that does not have any regular geometric pattern. In addition, Cladoxylopsids do not have higher-order axes that are inserted on a larger axis, as is the case with the iridopteridaleans; rather, the branches divide by dichotomous division or in a digitate fashion (Leclercq and Andrews 1960; Leclercq and Banks 1962). Spines are unknown in cladoxylopsids, whereas distinctive "nests" of cortical sclerenchyma (which provide the typical speckled or nodose pattern to the surface of compressions of cladoxylopsids) (Leclercq and Banks 1962; Stein and Hueber 1989) are unknown in iridopteridaleans. The sterile tips of distal dichotomizing lateral branching systems are never recurved in cladoxylopsids; rather, they have an expanded and somewhat fleshy but nevertheless straight tip (Leclercq and Andrews 1960; Leclercq and Banks 1962; Berry and Fairon-Demaret 1997).

Discussion

Justification of New Genus within Iridopteridales

The concept of Iridopteridales, as diagnosed by Stein (1982), is based on purely anatomical characteristics. The present morphological concept of Iridopteridales (Berry and Edwards 1996*a*; Berry et al. 1997; Berry and Fairon-Demaret, in press) allows for up to four axis orders, each of which bears whorls that are composed of higher-order branches and appendages, the insertion of these whorls being superposed along the axis. *Ibyka*, *Anapaulia*, and "*Hyenia*" *vogtii* all have these characteristics. They also bear spines. In addition, the first two have fertile ultimate appendages that are essentially identical to the sterile ones but that are terminated by paired sporangia (character unknown in "*Hyenia*" *vogtii*). In both, tips of sterile ultimate appendages are also recurved. In *Anapaulia*, recurved tips appear to develop from the determinate growth of small circinate axes (see Berry and Edwards 1996*a*, their fig. 2*a*), and this is probably characteristic for the order.

For the material described in this essay, we propose the name *Compsocradus laevigatus* gen. et sp. nov. We believe the characteristic whorled and regularly alternate phyllotaxis justifies this classification. The plant is also the only iridopteridalean to have naked, spineless axes. In addition, the comparatively acute insertion of the laterals is distinct from that of other iridopteridaleans.

The apparent similarity of the stele of *Compsocradus* to that of the type specimen of *Arachnoxylon kopfii* is of taxonomic concern. However, we note that a similar stelar architecture is also seen in *Ibyka amphikoma*. *Ibyka* is morphologically and anatomically distinct from *Compsocradus* because laterals appear in whorls, with one trace from each xylem rib supplying a branch or appendage. It is also a spiny plant.

Phylogenetic Relationships

Phylogenetic relationships among basal euphyllophytes (Kenrick and Crane 1997) remain highly problematic. A widespread, diverse, and reasonably abundant assemblage of plants apparently bridges the gap between late Early Devonian plants, such as *Psilophyton* and *Pertica* (traditionally trimerophytes), and Late Devonian to Early Carboniferous representatives of modern major plant groups, such as horsetails, ferns, and seed plants. However, phylogenetic resolution remains poor as a result of the transitional morphology of these forms, which often involves quantitative, as opposed to qualitative, differences between taxa. Perhaps this explains the difficulty typically encountered in proposing cladistic characters without significant levels of homoplasy in important phylogenetic characters, such as the organization of lateral branches on the shoot and stelar architecture. Another problem is the fact that the fossil record, especially in the Middle Devonian, contains many specimens and whole groups that are either anatomically or morphologically preserved, but not both; no convincing whole-plant concept for analyzing these specimens has yet been established. Until now, this has been true for Iridopteridales as well. The work on *Compsocradus* gen. nov. reported here combined with new information on *Ibyka* Skog and Banks (C. M. Berry, J. Cordi, and W. E. Stein, unpublished data) establish for the first time a concrete concept of Iridopteridales, thereby allowing one to realistically address whole-plant form from a combined anatomical and morphological perspective. The main characteristics of the order Iridopteridales are as follows: (1) the characteristic stelar architecture (in which the primary xylem forms a solid column containing "permanent" peripheral protoxylem strands [Beck and Stein 1993] near rib tips); (2) iterative branch system architecture reflecting the presence of "major" and "minor" trace types observed anatomically; and (3) the presence of both branches and ultimate appendages in whorls. Within this general pattern, one can also distinguish a subgroup of plants (*Compsocradus* and "*Cladoxylon*" *dawsonii*), in which the lateral organs are regularly offset within successive whorls (Cordi and Stein 1997). These characters are potential synapomorphies for or within the Iridopteridales in the context of the Devonian euphyllophytes of Kenrick and Crane (1997). Other characteristics of the Iridopteridales, such as paired sporangia and isodichotomous ultimate appendages, clarify the outward appearance of the plant but are likely to be neither shared derived features of the group nor phylogenetically informative characteristics.

