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GLEICHENIA APPIANENSIS SP. NOV. (GLEICHENIACEAE): A PERMINERALIZED RHIZOME AND ASSOCIATED VEGETATIVE REMAINS FROM THE EOCENE OF VANCOUVER ISLAND, BRITISH COLUMBIA

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A permineralized gleicheniaceous rhizome with an attached stipe base has been identified from the Appian Way locality on Vancouver Island, British Columbia, Canada. The specimens are preserved in Middle Eocene marine calcareous concretions that are studied using the cellulose acetate peel technique. The marginally mesarch rhizome has a vitalized protostele, protoxylem elements with helical wall thickenings, and scalariform metaxylem tracheids that occur in clusters. A continuous band of phloem and pericycle surrounds the xylem. The inner cortex consists of a layer of small-diameter sclerenchyma fibers, and the outer cortex is composed of larger parenchyma cells. A nodal island of sclerenchyma is present between the leaf trace and protostele at the level of frond-trace divergence. Long metaxylem tracheids in the frond trace show septa in longitudinal section that likely represent tyloses. Roots diverge from all sides of the rhizome with traces that run obliquely through the cortex. Numerous associated but isolated frond segments are found in the Appian Way nodules that show a pinched and inrolled C-shaped vascular trace and pseudodichotomous bifurcation. The frond traces have numerous protoxylem strands, and the general anatomy is comparable to that of gleicheniaceous stipes. The rhizome is described as a new species of *Gleichenia*, *Gleichenia appianensis* Mindell, Stockey, Rothwell, et Beard sp. nov., and represents the first record of Gleicheniaceae in the Tertiary of North America.

Keywords: Eocene, fern, Gleicheniaceae, Hymenophyllaceae, *Lygodium*, Schizaeaceae.

Introduction

Gleicheniaceae is a tropical to subtropical family of three to five living genera (Tryon and Tryon 1982; Kramer 1990) that have long been considered to be basal leptosporangiate ferns, based on morphological and anatomical characters (Bower 1926; Copeland 1947). Most notable of these characters are the protostelic rhizomes, exindusiate sori with simultaneous maturation, and large sporangia (Bower 1926). Phylogenetic relationships of the Gleicheniaceae have been clarified by recent cladistic analyses using morphological and molecular characters (Hasebe et al. 1995; Pryer et al. 1995; Stevenson and Loconte 1996; Rothwell 1999).

Probable gleicheniaceous fossil remains are known as early as the Permian (Yao and Taylor 1988). Mesozoic records of the family are more common, including fronds, rhizomes with attached stipes, and isolated fertile material (Tidwell and Ash 1994; Collinson 1996; Skog 2001). By the mid-Cretaceous, gleicheniaceous fossils are abundant, with a large number of specimens being assigned to *Gleichenia* (Berry 1922; Andrews and Pearsall 1941). Despite this relatively rich Mesozoic history, there are no Tertiary records of the family in the New World (Tidwell and Ash 1994; Collinson 2001). The Eocene Appian Way flora of Vancouver Island is dominated by angiosperm fruits and seeds (Little et al. 2001), but several kinds of taxodiaceous conifers are present (Hernandez-Castillo et al. 2005) as well as a polypore fungus (Smith et al. 2004) and many types of filicalean ferns. The ferns of Appian Way have only recently begun to be investigated in detail. Sori of a schizaeaceous fern have been described (Trivett et al. 2002; Trivett 2006), and a general description of fern diversity is underway. In this article we describe *Gleichenia appianensis* sp. nov., a new species of gleicheniaceous ferns based on a permineralized rhizome with an attached stipe. This rhizome and several associated stipes represent the first record of Gleicheniaceae in the Tertiary of North America.

