

KAPLANOPTERIDACEAE FAM. NOV., ADDITIONAL DIVERSITY IN THE INITIAL RADIATION OF FILICALEAN FERNS

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The Pennsylvanian filicalean fern *Kaplanopteris clavata* gen. et comb. nov. is reconstructed on the basis of permineralized vegetative and fertile frond segments and rhizomes. Characteristic anatomy conforming to morphospecies *Anachoropteris clavata* Graham allows for integration of new observations and reevaluation of material from Ohio with published data into the whole-plant reconstruction. Epiphyllous rhizomes arise laterally along frond rachides and feature terete exarch protosteles. Fronds are planar, tripinnate-pinnatifid, with alternate division. Vascular traces of all frond members have adaxial, exarch protoxylem. Rachides and primary pinnae have adaxially convex C-shaped traces; secondary pinna traces are terete. Pinnules are laminar, with lobed margins and open dichotomous venation. Tripinnate latent croziers equivalent in complexity to whole fronds arise on otherwise mature frond segments at the position of primary pinnae. Superficial abaxial indusiate sori exhibit gradate maturation and include numerous leptosporangia producing trilete spores. Sporangial capsules are bent away from the center of the sorus at the juncture with the long, uniseriate stalks. The annulus is a band of two to three rows of interfingering cells, wrapped around the long axis of the sporangium and covering most of it. The longitudinal stomium faces toward the apex of the sorus. *Kaplanopteris clavata* is reconstructed as a primarily vining plant with organography overwhelmingly dominated by the frond and a unique life-history pattern influenced by growth from two types of foliar-borne reiterative units: latent croziers and rhizomes. *Kaplanopteris* combines characters known exclusively in fossil filicaleans with both plesiomorphic and derived characters of living filicaleans. This novel combination reveals the existence of a previously unrecognized lineage of basal filicaleans and justifies placement in a new family. *Kaplanopteris* illustrates the diversity and complexity reached during the first major evolutionary radiation of filicaleans.

Keywords: *Kaplanopteris*, *Anachoropteris clavata*, fossil, fern, Filicales, Pennsylvanian, epiphyllous rhizome, latent crozier, reiterative growth, indusiate, gradate soral maturation.

Introduction

Filicaleans are homosporous ferns whose most characteristic feature is the leptosporangium provided with an annulus as the dehiscence mechanism. The deep roots of filicalean fern phylogeny go back at least 345 million years to the beginning of the Carboniferous (Tournaisian; Galtier 1981), but unequivocal representatives of living filicalean families are not known before the Late Permian (Rothwell 1987; Stewart and Rothwell 1993). Although fertile foliage with sori similar to the Gleicheniaceae occurs in the Early Permian of China (Yao and Taylor 1988), the oldest fossils that can be unequivocally assigned to an extant filicalean family are the Late Permian osmundaceous cauline morphogenera *Thamnopteris* and *Zalesskya* (Miller 1971). The interval between these two benchmark occurrences witnessed tremendous evolutionary radiation and turnover among the Filicales (Rothwell 1987). Although often ignored by those who attempt to resolve patterns of phylogeny from the study of modern species, fossils with filicalean affinities provide evidence of a complex evolu-

tionary history (Eggert and Taylor 1966; Eggert and Delevoryas 1967; Phillips 1974; Scott et al. 1985) that predates the origin of all families with living representatives and that reveals the earliest stages of filicalean evolution.

In this article, we reconstruct a Late Pennsylvanian fern illustrative of the complexity and diversity reached by filicaleans during the Carboniferous radiation. This fern is characterized by vegetative anatomy previously associated with the coenopterids (Seward 1910; Delevoryas and Morgan 1954; Eggert 1964), a now-abandoned heterogeneous group of Paleozoic fern morphotaxa (Rothwell 1987, 1999). The defining vascular anatomy of the plant conforms to morphospecies *Anachoropteris clavata* Graham. This characteristic anatomy allows for integration of previously described vegetative frond and rhizome material from Illinois (Graham 1935; Delevoryas and Morgan 1954; Smoot 1985) with vegetative and fertile frond and rhizome material from Ohio (Rothwell 1987; Trivett and Rothwell 1988), for the purpose of developing a whole-plant concept for this distinctive Paleozoic filicalean. Several aspects of the anatomy and morphology of the plant described by previous authors are summarized along with presentation of new data. All of these are integrated in the current whole-plant reconstruction and are employed in diagnoses of Kaplanopteridaceae fam. nov., *Kaplanopteris* gen. nov., and *Kaplanopteris clavata* (Graham)

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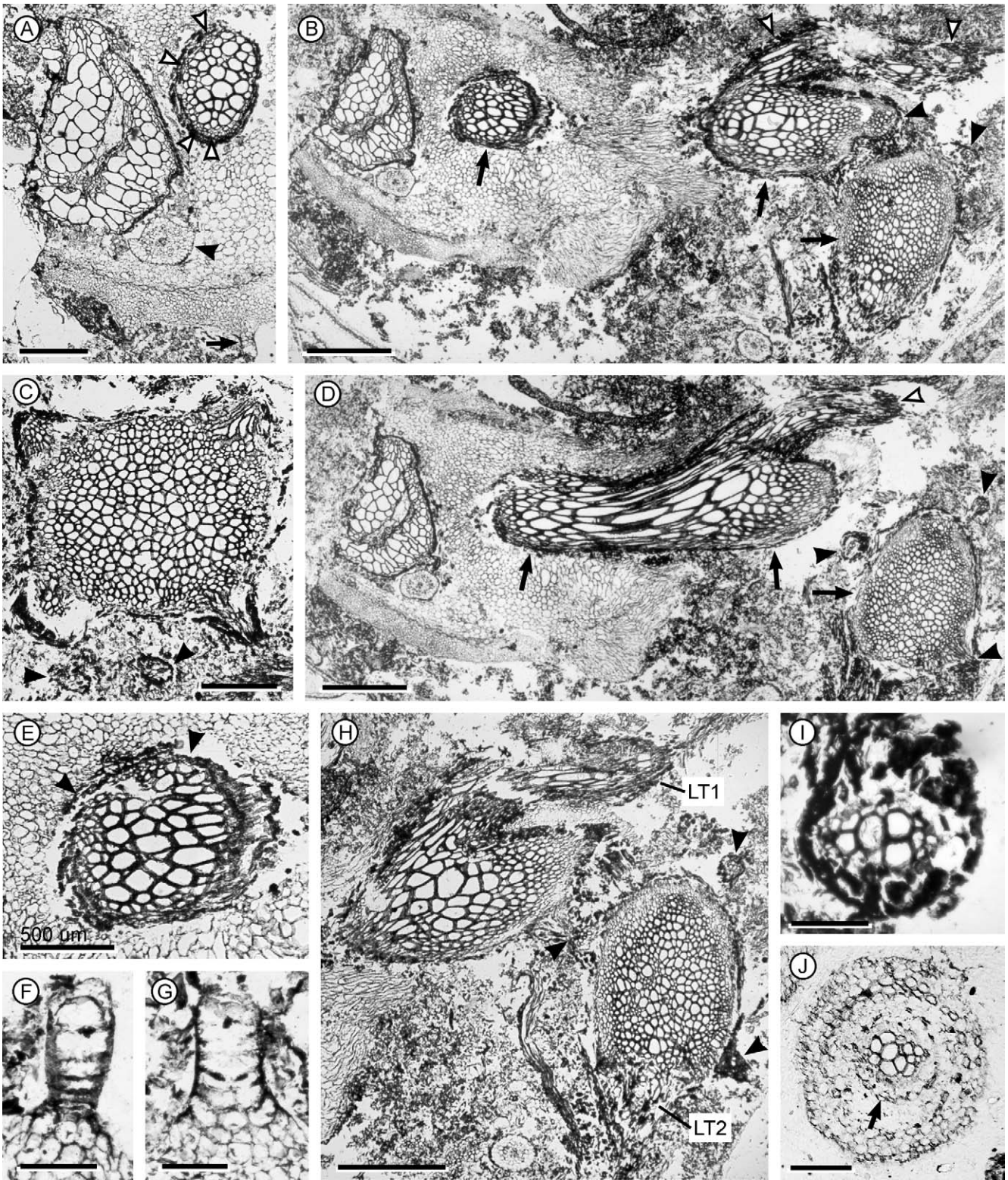


Fig. 1 *Kaplanopteris clavata* gen. et comb. nov. Epiphyllous rhizome, root, and frond divergence. **A**, Cross section of frond rachis with vascular trace and rhizome stele in common cortex. Epiphyllous rhizome has diverged laterally from the trace and has elliptical stele at this level. Protoxylem strands (white arrowheads) are present only on one side of the rhizome. Rachis cortex has two distinct zones and is penetrated by a *Psaronius* root (black arrowhead). Note short uniseriate epidermal trichomes (arrow). Ohio University Paleobotanical Herbarium (OUPH) 16812; scale = 500 μm . **B**, Section distal to **A** showing the vascular trace of rachis (far left) and three progressively more distal sections (left to right) of the same rhizome (arrows). Note divergence of basalmost frond trace (sectioned oblique-longitudinally) between white arrowheads, and adventitious roots (black

comb. nov. New data contributed by this study include the reconstruction of frond architecture (with the division pattern of the fronds and pinnule form), reinterpretation of the insertion position of latent croziers, documentation of epiphyllous rhizomes from an additional locality, supplementary evidence for the pattern of soral maturation, reconstruction of sporangial morphology, as well as the whole-plant reconstruction.

The novel combination of characters exhibited by *Kaplanopteris* demonstrates that vegetative parts assignable to morphogenus *Anachoropteris* were produced by at least two filicalean families, the Sermayaceae Eggert and Delevoryas and the Kaplanopteridaceae. Developmental patterns of the *K. clavata* plant are recognized as a distinctive mode of reiterative growth that allows for interpreting the role of this plant in the tropical wetland ecosystems of the Late Pennsylvanian.

Material and Methods

Specimens of *Kaplanopteris clavata* are preserved by calcareous cellular permineralization in coal balls from Late Pennsylvanian deposits of North America (Graham 1935; Delevoryas and Morgan 1954; Rothwell 1987; Trivett and Rothwell 1988). Vegetative frond segments with a frond trace configuration characteristic of *Anachoropteris clavata* also have been reported from Middle Pennsylvanian coal balls (Phillips 1974, 1980), but the latter have not been described or figured. It remains uncertain whether the Middle Pennsylvanian specimens were produced by the same species as the Late Pennsylvanian fern described herein as *K. clavata*.