In the wider context of the Euphyllophytina of Kenrick and Crane, where might the Iridopteridales fall? We suggest the presence of a more inclusive clade, one comprised of Devonian members of Cladoxylopsida (Pichi-Sermolli 1959; Leclercq 1970; Stein and Hueber 1989) plus Iridopteridales (Arnold 1940; Stein 1982), which might form the concept of a class-level taxon—Cladoxylopsida in an expanded sense. The history of the taxonomy of this group is complex. It should, however, be noted that as of yet, there is little evidence that the type species of the type genus *Cladoxylon* actually belongs to the group that is otherwise substantially defined by Middle Devonian taxa. Table 2 represents our current view. Presently known members of Pseudosporochnales (in our sense) include *Calamophyton* Kräusel and Weyland (*sensu* Fairon-Demaret and Berry 2000), *Pseudosporochnus* Potonié and Bernard (Leclercq and Banks 1962; Stein and Hueber 1989; Berry and Fairon-Demaret 1997), *Lorophyton* Fairon-Demaret and Li (1993), and *Wattieza* Stockmans (*sensu* C. M. Berry, unpublished data). A potential synapomorphy to diagnose the base of this clade is the presence of stelar systems with radially directed, deeply bifurcate/trifurcate (or more complexly divided) primary ribs (see fig. 13). Within the Devonian Pseudosporochnales, where known, the primary xylem column is dissected. In addition, in several taxa there appears to be a range of protoxylem architectures that effectively bridge the proposed distinction between "radiate" and "peripheral" protoxylem groups (Beck and Stein 1993) that currently forms the substantial basis for Kenrick and Crane's (1997) euphyllophyte "Moniliformopses" and "Radiatopses" subclades. For example, *Pseudosporochnus hueberi* (Stein and Hueber 1989) demonstrates conspicuous peripheral protoxylem strands near the tips of xylem ribs as well as additional strands along midplanes, but apparently these protoxylem strands do not emanate from a single strand at the center of the stele. *Calamophyton primaevum* (Mustafa 1978), by contrast, apparently lacks internal protoxylem altogether, and with further study, it may be shown to exhibit the "permanent" protoxylem condition. Clearly, more remains to be learned before the significance of this character is clarified.

Table 2

Summary of Genera and Higher-Order Taxa of Devonian Cladoxylopsida for Which a Whole-Plant Concept Is Established

Cladoxylopsida	
Pseudosporochnales	*Iridopteridales*
Calamophyton Kräusel & Weyland	*Ibyka* Skog & Banks
Pseudosporochnus Potonié & Bernard	*Compsocradus* gen. nov.
Lorophyton Fairon-Demaret & Li	
Wattieza Stockmans	

Within our expanded concept of Cladoxylopsida, there are distinct differences between the two recognizable subgroups, here termed Pseudosporochnales and Iridopteridales (table 2; fig. 13); these differences have both phylogenetic and functional significance. There is an emerging concept of pseudosporochnalean architecture (Berry and Fairon-Demaret 1997, in press) in which dichotomous and digitate branches, sometimes considered to be the whole plant, arise from a stout trunk. Branches are supplied by multiple traces from adjoining xylem ribs in the trunk. Ultimate appendages are borne on branches that are supplied by one or more traces from adjacent ribs in a pattern that lacks obvious phyllotaxis. Evidence clearly indicates that within branch systems borne by the trunk, further branches arise only by dichotomy or digitate branching in this group. This unique architecture can perhaps be considered a unique evolutionary solution to the problem of obtaining large size in these early trees, to be contrasted with the secondary growth typically observed in the lignophyte clade. Other characters that may distinguish the Pseudosporochnales from other Devonian taxa are the presence of cortical sclereid nests and the unique form of the terminations of lateral appendages, which appear to grow linearly from slightly fleshy, expanded, terete tips rather than via the the recurved and probably circinate mode of development observed in all other Early and Middle Devonian euphyllophyte taxa.