Material and Methods

Specimens were collected from the Appian Way fossil locality south of Campbell River on the east coast of Vancouver Island, British Columbia, Canada (lat. 49°54′42″N, long. 125°10′40″W; UTM 10U CA 5531083N, 343646E). Plant remains occur in marine calcareous concretions in a sandy-siltstone matrix. These shallow marine sediments have been dated as Eocene based on fossil molluscs, decapods, and shark teeth (Haggart et al. 1997), and stratigraphic studies are currently being conducted at the site (J. W. Haggart, personal communication, 2004).

The fossiliferous concretions were cut into slabs, and peels were made using the cellulose acetate peel technique (Joy et al. 1956). Slides were mounted using xylene-soluble Eukitt

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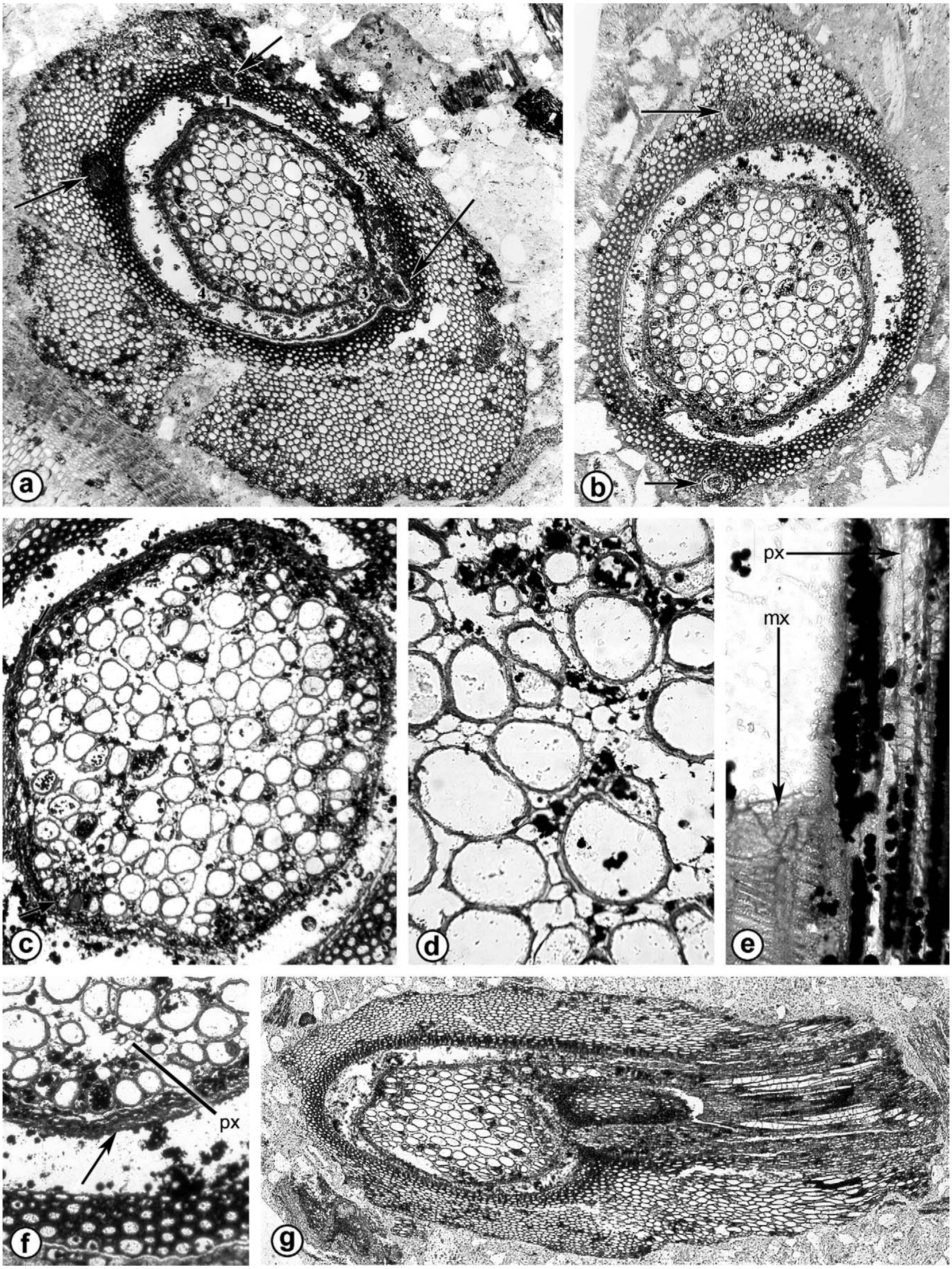