The interconnected vegetative and fertile frond parts that provide new data for the whole-plant reconstruction occur in coal balls collected from an exposed seam of the Late Pennsylvanian (Kasimovian; mid-Stephanian) Duquesne Coal along the south side of Ohio State Route 22, approximately 8 km west of Steubenville, Ohio (NE1/4 SE1/4 SE1/4, Sect. 6, Wayne Twp., Jefferson Co.; Rothwell 1976). Together with the previously described specimens from the stratigraphically equivalent Calhoun Coal of Illinois (Phillips 1980), the material includes frond segments representing four orders of division with attached croziers, abaxially borne indusiate sori, and epiphyllous rhizomes ("rhizome" is used to designate the stems following traditional fern terminology). The Duquesne Coal material has been studied in two coal balls (Ohio University coal balls 422 [figs. 3–7, 9] and 2190 [figs. 1A–1I, 2C–2F]) and includes nine frond segments with three latent croziers, one epiphyllous rhizome, and numerous sori. Specimens from Delevoryas and Morgan's (1954) Washington University coal ball are also figured (fig. 1J; fig. 2A, 2B).

Anatomical sections were prepared by the well-known cellulose acetate peel technique (Joy et al. 1956), and frond morphology was reconstructed from a series of closely spaced serial sections. Spores were prepared for scanning electron microscopy by maceration of sporangia from the coal ball matrix with dilute (2%) HCl, rinsing in distilled water, and drying of specimen stubs. Reconstructions were realized by mapping individual specimens through coal balls and serial peel sections. Images were captured using Photo-phase digital scanning (Phase One, Denmark) and Nikon digital cameras and processed using Adobe Photoshop. Coal ball slabs, acetate peels, and slides are housed in the Ohio University Paleobotanical Herbarium (OUPH). Microscope slides mounted from the peels bear numbers 16812–16859.

The terminology used to describe the morphology of compound, pinnately dissected fern fronds is determined by the position of the different frond segments relative to the rhizome. For a frond with four orders of division (tripinnate), these are the rachis (attached to the rhizome through the stipe or petiole), primary pinnae, secondary pinnae, and pinnules. This determinate terminology raises problems when the various frond parts are found detached from the rhizome or from each other. In such instances, an open-ended terminology is used, based simply on numbering of the orders of division, starting with the most basal as the first order.

Although the *K. clavata* fronds described here occur as detached fragments, two lines of evidence provide a rationale for use of a determinate rather than an open-ended terminology in this case: the morphology of croziers and the maximum number of division orders documented for this plant. Croziers can be regarded as developmental time capsules in the sense that they represent the condensed expression of the mature frond architecture. As such, they are extremely valuable in cases when frond development cannot be observed directly, as is the case in many plant fossils. *Kaplanopteris clavata* croziers feature four orders of division, indicating that mature fronds are characterized by four orders of division as well. This conclusion is concordant with the maximum number of division orders of the mature fronds of the plant, which also is four.

Systematic Description

Order—Filicales

Family—Kaplanopteridaceae fam. nov.

Familial diagnosis. Ferns with exarch protostelic rhizomes bearing helically arranged fronds and diarch adventitious

arrowheads). OUPH 16813; scale = 1 mm. C, Rhizome stele in more distal section, with circular outline and exarch xylem maturation. At this level, protoxylem strands extend around the periphery of the metaxylem and four root traces are diverging from the stele. Note two other root traces in cortex (black arrowheads). OUPH 16814; scale = 500 μ m. D, Section distal to B showing same three rhizome sections (arrows). Note basalmost frond trace (white arrowhead) and several roots (black arrowheads) diverging from the rhizome. OUPH 16815; scale = 1 mm. E, Detail of proximal rhizome stele in B showing incipient lateral arms of basalmost frond trace (black arrowheads). Dark debris in the space between stele and cortex may represent remnants of the endodermis. OUPH 16813; scale = 500 μ m. F, Uniseriate epidermal trichome with caplike cell at the tip. OUPH 16816; scale = 100 μ m. G, Uniseriate epidermal trichome. OUPH 16816; scale = 100 μ m. H, Section between levels in B and D showing the traces of the first two leaves (LT1 and LT2) at base of rhizome. Adventitious root traces (black arrowheads) are preserved in cortex. OUPH 16817; scale = 1 mm. I, Detail of diarch adventitious root trace in the rhizome cortex. OUPH 16817; scale = 100 μ m. J, Cross section of diarch root (detail of B). Note incomplete ring of minute dark cells of the endodermis (arrow). OUPH 16818; scale = 100 μ m.

roots. Fronds planar, with up to four orders of alternate pinnate dissection. Vascular strand of frond segments diverging laterally from strand of lower order segments. Stipe and rachis traces abaxially concave with adaxial protoxylem. Sporangia abaxial superficial and soral; indusiate, with gradate maturation. Sporangia with transverse two- to three-seriate annulus, and long, narrow stalk. Sporangial wall one cell layer thick at maturity, with longitudinal stomium.

Type Genus—*Kaplanopteris gen. nov.*

Generic diagnosis. Characters of the genus as those of the family. Rhizomes slender with closely spaced stipes; fronds pinnately dissected; frond architecture catadromous (*sensu* Kramer and Green 1990). Pinnules laminar with open dichotomous venation; sori radial, with numerous sporangia per sorus. Sporangia attached to vascularized conical receptacle. Metaxylem tracheids of rhizome range from multiseriate circular bordered pits to multiseriate scalariform pitting. Spores radial, trilete, subtriangular in polar view.

Etymology. *Kaplanopteris*, Kaplan + *pteris* (=fern), is named in honor of Donald R. Kaplan in recognition of the contributions his research has made to our understanding of the organization and construction of the plant body in ferns.

Type Species—*Kaplanopteris clavata (Graham) comb. nov.*

Synonymy. *Anachoropteris clavata* Graham 1935, fig. 22; *A. clavata* Delevoryas and Morgan 1954, figs. 1–13; *A. clavata* Phillips 1974, fig. 43D; *A. clavata* Phillips 1980, table 2.8; *A. clavata* Smoot 1985, figs. 8, 15; *A. clavata* Rothwell 1987, figs. 1–8; *A. clavata* Trivett and Rothwell 1988, figs. 1, 2; *A. clavata* plant Rothwell 1999, table 1.

Amplified specific diagnosis. Characters of the species as those of the genus. Production of epiphyllous rhizomes laterally along frond rachides at positions of primary pinnae. Fronds tripinnate with pinnatifid pinnae, sparsely branched, with indeterminate growth from latent croziers that replace primary pinnae. Stipe and rachis traces horseshoe-shaped, abaxially concave; expanded arms with larger tracheids than in adaxial part of trace. Four to six protoxylem strands on convex, adaxial side. Primary pinna traces reniform at base, C-shaped distally, with three to four protoxylem strands on adaxial side. Secondary pinna traces oval with one to two adaxial protoxylem strands; pinnules with lobed margins. Sporangia tightly packed in globose to urn-shaped indusium, 0.4–0.6 mm in diameter. Sporangial capsule bent toward periphery of sorus, with stomium opening longitudinally toward distal side of sorus; stalks uniseriate. Spores scabrate, 18–25 μm in diameter, with triangular contour in polar view.

Description

General Features

Kaplanopteris clavata is represented by epiphyllous rhizomes with helically arranged fronds and adventitious roots (figs. 1, 2, 8A) and by vegetative (fig. 2A, 2B; figs. 3, 4, 8A) and fertile frond segments with abaxially attached indusiate sori of annulate sporangia producing trilete spores (fig. 9A–9N). All of the plant parts have been found as interconnected

combinations of organs, many of which display diagnostic anatomical and histological characters that support their identification as parts of the same species of plant. Other isolated frond members and sori are scattered in the coal ball matrix. Epiphyllous rhizomes diverge laterally along rachides at the positions of primary pinnae. Fronds are tripinnately compound, with alternate divergence of pinnatifid pinnae (fig. 3C, 3H; figs. 4E–4G, 5, 8A) and lobed pinnules with open dichotomous venation (fig. 4C, 4D). Latent croziers replace some primary pinnae (figs. 7, 8A), and each crozier displays the entire complexity (approximately four orders of division) of the frond (fig. 6).

The Rhizome

In agreement with specimens described as *Anachoropteris clavata* by Delevoryas and Morgan (1954; fig. 1), a new epiphyllous rhizome of *K. clavata* originates as an elliptical vascular bundle that diverges laterally from one of the lateral arms of the rachis trace and that shows protoxylem tracheids on the side facing the adaxial surface of the rachis (fig. 1A). This terete vascular bundle is very different from the strands that supply primary pinnae. Although the latter arise in the same position on rachides, they exhibit characteristic abaxially concave reniform traces at the base. In progressively more distal sections, the stele of the rhizome becomes round (fig. 1C) and increases in diameter, and protoxylem strands extend around the entire periphery of the metaxylem (fig. 1C, 1H).

The rhizome is thus protostelic with exarch xylem maturation. Both frond and root traces diverge from the stele, which ranges 1.0–1.3 mm in diameter distal to the divergence of the first stipe bundle (fig. 1B, 1D, 1H). In this section, the largest metaxylem tracheids of the stele are 140–230 μm in diameter. Wall-thickening patterns range from multiseriate, alternate circular-elliptical bordered pits at the center of the stele to scalariform thickenings with uniseriate rows of circular-oval pits in between, to simple scalariform pitting toward the protoxylem (fig. 2D–2F). Protoxylem elements (fig. 2C) range 17–28 μm in diameter. Phloem of the Duquesne Coal specimens is typically incompletely preserved and represented by spaces between the xylem and the cortex (fig. 1C, 1E; fig. 3D). Cortex consists of relatively thin-walled cells that, in some sections, become smaller with thicker walls toward the periphery (fig. 2A, 2B). In areas where the epidermis is preserved, there are short uniseriate, multicellular trichomes at the periphery of the rhizome and at the base of the rachis (fig. 1A, 1E, 1G).