By contrast, the iridopteridales exhibit a unique architecture among their contemporaries in terms of the whorled insertion of appendages and the presence of lateral branches that are at times borne within the whorls. This architecture makes it relatively easy to spot compression taxa that, in our opinion, likely belong in the order. Examples include *Anapaulia* Berry and Edwards, "*Hyenia*" *vogtii* Høeg, and "*Hyenia*" *banksii* Arnold (Berry and Fairon-Demaret, in press). Although much

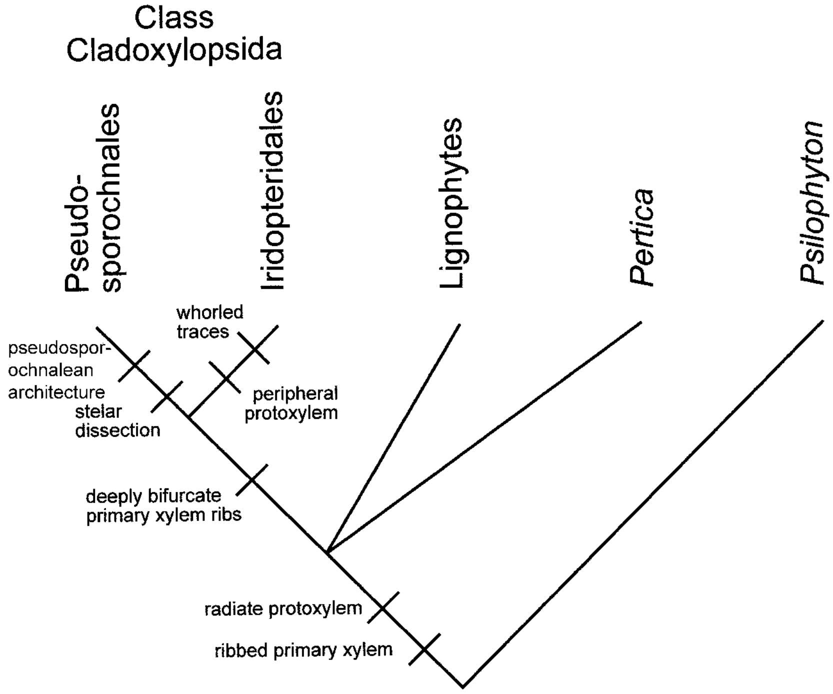

Fig. 13 Summary of cladistic relationships among selected basal taxa (see text). This cladogram is derived informally to demonstrate the basic characters that are recognized in our current classification of the named plant groups.

remains to be learned, the presence of whorls in iridopteridaleans together with the position of the protoxylem strands makes them the best candidate (among euphyllophytes) for sphenopsid (at least equisetalean) ancestors (Berry and Edwards 1996*a*; Kenrick and Crane 1997; C. M. Berry, J. Cordi, and W. G. Stein, unpublished data).