The basalmost foliar bundle starts taking shape at a level where the rhizome stele is still within the cortex of the subtending rachis (fig. 1B, 1E). The foliar bundle separates from the stele close to the level where the rhizome has separated from the subtending rachis (fig. 1B, 1D) or above this level (fig. 2B) and is clearly abaxially concave (fig. 2B). Root traces with diarch steles (fig. 1I, 1J) are produced in conjunction with the inversicatenalean (i.e., abaxially concave) foliar vascular bundles (fig. 1B–1D, 1H), sometimes starting slightly below the point of separation of the basalmost stipe (fig. 2A). Only two stipes are preserved diverging from the Duquesne Coal rhizome (fig. 1H). This rhizome could be

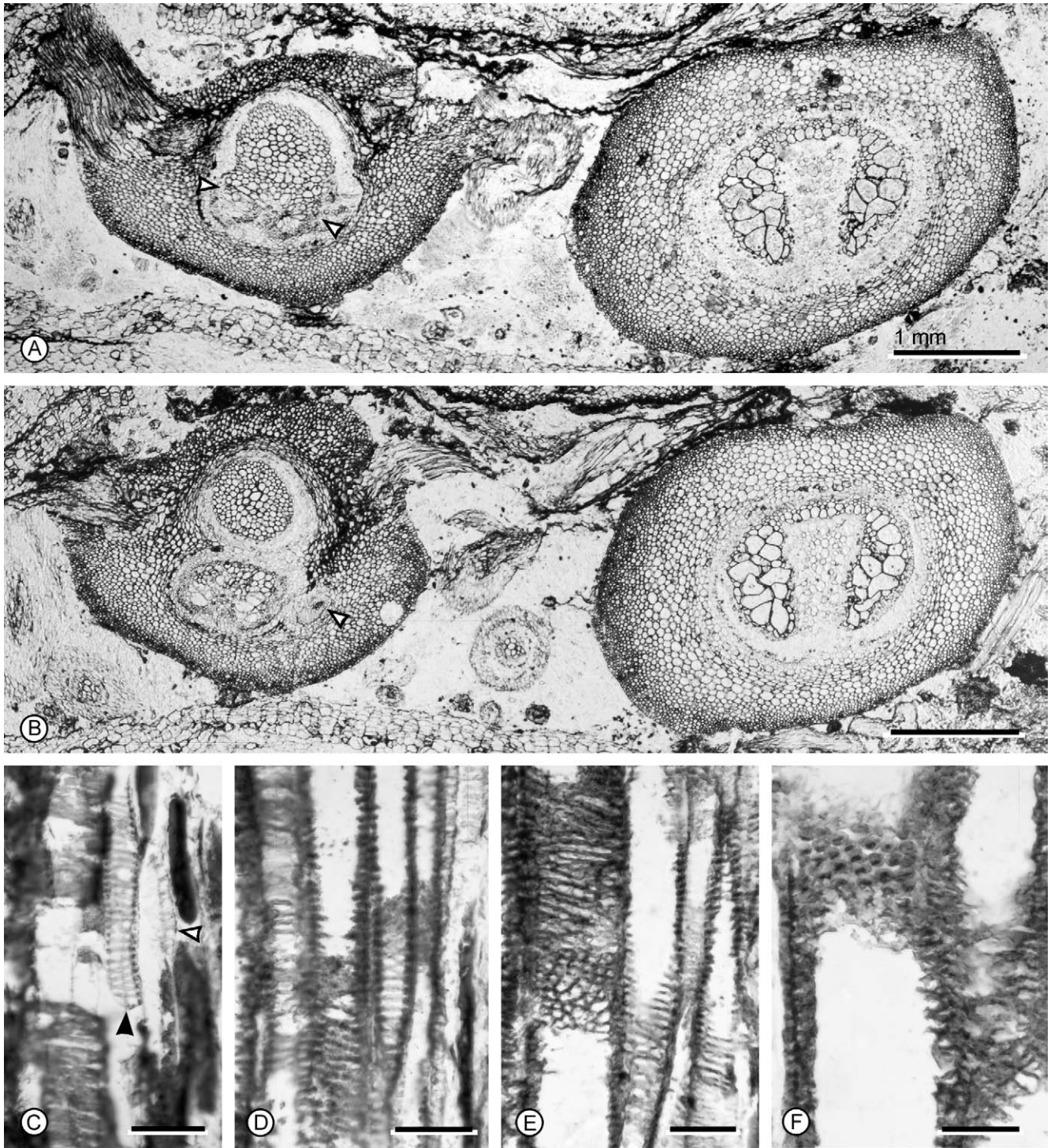


Fig. 2 *Kaplanopteris clavata* gen. et comb. nov. Frond rachis, epiphyllous rhizome, and leaf trace divergence. *A, B*, Cross sections of epiphyllous rhizome (left) and subtending rachis (right). Two adventitious roots are diverging laterally (left and right) from the rhizome. The two lateral arms of an incipient leaf trace (white arrowheads) protrude from the rhizome stele (*A*) below level of divergence. A root trace (white arrowhead) diverges from the rhizome stele (*B*). Note *Kaplanopteris* roots between rachis and rhizome. OUPH 16819 and 16818; scale = 1 mm. *C*, Annular (white arrowhead) and helical (black arrowhead) protoxylem tracheids of rhizome. OUPH 16820; scale = 20 μm . *D*, Narrow metaxylem tracheids of rhizome, with simple scalariform wall thickenings. OUPH 16821; scale = 20 μm . *E*, Metaxylem tracheids of rhizome, with scalariform thickenings (right), transitional scalariform/pitted (upper left), and alternate multiserial bordered pits (lower left). OUPH 16821; scale = 20 μm . *F*, Metaxylem tracheids of rhizome, with circular-elliptical alternate bordered pits showing horizontally elongated apertures. OUPH 16821; scale = 20 μm .

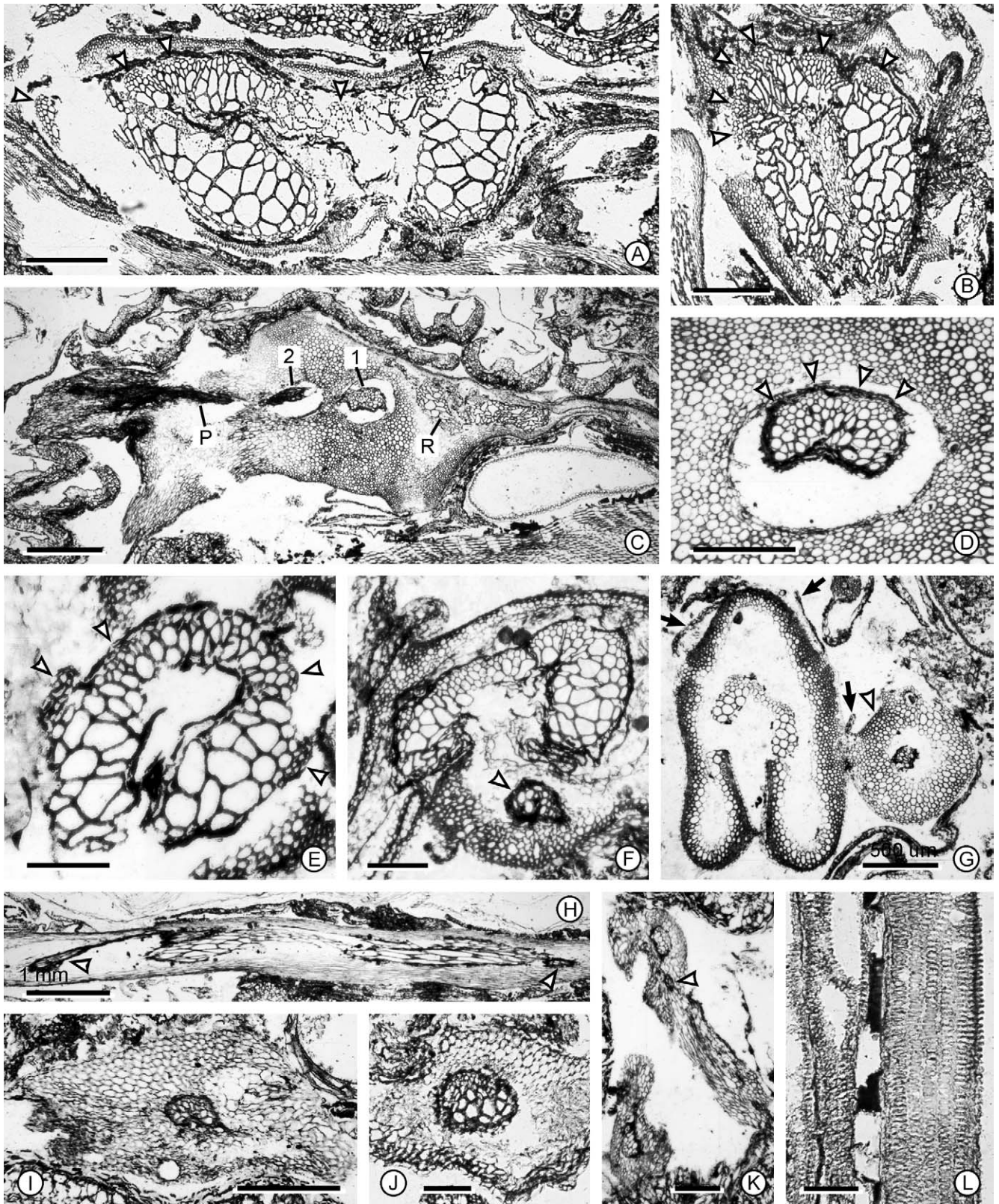


Fig. 3 *Kaplanopteris clavata* gen. et comb. nov. Frond anatomy. A, Cross section of frond rachis with dorsiventrally compressed trace. Note adaxial protoxylem strands (white arrowheads). OUPH 16822; scale = 500 μm . B, Cross section of frond rachis with laterally compressed trace and adaxial protoxylem strands (white arrowheads). OUPH 16823; scale = 500 μm . C, Cross section of frond with traces to all orders of division in common cortex. Highly distorted rachis strand (R) and the primary pinna strand (1) are sectioned transversally, secondary pinna strand (2) is in

followed in serial sections for about 10 mm distal to divergence from the parent rachis, but Delevoryas and Morgan (1954) were able to follow an epiphyllous rhizome, in serial sections, as it produced four helically arranged fronds.

The morphology of branching of the Duquesne Coal rhizome, as reconstructed from serial sections (e.g., fig. 1B, 1D), is highly reminiscent of the S-shaped epiphyllous rhizomes described in *Anachoropteris involuta* Hoskins by Galtier and Holmes (1984). However, close examination of the Duquesne Coal specimen shows that this apparent similarity is a taphonomic artifact where the second bend of the S is due to breaking of the rhizome. *Anachoropteris clavata* epiphyllous rhizomes do not exhibit S-shaped branching, as illustrated by the specimens described by Delevoryas and Morgan (1954), all of which have straight rhizomes (one of these specimens is illustrated in fig. 2A, 2B). It is also important to note that such epiphyllous rhizomes arise laterally at any position along frond rachides (Delevoryas and Morgan 1954).

The Frond

The most obvious diagnostic vegetative organ of the *K. clavata* plant is the rachis, which displays a horseshoe-shaped trace with inflated lateral arms made up of tracheids that are larger than those in the connecting adaxial xylem (fig. 1A; fig. 2A, 2B; fig. 3A, 3B), a configuration characteristic of the morphospecies *A. clavata* Graham. As documented by Trivett and Rothwell (1988), frond segments display four orders of division (figs. 3–5, 8A), and latent croziers replace lateral frond members (figs. 7, 8A).

The overall frond morphology of *K. clavata* is based on mature frond segments comprising all four interconnected division orders, thus representing the entire complexity of the tripinnately dissected fronds (figs. 3C, 4E–4G, 5), and on the structure of croziers that are attached to the fronds (figs. 6, 7). In mature fronds, the basalmost vascular strands of all four orders of division diverge within a short distance while they are all still within a common cortex (fig. 3C). The alignment of the vascular traces (figs. 3C, 5) clearly demonstrates the planar morphology of the frond. Frond architecture is catadromous, in the sense that the first lobe or segment of a pinna arises basiscopically (on the side facing away from the lower-order segment that bears that pinna). Both primary and secondary pinnae are pinnatifid, with thin narrow lami-

nae extending laterally from the adaxial surface of the frond members (fig. 3G at arrows). Such laminae are absent from the base of each frond member, becoming pronounced at more distal levels. Cells in the outer cortical layers are thick walled (fig. 4A, 4B).

Primary pinna traces arise laterally from the rachis trace at the outer side of one of the clavate arms and toward the adaxial face, as described by Delevoryas and Morgan (1954, their fig. 12). Rachis sections are about 2.4×3.6 mm, with rachis traces that are 1.0×1.5 mm. The expanded portion of each of the xylem arms is 0.4–0.6 mm wide (fig. 2A, 2B; fig. 3A). Proximal to the divergence of a primary pinna from the rachis, the primary pinna trace is reniform in cross section (360×680 μm), with an abaxially oriented concavity (fig. 3D). Metaxylem tracheids are narrow (50–65 μm diameter), and three to four protoxylem strands are present on the adaxial side (fig. 3D). Following an epidogenetic pattern, the xylem strand becomes progressively wider distally, with larger tracheids, and acquires an abaxially concave horseshoe-shaped cross section above the divergence of the primary pinna from the rachis (fig. 1E–1G). Over a distance of 20–25 mm (measured between divergences of vascular strands), one primary pinna produces five alternate secondary pinnae (fig. 5).

Secondary pinna traces arise laterally from primary pinna traces (fig. 3C, 3H). Secondary pinnae diverge at intervals of 4–6 mm in the illustrated specimen (fig. 5) and are about 0.8×0.9 mm in section. The basalmost secondary pinna diverges from the primary pinna proximally to divergence of the latter from the rachis and laterally on the side facing away from the rachis (figs. 3C, 5). Secondary pinna xylem strands are oval in cross section ($120\text{--}140 \times 160\text{--}220$ μm) and display narrow tracheids (fig. 3I–3K). One to two inconspicuous protoxylem strands are present on the adaxial side. Secondary pinnae bear alternate pinnules. The vascular trace to the first pinnule diverges from the basalmost secondary pinna trace, while the latter is still within a common cortex with the subtending primary pinna and rachis (figs. 3C, 5). Pinnules are laminar, 45–90 μm thick, and have relatively deeply lobed margins and open dichotomous venation (fig. 4C, 4D).

Latent Croziers

Tightly coiled croziers attached to the fronds were described by Trivett and Rothwell (1988) and used to propose an architectural model for this fern. The croziers (figs. 6, 7)

oblique section, and vascular strand of pinnule (*P*) is in longitudinal-oblique view. OUPH 16824; scale = 1 mm. *D*, Enlargement of vascular strand in primary pinna close to level of divergence from rachis. Note the reniform, abaxially concave outline of the primary pinna trace, the adaxial protoxylem strands (white arrowheads), and the space between the xylem and the cortex. OUPH 16825; scale = 500 μm . *E*, More distal, horseshoe-shaped primary pinna trace showing four adaxial protoxylem strands (white arrowheads). OUPH 16826; scale = 200 μm . *F*, Distorted primary pinna trace with diverging secondary pinna trace (white arrowhead) in transverse section. OUPH 16827; scale = 200 μm . *G*, Cross sections of primary pinna (left) and secondary pinna (right). Note horseshoe-shaped outlines of the primary pinna and primary pinna trace, circular outline of the secondary pinna with a flat adaxial surface (white arrowhead), and laminar tissue (arrows) attached laterally toward the adaxial sides of the primary and secondary pinnae. OUPH 16828; scale = 500 μm . *H*, Oblique section of a primary pinna (detail of section in fig. 4G) showing xylem strand and two diverging secondary pinna traces (white arrowheads). OUPH 16829; scale = 1 mm. *I*, Cross section of secondary pinna with adaxial protoxylem. OUPH 16830; scale = 500 μm . *J*, Detail of secondary pinna trace in cross section. Note adaxial protoxylem. OUPH 16831; scale = 100 μm . *K*, Two secondary pinnae (upper and lower left) in slightly oblique sections. Note divergence of pinnule (vascular bundle at white arrowhead) from upper pinna. OUPH 16832; scale = 200 μm . *L*, Metaxylem tracheids of primary pinna with multiseriate laterally elongated bordered pits. OUPH 16830; scale = 50 μm .

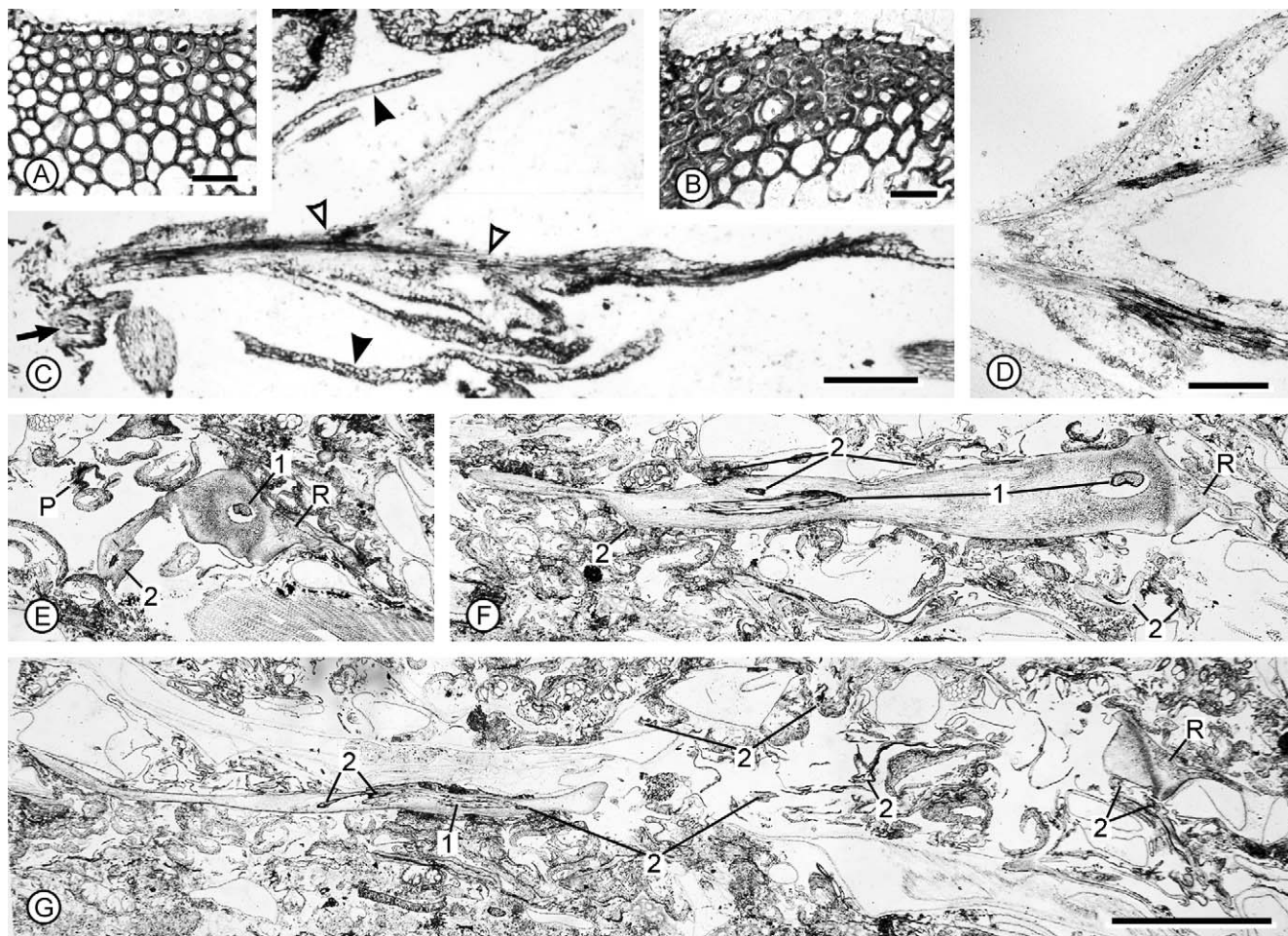


Fig. 4 *Kaplanopteris clavata* gen. et comb. nov. Frond anatomy. *A*, Cross section of cortex and adaxial epidermis of secondary pinna (detail of fig. 3G). Note progressively thicker cell walls toward outside of cortex. OUPH 16828; scale = 50 μm . *B*, Cross section of lateral cortex and epidermis of primary pinna (detail of fig. 3G). Note extremely thickened walls and narrow lumens of cells in outer cortical layers. OUPH 16828; scale = 50 μm . *C*, Pinnule in oblique-paradermal section, showing subtending secondary pinna (arrow) and unequal dichotomous venation (white arrowheads identify dividing veins). Black arrowheads indicate lobes of the same pinnule in cross sections. OUPH 16833; scale = 500 μm . *D*, Oblique paradermal section of pinnule with dichotomous venation. OUPH 16832; scale = 250 μm . *E*, Frond section (peel 49 in fig. 5) showing four orders of division. Secondary pinna (2) is almost separated from primary pinna (1) and highly distorted rachis (R). All traces are still within a common cortex. At this level, basalmost pinnule (P) has already separated from secondary pinna. OUPH 16834. *F*, Oblique section of frond division distal to section in fig. 4E (peel 198 in fig. 5). Rachis trace (R), primary pinna trace (1), and secondary pinna trace (2) within a common cortex. Two other secondary pinnae (2) are also present at this level. Numbers with more than one pointer bar indicate individual frond members that intersect the plane of the section more than once. OUPH 16835. *G*, Frond division distal to section in fig. 4F (peel 358 in fig. 5) showing rachis (R), primary pinna (1), five secondary pinnae (2), and numerous pinules (not labeled). OUPH 16829; scale = 5 mm for *E*, *F*, and *G*.

are 2.5–3.0 mm in diameter, and at least three are present in the coal ball. An unrolled primary pinna is present on the crozier stipe of one specimen (fig. 7). The croziers are attached directly to mature rachides (figs. 7, 8A), and therefore they replace primary pinnae. However, careful study of serial sections revealed that rather than consisting of three orders of division, like the primary pinnae, the structure of the croziers includes all four orders of alternate division that characterize complete *Kaplanopteris* fronds (rachis, primary and secondary pinnae, and laminar pinnules; fig. 6). This feature of the croziers, together with their occurrence on otherwise mature frond segments, reveals that they represent dormant meristems in the form of latent croziers (Trivett and Rothwell

1988), comparable to those seen in the climbing fern *Lygodium* (Schizaeaceae) (Mueller 1983).