Within the wider context of the relationships of Cladoxylopsida *sensu lato*, at the level of cladistic structure of Kenrick and Crane's (1997) Euphyllophytina, it is becoming increasingly evident that several currently problematic taxa will have a major role to play in assessing phylogenetic relationships of major subgroups. Specifically, renewed focus needs be placed upon taxa previously and vaguely considered to be "preferns." These include Stenokoleales (Matten 1992; Beck and Stein 1993), which is currently recognized only from anatomically preserved specimens, although possibly also represented by compression taxa such as *Protocephalopteris* (e.g., Schweitzer 1968). This group exhibits actinosteles with shallowly bifurcate primary xylem ribs and an apparent "radiate" pattern of protoxylem strands. Traces to lateral branches or appendages are borne in pairs, perhaps conferring upon the group a distinctive appearance that might allow them to be recognized from compressions. Reproductive structures are unknown, and unfortunately, few characters exhibited by these plants as yet appear to be derived and shared with other plant groups. Another important yet enigmatic plant is *Rhacophyton* Crépin (Leclercq 1951; Andrews and Phillips 1968; Cornet et al. 1976; Dittrich et al. 1983), which was grouped with *Pseudosporochnus* by Kenrick and Crane (1997) based on their "distinctive clepsydroid xylem shape." This putative "early fern" character is highly problematic. In *Pseudosporochnus*, the only traces that might conceivably be termed "clepsydroid" occur in pairs that are perpendicular to the dichotomous division of branches (Stein and Hueber 1989). These traces most likely supply the large dichotomous appendages that are observed in identical positions in compression taxa (Berry and Fairon-Demaret 1997, in press). Such structures are not homologous to the vascular supply in multiple orders of branching in *Rhacophyton*, and thus, the case for a close relationship between these two taxa is weak. If a relationship for *Rhacophyton* with the Cladoxylopsida, as defined here, is to be entertained at all, then we suggest that it shares none of the architectural characteristics of Pseudosporochnales. However, characters shared with Iridopteridales include iterative architecture, partially similar branch and trace morphologies, and a regular phyllotaxis involving recognizable nodes and internodes. On the other hand, there are multiple problems associated with any interpretation of *Rhacophyton* put forward to date. The lack of knowledge of the basal parts of the plant is perhaps sufficient reason to extend doubt in placing *Rhacophyton* in a phylogenetic scheme. However, a similar argument might also be expressed for *Ibyka* and Iridopteridales. If a relationship between *Rhacophyton* and Iridopteridales exists, then stratigraphic evidence indicates that Upper Devonian *Rhacophyton* (and its earlier relative, *Ellesmeris* Hill et al. [Hill et al. 1997]) may be a relatively reduced form, a branching system rather than a frond. Potential synapomorphies within Iridopteridales shared by *Compsocradus* and *Rhacophyton* might also include offset insertion of appendages (also present in "*Cladoxylon*" *dawsonii*, Cordi and Stein 1997) and the lack of spines (spines present in *Anapaulia*, *Ibyka*, *Metacladophyton*, "*Hyenia*" *vogtii*, and possibly *Arachnoxylon minor*).

Kenrick and Crane (1997) recognized that their cladistic analysis of basal euphyllophyte taxa was provisional and that much work needed to be done to resolve phylogenetic relationships between early members of this clade. Progress in this regard is certain to be made by studies of new and unusual taxa from new localities, such as those in China and South America. However, changes in our knowledge of already "known" groups from Europe and North America (i.e., Iridopteridales and Pseudosporochnales) seems equally likely to contribute toward future progress in the analysis of land-plant phylogeny.

Conclusions

The composition of the recorded flora from horizon 3 in the Devonian of Caño Colorado, western Venezuela, is increasingly diverse, containing zosterophylls, herbaceous lycopsids, aneurophytalean progymnosperms, a pseudosporochnalean, and the iridopteridalean *Compsocradus* gen. et sp. nov.

Compsocradus laevigatus Berry and Stein gen. et sp. nov. is preserved as both compressions and as a single permineralization. It has a typically iridopteridalean stele, yet it is unique among such plants because the branching pattern is both whorled and regularly offset. As a result of this, the concept of Middle and Late Devonian Iridopteridales is expanded.

Two examples of Iridopteridales are now known from both anatomically preserved and morphologically preserved remains—*Ibyka* Skog and Banks and *Compsocradus* gen. nov. The group may increasingly be viewed as representing an important group of land plants, forming part of the explosion of diversity within the euphyllophyte clade during the Early and Middle Devonian; these plants may also represent ancestors for major modern groups. Considering equisetopsids and "ferns," we believe the Iridopteridales to be the best candidates with regard to the ancestry of horsetails.

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Literature Cited

Andrews HN, TL Phillips 1968 *Rhacophyton* from the Upper Devonian of West Virginia. Bot J Linn Soc 61:37–64.