Fertile Structures

As described by Rothwell (1987), fertile structures borne on fronds with *A. clavata* anatomy consist of superficial indusiate sori on the abaxial faces of laminar pinnules (fig. 9A). Each sorus includes numerous sporangia tightly packed within a globose, urn-shaped indusium 0.4–0.6 mm in diameter (fig. 9A, 9C, 9M, 9N). There is a conical vascularized receptacle at the base of the sorus from which crowded sporangial stalks diverge (fig. 9D–9F). Sporangial stalks are long and uniseriate, and they terminate in a bell-shaped

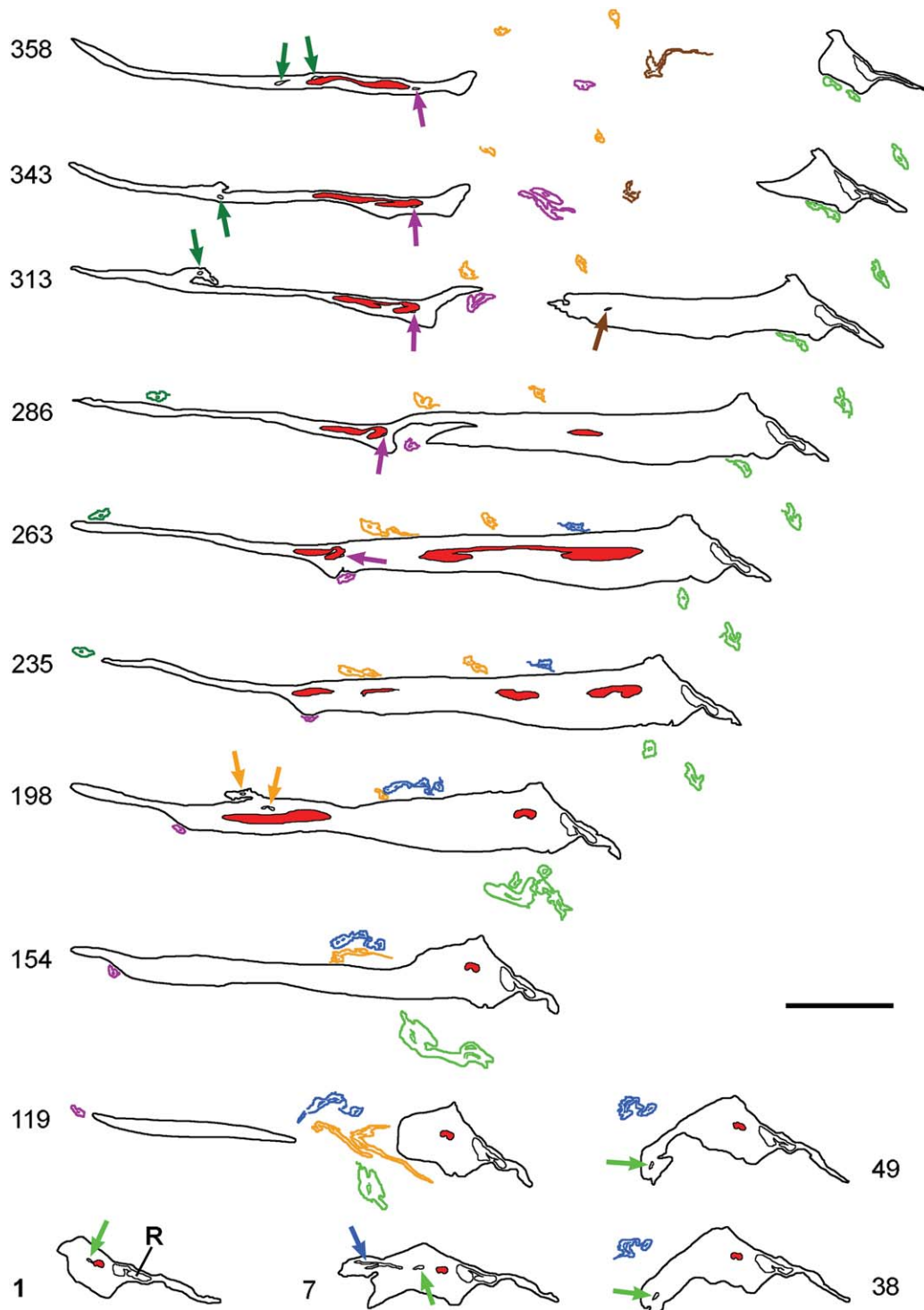


Fig. 5 *Kaplanopteris clavata* gen. et comb. nov. Digitized tracings of peel sections from coal ball slab 422Ctop documenting divergence of a primary pinna from the rachis (R) and alternate divergence of five secondary pinnae (color coded) from the primary pinna. Most pinnules have been omitted for clarity. Sections are identified by peel numbers, with the basalmost section at bottom left (peel 1). Arrows indicate vascular traces of frond segments proximal to their divergence from the subtending frond segment. Red = primary pinna trace. Light green = first (basalmost) secondary pinna trace and outline. Brown = second secondary pinna trace and outline. Orange = third secondary pinna trace and outline. Purple = fourth secondary pinna trace and outline. Dark green = fifth secondary pinna trace and outline. Blue = trace and outline of the basalmost pinnule on the basalmost (first) secondary pinna. Scale = 5 mm.

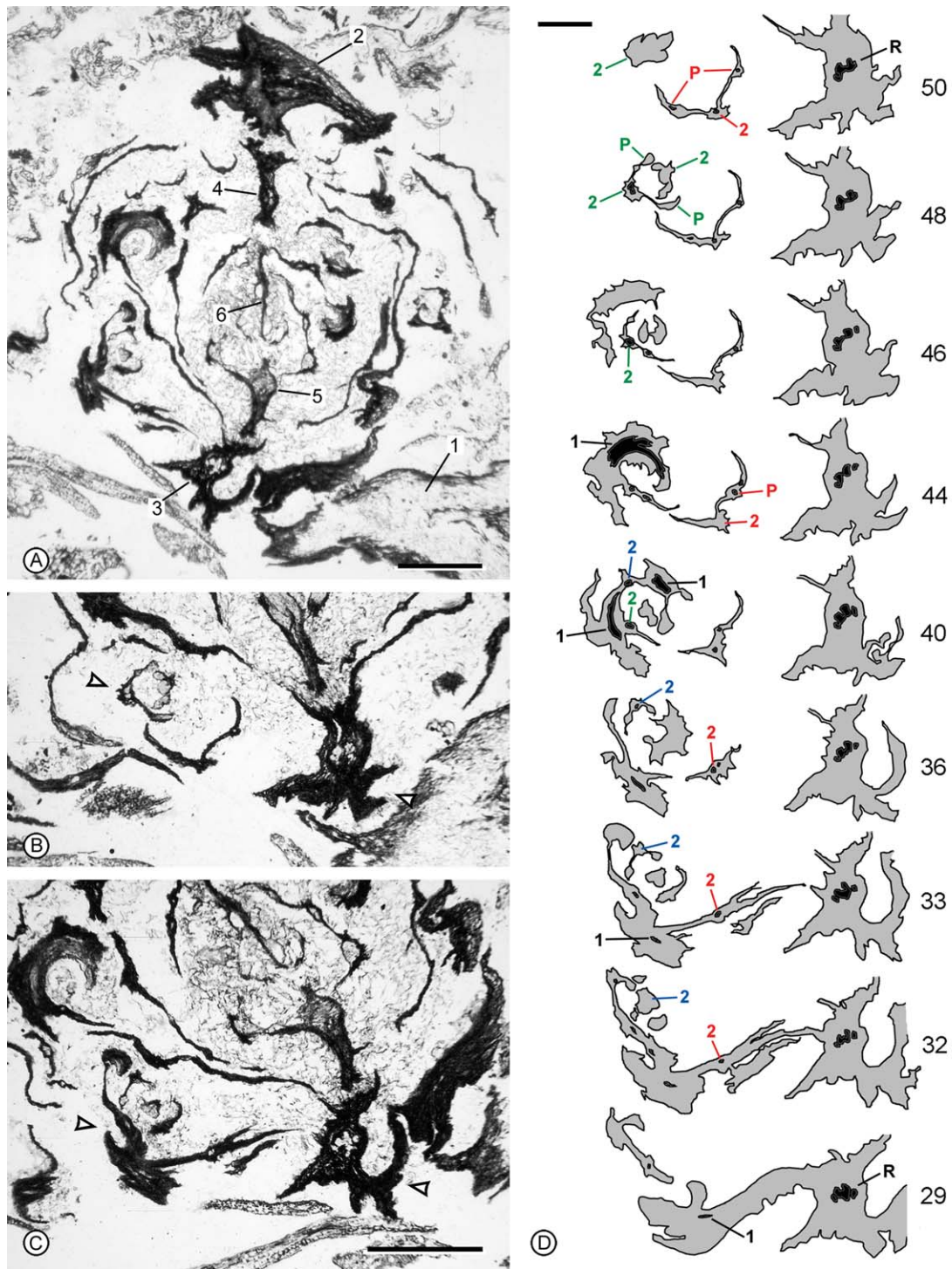


Fig. 6 *Kaplanopteris clavata* gen. et comb. nov. Latent crozier complexity. *A*, General view of latent crozier in oblique cross section. Coiled crozier stipe/rachis intersects plane of section six times, numbered 1–6 from most proximal to most distal. Stipe (seen in oblique section at 1) corresponds to position of primary pinna on frond (fig. 7). Numbers 2–5 are oblique sections, whereas 6 is tangential/grazing longitudinal section. OUPH 16841; scale = 500 μm . *B*, Detail of crozier section showing (between arrowheads) the part illustrated in *D*, peel 48. OUPH 16842; scale = 500 μm . *C*, Detail of crozier section in *A* showing (between arrowheads) the part illustrated in *D*, peel 33. OUPH 16841; scale = 500 μm . *D*, Digitized tracings of peel sections from coal ball slab 422G1top documenting the four orders of division of the latent crozier in *A*. The series includes only a selected portion of the crozier showing divergence of a primary pinna (1) from the crozier rachis (R) and three color-coded secondary pinnae (2) with pinnules (P), diverging from the primary pinna. Sections are identified by peel numbers. Red = first (basalmost) secondary pinna system. Green = third secondary pinna system. Blue = fourth secondary pinna system. Vascular traces in black. Second secondary pinna system not indicated for clarity. Scale = 250 μm .

capsule (fig. 9E, 9H, 9I). At the juncture of the stalk and capsule, the capsule is bent away from the center of the sorus (fig. 8B; fig. 9E, 9F).