Arnold CA 1935 Some new forms and new occurrences of fossil plants from the Middle and Upper Devonian of New York State. Bull Buffalo Soc Nat Sci 17:1–12.

——— 1940 Structure and relationships of some Middle Devonian plants from western New York. Am J Bot 27:57–63.

——— 1941 Observations on fossil plants from the Devonian of eastern North America. V. *Hyenia banksii* sp. nov. Contrib Mus Paleontol Univ Mich 6:53–57.

——— 1947 An introduction to palaeobotany. McGraw-Hill, New York. 433 pp.

Beck CB, W Stein 1993 *Crossia virginiana* gen. et sp. nov., a new member of the Stenokoleales from the Middle Devonian of southwestern Virginia. Palaeontographica 229:115–134.

Benedetto J-L 1984 Les brachiopodes Devoniens de la Sierra de Perijá (Venezuela). Biostratigr Paleo 1:1–191.

Berry CM, JE Casas, JM Moody 1993 Diverse Devonian plant assemblages from Venezuela. Doc Lab Geol Fac Sci Lyon 125:29–42.

Berry CM, J Cordi, WE Stein 1997 Morphological models of Devonian Iridopteridales. Am J Bot 84(suppl):129.

Berry CM, D Edwards 1994 New data on the morphology and anatomy of the Devonian zosterophyll *Serrulacaulis* Hueber and Banks from Venezuela. Rev Palaeobot Palynol 81:141–150.

——— 1995 New species of the Devonian lycophyte *Colpodexylon* from the Devonian of Venezuela. Palaeontographica 137:59–74.

——— 1996*a* *Anapaulia moodyi* gen. et sp. nov., a probable iridopteridalean compression fossil from the Devonian of Venezuela. Rev Palaeobot Palynol 93:127–145.

——— 1996*b* The herbaceous lycophyte genus *Haskinsia* Grierson and Banks from the Devonian of western Venezuela, with observations on the leaf morphology and fertile specimens. Bot J Linn Soc 122:103–122.

Berry CM, M Fairon-Demaret 1997 A reinvestigation of the cladoxylopsid *Pseudosporochnus nodosus* Leclercq et Banks from the Middle Devonian of Goé, Belgium. Int J Plant Sci 158:350–372.

——— In press The Middle Devonian flora revisited. *In* P Gensel, D Edwards, eds. Plants invade the land. Columbia University Press, New York.

Cordi J, WE Stein 1997 A reinvestigation of *Cladoxylon dawsonii* Read: new data question taxonomic and phylogenetic distinctions between the Devonian Cladoxylopsida and Iridopteridales. Am J Bot 84(suppl):132.

Cornet B, TL Phillips, HN Andrews 1976 The morphology and variation in *Rhacophyton ceratangium* from the Upper Devonian and its bearing on frond evolution. Palaeontographica 158:105–129.

Dawson JW 1881 Notes on new Erian (Devonian) plants. Q J Geol Soc Lond 37:299–308.

Dittrich HS, LC Matten, TL Phillips 1983 Anatomy of *Rhacophyton ceratangium* from the Upper Devonian (Fammenian) of West Virginia. Rev Palaeobot Palynol 40:127–147.

Edwards D, J-L Benedetto 1985 Two new species of herbaceous lycopods from the Devonian of Venezuela with comments on their taphonomy. Palaeontology 28:599–618.

Fairon-Demaret M, CM Berry 2000 A reconsideration of *Hyenia elegans* Kräusel and Weyland and *Hyenia* "*complexa*" Leclercq: two Middle Devonian cladoxylopsids from western Europe. Int J Plant Sci 161:473–494.

Fairon-Demaret M, JM Hilton, CM Berry 1999 Morphology: surface preparation of fossils. Pages 33–35 *in* Fossil plants and spores: modern techniques. TP Jones, NP Rowe, eds. Geological Society of London, London.

Fairon-Demaret M, C-S Li 1993 *Lorophyton goense* gen. et sp. nov.

from the Lower Givetian of Belgium and a discussion of the Middle Devonian Cladoxylopsida. Rev Palaeobot Palynol 77:1–22.