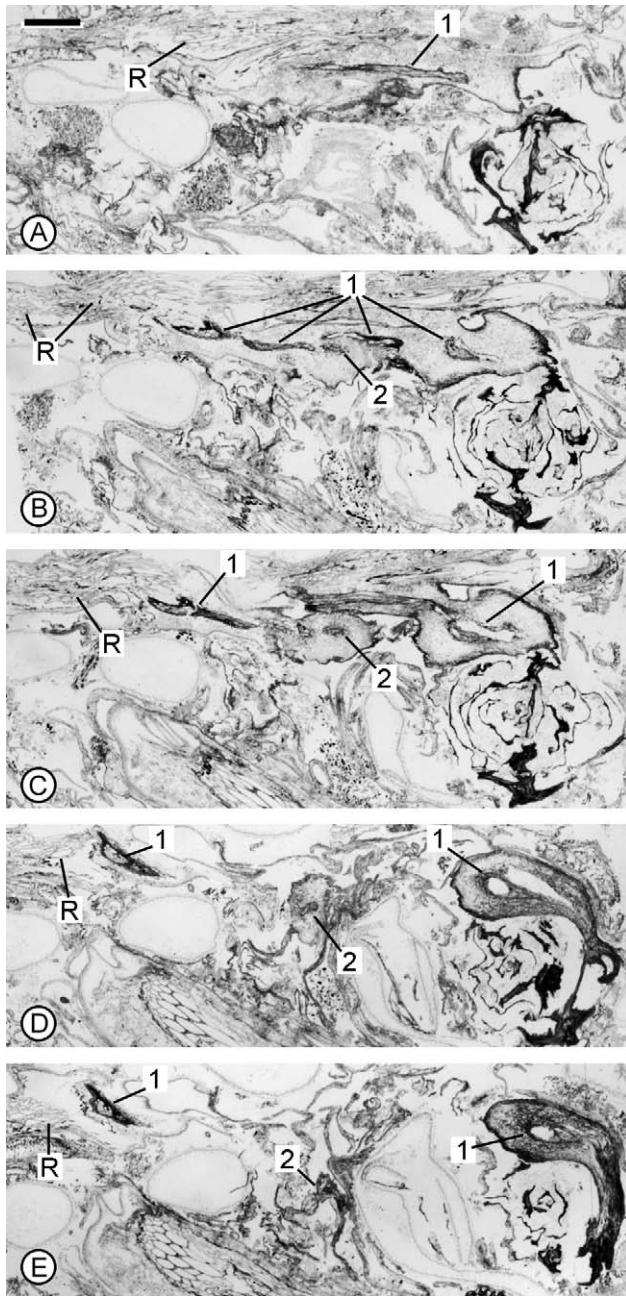


Fig. 7 *Kaplanopteris clavata* gen. et comb. nov. Series of sections illustrating attachment of latent crozier (at right) to frond rachis/stipe (R). Primary pinna trace (1) seen in grazing longitudinal section in A intersects plane of section at four places in B and at two places in C–E. Left side of panel shows successively more proximal sections toward bottom, with primary pinna trace rejoining the rachis trace (both sectioned obliquely). Right side of panel shows successively more distal sections toward bottom, with the primary pinna trace entering the base of the crozier and becoming the vascular trace of the crozier rachis. The primary pinna trace also produces a vascular strand that supplies a secondary pinna (2) with attached pinnules. OUPH 16849–16853; scale = 1 mm.

The sporangia have one-cell-thick walls (fig. 9C, 9J) and are annulate, with the annulus consisting of two to three rows of longitudinally elongated interfingering cells (fig. 8B; fig. 9B, 9G, 9K) with thickenings on the internal and anticlinal walls (fig. 9J). The annulus is a wide band wrapped around the long axis of the sporangium and covering most of it, and therefore it is not interrupted by the stalk (fig. 8B; fig. 9E, 9H, 9J). The longitudinally oriented stomium faces toward the distal part of the sorus (figs. 8B, 9J). Each sporangium produces 64–128 spores approximately 18–25 μm in diameter. The spores are radial, trilete, triangular in polar view, and scabrate (fig. 9L).

A series of specimens that includes those with all sporangia undehisced (fig. 9C, 9E, 9F, 9M), those with the apical-most sporangia dehisced and more basal sporangia immature and undehisced (fig. 9G), and those with entirely senescent dehisced sporangia (fig. 9O) documents that sporangia at the apex of the sorus mature (with elongation of the stalk) and dehisce first, with progressively more proximal sporangia maturing and dehiscing at successively later times. This demonstrates the basipetally gradate development of the sori (Rothwell 1987). Likewise, the occurrence of spore tetrads in basal sporangia of indusia with senescent apical sporangia (fig. 9N) supports this developmental interpretation.

Discussion

The Genus Anachoropteris

Anachoropteris as erected by Corda (1845) is a morphogenus consisting of vegetative frond fragments characterized by a C-shaped vascular strand in cross section. The genus was assigned by Seward (1910) to the now-abandoned order Coenopteridales, and it now includes over a dozen morphospecies (Phillips 1974). Species of *Anachoropteris* have been described from Europe and North America and cover a stratigraphic range spanning the Namurian C (Early Pennsylvanian) through Early Permian (Galtier and Holmes 1984). Fertile fronds with the *Anachoropteris* trace configuration were described by Eggert and Delevoryas (1967) as *Sermaya biseriata* Delevoryas and Morgan and recognized as a new filiclean family, the Sermayaceae Eggert and Delevoryas. A second genus of the Sermayaceae, *Doneggia* has subsequently also been described (Rothwell 1978).

Eggert and Delevoryas (1967) suggested that *Anachoropteris* is an unnatural taxon (i.e., a morphotaxon) that defines frond members of a heterogeneous group of ferns with similar foliar anatomy, a suggestion that is confirmed by the features of *Kaplanopteris*. In agreement with *Sermaya* and *Doneggia*, the fronds of *Kaplanopteris* have frond anatomy of the *Anachoropteris* type and bear sori of annulate leptosporangia that are indicative of filiclean affinities. In contrast to the other two genera, the sori of *Kaplanopteris* are indusiate, display gradate maturation, and have sporangia with long, narrow stalks. It is therefore confirmed that fertile fronds with *Anachoropteris* anatomy characterize at least two distinct filiclean fern genera of the family Sermayaceae (i.e., *Sermaya* and *Doneggia*) as well as *Kaplanopteris* of the Kaplanopteridaceae.

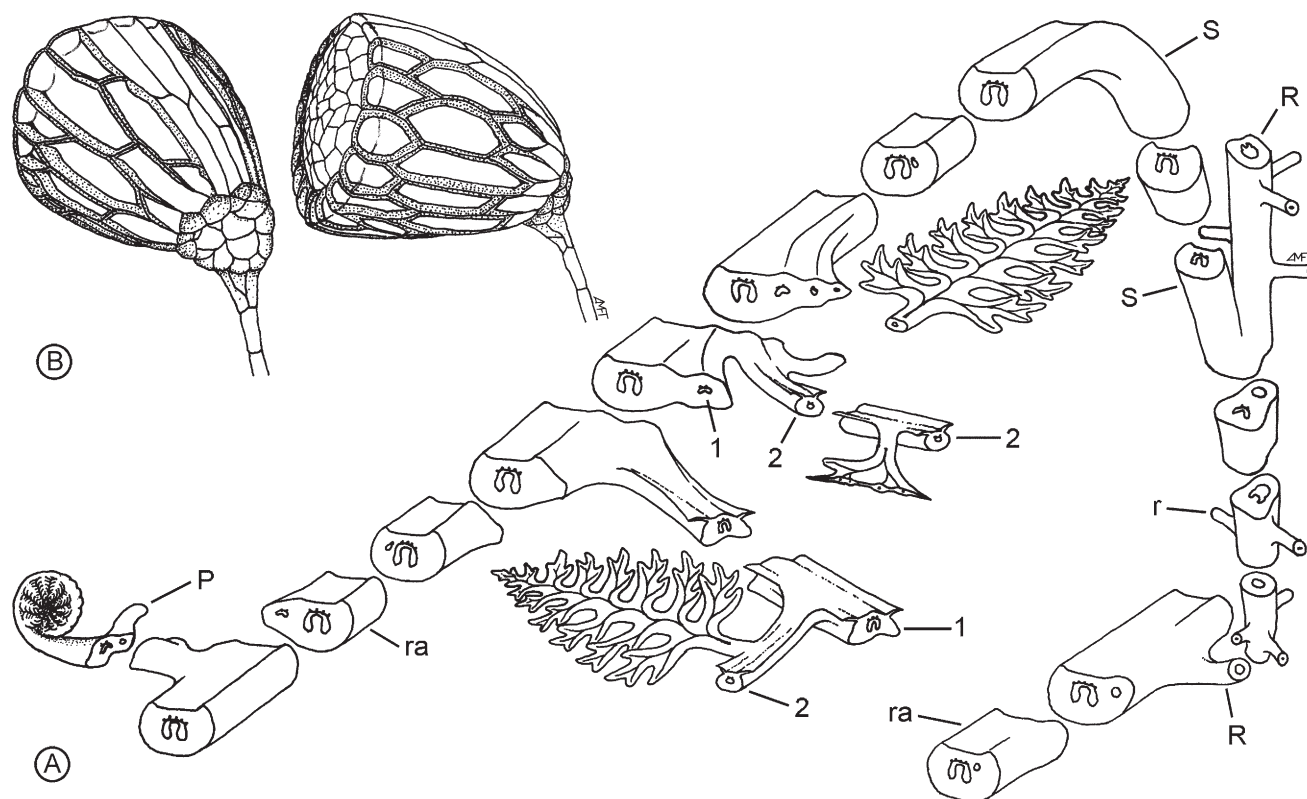


Fig. 8 *Kaplanopteris clavata* gen. et comb. nov. A, Reconstruction of epiphyllous rhizome and frond divergence. The rhizome (R) diverges laterally from a frond rachis (ra). The stipe (S) extends distally and then bears a primary pinna (1) that produces two secondary pinnae (2) with pinnules. A latent crozier is attached to the frond rachis in the position of a primary pinna, and a pinna (P) diverges from the crozier rachis. Protoxylem strands represented by dots at vascular trace margins, except for rhizome stele, which is exarch. Length of the rhizome is exaggerated for clarity; r = adventitious roots. B, Reconstructions of sporangia seen from side (right) and from base (left) of capsule. Wide two- to three-seriate annulus covers most of the sporangial surface (cell walls of annulus stippled). Stomium runs longitudinally from apex to base on the upper side of capsule.

Building the Concept of Kaplanopteris clavata

The morphospecies of frond parts that is herein amplified to the new fossil plant genus *Kaplanopteris* was originally described as *Anachoropteris clavata* Graham (Graham 1935) on the basis of the frond trace configuration of specimens from the Calhoun Coal (Upper Conemaugh Group, Late Stephanian) of Illinois and is known only from North America. The species is primarily or exclusively Late Pennsylvanian and is best known from coal balls of the Calhoun Coal of Illinois and the Duquesne Coal of Ohio (Phillips 1980). Pinnae with a trace configuration similar to that of *A. clavata* have been reported from Middle and Upper Pennsylvanian coal balls associated with the Springfield, Herrin, Baker, Parker, and Friendsville Coals of Illinois, Indiana, and Kentucky (Phillips 1980). To date, these have not been described or figured, and other organs of the plants with *A. clavata*-type anatomy from those localities are unknown. Therefore, it remains uncertain whether the older specimens were produced by the same species as the Late Pennsylvanian fern described herein as *Kaplanopteris clavata*.

In his original description of *A. clavata*, Graham (1935) described the distinctive clavate configuration of the rachis

trace as well as the lateral divergence of the primary pinna trace. Studying additional coal balls from the same coal, Delevoryas and Morgan (1954) also described two orders of division for the *A. clavata* frond and documented unequivocally the inversicatenalean orientation of the frond traces. Perhaps more important, those authors described frond members that produced in lateral positions *Tubicaulis*-type protostelic rhizomes, complete with adventitious roots and helically arranged stipes with the diagnostic *A. clavata* xylem configuration (Delevoryas and Morgan 1954). The epiphyllous rhizomes in the Duquesne Coal from Steubenville, Ohio, are comparable to those described by Delevoryas and Morgan in every respect.

Smoot (1985) gave a detailed description of the phloem of *A. clavata*. She emphasized the very complex cellular composition of the phloem in this species, which is comparable to that of only a few other vascular cryptogams (Smoot 1985). Preservation of specimens from the Duquesne Coal is inadequate to confirm a similar phloem composition for the Ohio specimens.

Fertile parts of *Kaplanopteris* were first described from the Duquesne Coal of Ohio and recognized as evidence of a new family of Paleozoic Filicales with indusiate sori of leptosporangia that display a biseriate annulus and long, narrow stalk

(Rothwell 1987), but the new fern was not named in that article. On the basis of the same material, Trivett and Rothwell (1988) documented the four orders of division of *A. clavata* fronds as well as reiterative indeterminate frond growth by production of latent croziers. Those authors also proposed a new architectural model based on the growth and development of the *A. clavata* frond.

Frond segments of the plant reconstructed here conform to the genus *Anachoropteris*, whereas rhizomes of the plant are similar to the genus *Tubicaulis*. However, neither of these names can be used for the whole *Kaplanopteris* plant, because both *Anachoropteris* and *Tubicaulis* designate morphotaxa that represent well-delimited vegetative plant parts that are common to at least two different families of ferns. The importance of restricting *Anachoropteris* and *Tubicaulis* to the organs that they were originally meant to define has been fully explained and justified by Eggert and Delevoryas (1967). Those authors used this approach when describing the new filiclean genus *Sermaya* and stressed that plant parts included within the genera *Anachoropteris* and *Tubicaulis* very likely came from a variety of plants (Eggert and Delevoryas 1967). The subsequent description of *Doneggia* (Rothwell 1978), another filiclean genus included in the Sermayaceae and characterized by *Anachoropteris* frond structure, made it clear that this feature is common to at least two genera of ferns. The reconstruction of *Kaplanopteris* as a genus of extinct fern plants now documents that *Anachoropteris*- and *Tubicaulis*-type organs were produced by at least two families of filiclean ferns, the Sermayaceae and the Kaplanopteridaceae.

New data provided for the plant reconstruction of *K. clavata* by specimens in coal balls from the Duquesne Coal document (1) overall frond architecture and division pattern, (2) pinnule form, (3) latent croziers that form reiterative buds (Trivett and Rothwell 1988), and (4) fertile frond segments with indusiate sori of (5) annulate leptosporangia with (6) gradate soral maturation and (7) radial trilete spores (Rothwell 1987).

Phylogenetic Context

Planar dissected fronds with laminar pinnules, along with superficial soral leptosporangia with a well-defined annulus, reveal that *Kaplanopteris* is a true filiclean fern (Rothwell 1999). The fertile parts of this plant exhibit a novel combination of characters that places it outside the circumscription of all currently recognized filiclean families (Rothwell 1987) and documents the existence of a previously unrecognized extinct lineage of basal filicleans. *Kaplanopteris clavata* combines (1) features restricted to Paleozoic filicleans, such as inversicatenalean leaf trace orientation; and (2) traits considered plesiomorphic in living filicleans (e.g., multiseriata sporangial annulus), with (3) a considerable number of characters of more derived filiclean groups, such as long, uniseriate sporangial stalks and indusiate sori with gradate maturation. *Kaplanopteris* demonstrates that many presumably derived filiclean traits evolved by the Late Carboniferous in basal lineages during the first major evolutionary radiation of filiclean ferns (Rothwell 1987).

Reconstructive Paradigms

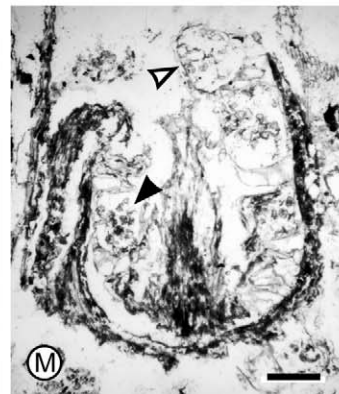
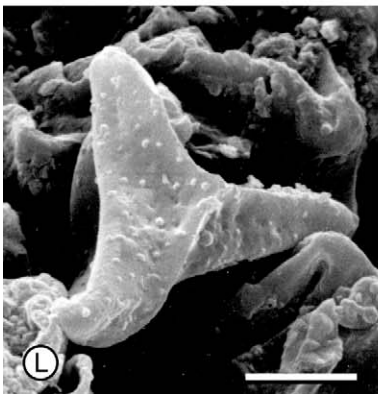
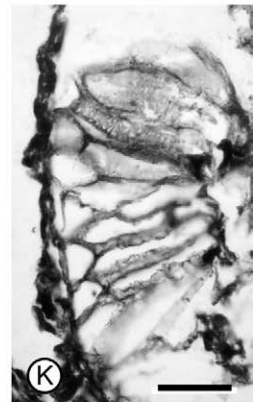
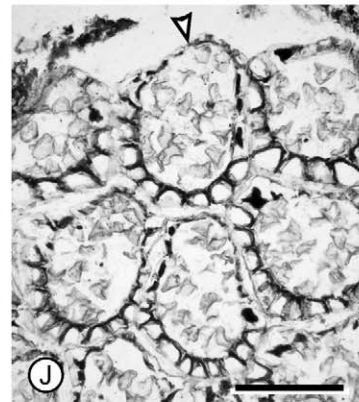
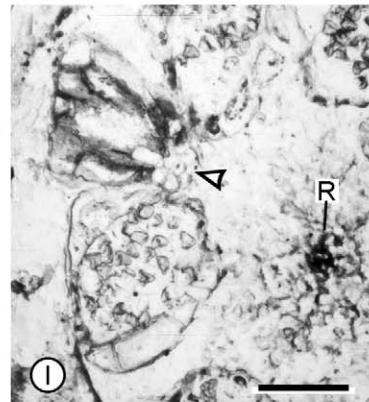
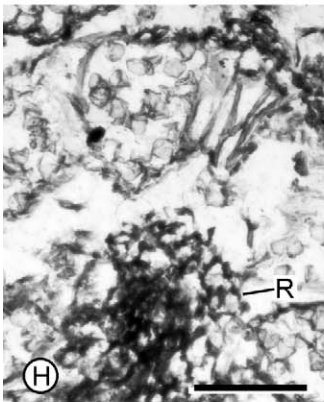
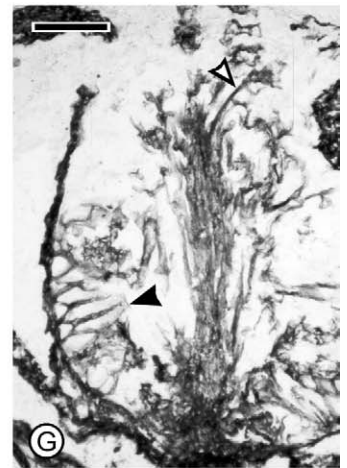
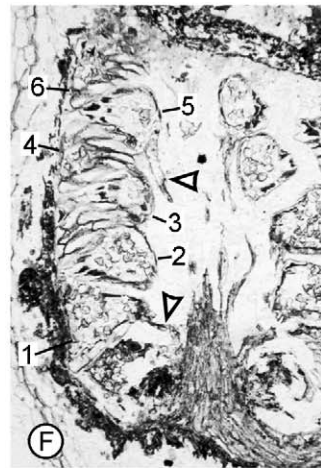
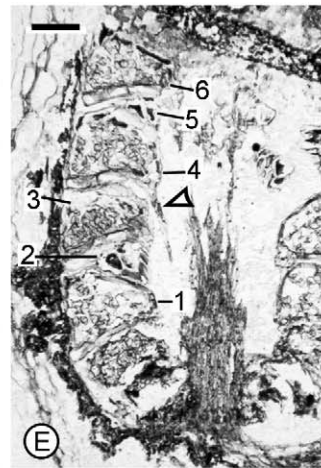
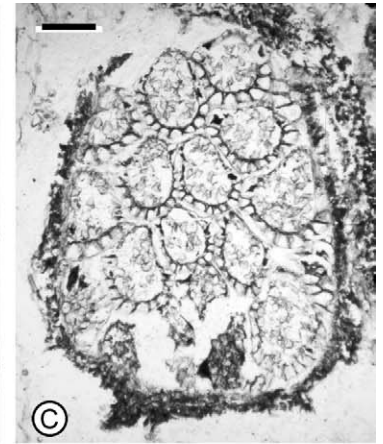
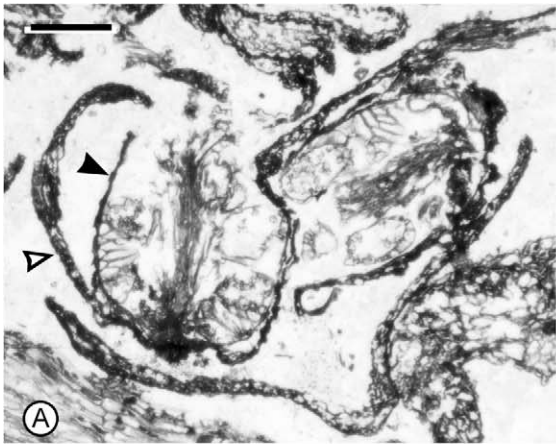
As a result of disarticulation of the parent plants after death, fossil plant remains that represent fragments of the same extinct species of plant are usually found detached, sometimes at distant locations and at different moments in time, possibly fossilized in different modes, and are described as distinct morphotaxa, often by different workers. Long periods of time may pass before two or more such morphotaxa are found connected to each other and can be recognized as being parts of the same taxon (e.g., *Archaeopteris*; Beck 1960). As an alternative to this connectivity paradigm, shared characteristic anatomical features (e.g., glandular trichomes in the now classical reconstruction of the seed fern *Lyginopteris*; Oliver and Scott 1904) have been used to demonstrate the con-specificity of distinct morphotaxa.