Hill SA, SE Scheckler, JF Basinger 1997 *Ellesmeris sphenopteroides*, gen. et sp. nov., a new zygopterid fern from the Upper Devonian (Frasnian) of Ellesmere, N.W.T., Arctic Canada. Am J Bot 84: 85–103.

Høeg OA 1942 The Downtonian and Devonian flora of Spitzbergen. Nor Svalbard Ishavs Unders Skr 83:1–228.

Kenrick P, PR Crane 1997 The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington, D.C. 441 pp.

Kräusel R, H Weyland 1932 Pflanzenreste aus dem Devon. III. Über *Hyenia* Nathorst. Senckenbergiana 14:274–280.

Leclercq S 1940 Contribution à l'étude de la flore du Dévonien de Belgique. Mem Acad R Belg Cl Sci 12:1–65.

——— 1951 Étude morphologique et anatomique d'une fougère du Dévonien Supérieur. Ann Soc Geol Belg Mem 9:1–62.

——— 1960 Réfendage d'une roche fossilifière et dégagement de ses fossiles sous binoculaire. Senckenb Lethaea 41:483–487.

——— 1970 Classe des Cladoxylopsida Pichi-Sermolli, 1959. Pages 120–177 *in* E Boureau, ed. Traité de paléobotanique. Vol 4. Masson & Cie, Paris.

Leclercq S, HN Andrews 1960 *Calamophyton bicephalum*, a new species from the Middle Devonian of Belgium. Ann Mo Bot Gard 47:1–23.

Leclercq S, HP Banks 1962 *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with Cladoxylalean affinities. Palaeontographica 110:1–34.

Li C-S, J Hsü 1987 Studies on a new Devonian plant *Protopteridophyton devonicum* assigned to primitive fern from China. Palaeontographica 207:111–131.

Matten LC 1992 Studies on Devonian plants from New York State: *Stenokoleos holmesii* n. sp. from the Cairo flora (Givetian) with an alternative model for lyginopterid seed fern evolution. Cour Forsch Inst Senckenb 147:75–85.

Mustafa H 1978 Beiträge zur Devonflora III. Argumenta Palaeobot 5:91–132.

Pichi-Sermolli REG 1959 Pteridophyta. Pages 421–493 *in* WB Turrill, ed. Vistas in botany. Pergamon, London.

Read CB 1938 Some Psilophytales from the Hamilton group in western New York. Bull Torrey Bot Club 65:599–606.

Rowe NP, J Galtier 1989 A Lower Carboniferous plant assemblage from La Serre (Montagne Noire, France). Part I. Rev Palaeobot Palynol 61:239–271.

Schweitzer H-J 1968 Pflanzenreste aus dem Devon Nord-Westspitzbergens. Palaeontographica 123:43–75.

Skog JE, HP Banks 1973 *Ibyka amphikoma*, gen. et sp. n., a new protoarticulate precursor from the late Middle Devonian of New York State. Am J Bot 60:366–380.

Stein WE 1981 Reinvestigation of *Arachnoxylon kopfii* from the Middle Devonian of New York State, U.S.A. Palaeontographica 147: 90–117.

——— 1982 *Iridopteris eriensis* from the Middle Devonian with systematics of apparently related taxa. Bot Gaz 143:401–416.

Stein WE, FM Hueber 1989 The anatomy of *Pseudosporochnus*: *P. hueberi* from the Devonian of New York. Rev Palaeobot Palynol 60:311–359.

Stein WE, DC Wight, CB Beck 1982 Techniques for preparation of pyrite and limonite permineralizations. Rev Palaeobot Palynol 36: 185–194.

——— 1983 *Arachnoxylon* from the Middle Devonian of southwestern Virginia. Can J Bot 61:1283–1299.

——— 1984 Possible alternatives for the origin of sphenopsida. Syst Bot 9:102–118.

Stockmans F 1968 Végétaux Mésodévoniens récoltés aux confins du Massif du Brabant (Belgique). Mem Mus R Hist Nat Belg 159:1–49.

Wang Z, B-Y Geng 1997 A new Middle Devonian plant: *Metacladophyton tetrapetalum* gen. et sp. nov. Palaeontographica 243: 85–102.