The current study makes use of both of these paradigms to bring together the whole-plant reconstruction of *K. clavata*. Interconnected parts have been used to document the attachment of several *K. clavata* organs to frond segments characterized by *A. clavata* anatomy. These are (1) the protostelic, *Tubicaulis*-like rhizomes borne on first order frond members; (2) four orders of attached mature frond parts; (3) leptosporangiate indusiate sori with gradate maturation, borne on pinnules; and (4) latent croziers preserved on otherwise mature frond segments. Shared anatomical characters have been used to bring together under the same species frond fragments from two collecting localities, as well as Smoot's (1985) description of phloem anatomy, on the basis of the shared and very characteristic xylem anatomy conforming to morphospecies *A. clavata*. All of these have made possible the reconstruction of the whole plant, have allowed for an understanding of systematic affinities, and have provided the basis for interpreting frond architecture, growth habit, and phylogenetic significance of this distinctive species of extinct plants.

Whole-Plant Reconstruction

The organography of *K. clavata* plants is overwhelmingly dominated by the frond. This is indicated by the rarity of rhizomes in the fossil material; the only *K. clavata* rhizomes known are epiphyllous rhizomes that conform to the morphogenus *Tubicaulis*. *Kaplanopteris clavata* fronds are planar, tripinnately pinnatifid dissected, with laminar pinnules. The limited record of frond division available suggests that the fronds are relatively sparsely divided. On the other hand, *K. clavata* fronds have potential for indeterminate growth by production of reiterative modules of two types, epiphyllous rhizomes and latent croziers. Epiphyllous rhizomes and latent croziers both occur at the positions of primary pinnae.

Morphologically, whether they are entire fronds or just frond segments, the fertile parts of ferns can be divided into two main categories. In taxa with dimorphic fronds or frond segments, the fertile regions are specialized in that they are modified with respect to vegetative parts. In these taxa, the pinnule lamina is typically reduced, often dramatically, so that the fertile foliar member consists mainly of axial components (e.g., *Osmunda* spp.; Hewitson 1962). By contrast, in other taxa (e.g., species of *Polypodium*) the



fertile parts have roughly the same morphology as the vegetative parts, the greatest difference being marked by the presence of sporangia on the fertile pinnules. *Kaplanopteris clavata* belongs to the second category: fertile pinnules are laminar and have sizes comparable to those of vegetative pinnules (fig. 9A).

In contrast to seed plants, where organography is mainly an expression of shoot development, fern architecture is characterized by the organographic dominance of the frond (Kaplan and Groff 1995). Kaplan and Groff have used different fern taxa as examples to illustrate extensive morphological parallelism between the shoots of seed plants and the fronds of ferns (i.e., what they call the construction of the plant body). They have shown that fern fronds parallel most of the growth architectural and adaptive roles fulfilled by shoots in seed plants. *Kaplanopteris clavata* is a dramatic example of this constructional parallelism, in that the fronds of the plant produce both latent croziers, associated by Kaplan and Groff (1995) with an indeterminate, vining growth habit, and epiphyllous rhizomes, usually associated with stoloniferous growth.

We reconstruct *K. clavata* as a primarily vining, or climbing, plant whose life-history pattern is influenced significantly by indeterminate fronds featuring reiterative modules, much like in the climbing fern *Lygodium* (Trivett and Rothwell 1988). By contrast to the latter, *K. clavata* reiterative modules occur not only in the form of latent croziers but also as epiphyllous rhizomes. We base our reconstruction on several lines of evidence. One of these is the rarity of rhizomes, invoked by Hall (1961) to advocate indeterminate growth of the fronds in another *Anachoropteris* species, *Anachoropteris involuta*. The fact that the organography of the plant body is dominated by fronds as well as the extended distance between successive frond divisions in *K. clavata* also suggest indeterminate growth of the fronds. Such inde-

terminate growth fits both climbing and scrambling growth habits.

The presence of epiphyllous rhizomes, known in several living and fossil fern species (e.g., Troop and Mickel 1968; Phillips 1974; Galtier and Holmes 1982), has been used to infer stoloniferous, scrambling habits for both anachoropteroid (Hall 1961; Holmes 1989) and botryopteroid (Rothwell and Good 2000) plants. However, a survey of growth habits among the living fern taxa with leaf-borne rhizomes reported by Troop and Mickel (1968) reveals that the feature is not limited to scrambling forms. Leaf-borne rhizomes are also present in climbing and epiphytic species as well as in species with erect rhizomes (Kramer and Green 1990). Latent croziers replacing primary pinnae, on the other hand, are reiterative growth features characteristic of the vining habit of *Lygodium*. In this genus, twining frond rachides tend to produce mainly latent croziers and to elongate considerably before they establish a good hold onto their support and start producing fully developed pinnae (Mueller 1983). The latent croziers of *K. clavata* very likely reflect a similar vining growth habit. In fact, vining and scrambling habits are not mutually exclusive and are known to co-occur in ferns with opportunistic rhizome growth (e.g., *Lomagramma guianensis*; Gay 1993).

The biomass of *K. clavata* plants consisted principally of indeterminate vining fronds produced by scanty, small erect rhizomes. The frequent co-occurrence of *Kaplanopteris* organs with pectopterid pinnules and scoleopterid synangia implies that *K. clavata* may have used the tree fern *Psaronius* for support. In such cases, *K. clavata* plants would have displayed opportunistic growth and could have propagated clonally by production of epiphyllous rhizomes where frond rachides touched the ground. They also could have been facultative epiphytes (as proposed for *Anachoropteris*-type plants by Galtier and Phillips 1996), rooted within the root mantle of *Psaronius* trunks.

Fig. 9 *Kaplanopteris clavata* gen. et comb. nov. Indusiate sori, sporangia, and spores. A, Pinnules with two sori in radial section. Sorus at left is attached to laminar pinnule (white arrowhead). Urn-shaped indusium indicated by black arrowhead. OUPH 16827; scale = 200 μm . B, Cross section of sorus showing receptacle surrounded by sporangial stalks at center, surrounded by radially oriented sporangia, and with indusium enclosing the ring of sporangia. Note multiseriate annulus of sporangium at top. OUPH 16854; scale = 100 μm . C, Tangential section of sorus showing tightly packed sporangia enclosed by urn-shaped indusium. OUPH 16855; scale = 100 μm . D, Longitudinal section of soral receptacle (detail of F). Note overall conical shape of the receptacle, vascular tissue in receptacle, and bases of uniseriate sporangial stalks (white arrowheads). OUPH 16856; scale = 100 μm . E, F, Closely spaced radial sections of sorus with sporangia (numbered 1–6) tightly packed inside indusium. Slightly different sagittal and tangential sections of the various sporangia reveal sporangial geometry and uniseriate stalks (white arrowheads). Note sporangial capsules bent away from the center of the sorus at juncture with stalk. OUPH 16857 and 16856; scale = 100 μm . G, Radial section of sorus. Note urn-shaped indusium and apparently biseriate annulus (black arrowhead). Sporangia toward apex of sorus are borne on elongated, uniseriate stalks and have already dehisced (e.g., white arrowhead). Compare with sorus in *M*. OUPH 16827; scale = 100 μm . H, Detail of sorus in cross section showing receptacle and sporangial stalks (R), and sporangium in longitudinal section (top). Note bell-shaped outline of sporangium; long, broad cells of annulus on the lateral walls of the sporangium; and short, narrow cells at the apical and basal ends of capsule. OUPH 16854; scale = 100 μm . I, Cross section of sorus with receptacle (R) and sporangial capsules seen in longitudinal sections. Note bell-shaped capsule outlines and cluster of circular cells forming base of capsule (white arrowhead). OUPH 16854; scale = 100 μm . J, Tangential section of sorus (detail of C) showing tightly packed sporangial capsules in cross section, each with a conspicuous annulus and thin-walled, much smaller cells of the stomium at top (e.g., white arrowhead). OUPH 16855; scale = 100 μm . K, Longitudinal section of sorus showing indusium (at left) and face view of lateral sporangial wall with two- to three-seriate annulus. OUPH 16858; scale = 100 μm . L, SEM of spore. Scale = 5 μm . M, Radial section of sorus with mature but undehisced sporangia at apex (white arrowhead) and less mature sporangia containing spores in tetrad stage at base (black arrowhead). Compare with sori in G and O. OUPH 16859; scale = 100 μm . N, Sporangium at base of sorus in *M* containing spores in tetrad stage. OUPH 16859; scale = 10 μm . O, Radial section of sorus in a later developmental stage. Apical sporangia, borne on much elongated stalks, have dehisced, whereas basal sporangia are still undehisced. Compare with sorus in *M*. OUPH 16854; scale = 100 μm .

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