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(O. Kindler, Freiburg, Germany) mounting medium. Images were captured using a PowerPhase digital scanning camera (Phase One, Copenhagen, Denmark) and processed using Adobe Photoshop 7.0.

Systematics

Order—Filicales

Family—Gleicheniaceae

*Genus—*Gleichenia

*Species—*Gleichenia appianensis *Mindell, Stockey, Rothwell, et Beard sp. nov. (Figs. 1, 2*a*–2*f)

Specific diagnosis. Rhizome small, at least 3.4 mm in diameter. Protostele mixed, ca. 1.4 mm in diameter; tracheids in chains or groups. Parenchyma cells between tracheids, thin walled, 10–20 μm in diameter. Protoxylem strands 5–6; stele marginally mesarch; protoxylem tracheids ca. 10 μm in diameter, thickenings helical. Metaxylem tracheids scalariform, 25–63 μm in diameter. Cortex two-zoned, at least 1 mm thick; outer parenchymatous, up to 950 μm thick, cells 25–63 μm in diameter; inner sclerenchymatous, 125–188 μm wide, fibers 13–38 μm in diameter. Roots diarch, numerous, arising on all sides of rhizome. Frond trace C-shaped, originating as an arc, forming nodal island of sclerenchyma fibers on divergence; metaxylem tracheids scalariform, up to 200 μm in diameter, some with numerous regularly spaced horizontal to slightly oblique septations.

Holotype. Rhizome with diverging stipe; specimen AW 258 C_2 bot and D_2 top, University of Alberta Paleobotanical Collections (UAPC-ALTA).

Stratigraphic position and age. Oyster Bay Formation, Middle Eocene.

Description. The rhizome of *G. appianensis* is 7.5 mm long and 3.0 mm in diameter (fig. 1*a*, 1*b*), but the specimen has been abraded and was probably at least 3.4 mm in diameter in life. No epidermis is preserved on the specimen. Therefore, the presence of possible scales or trichomes cannot be determined. The cortex is at least 1.1 mm thick and shows two distinct zones (fig. 1*a*). The outer cortex is up to 950 μm in thickness and up to 25 cells wide in the most completely preserved area. Cells in this zone are thick-walled parenchyma, 25–63 μm in diameter. The inner cortex measures 125–188 μm in thickness and is composed of thick-walled sclerenchyma fibers, 13–38 μm in diameter.

The rhizome has a mixed protostele up to 1.4 mm in diameter (fig. 1*a*–1*c*, 1*g*). In cross sections, metaxylem tracheids, 25–63 μm wide, appear to be arranged in chains up to five cells long (fig. 1*a*–1*d*). Thin-walled parenchyma cells 10–20 μm in diameter occur between groups of metaxylem tracheids (fig. 1*d*). Five to six marginally mesarch protoxylem strands correspond to subtle lobes of the stele (fig. 1*a*, 1*b*, 1*f*). Helically thickened protoxylem elements 10 μm in diameter (fig. 1*e*, right) occur in clusters among scalariform metaxylem tracheids near the periphery of the xylem (fig. 1*e*, 1*f*). Encircling the xylem is a poorly preserved layer of putative phloem and pericycle up to five cells wide and 60 μm across (fig. 2*f*, arrow).

Diarch root traces occur on all sides of the rhizome (fig. 1*a*, 1*b*, arrows) except in the area of leaf-trace divergence (fig. 1*g*). Root traces are surrounded by thick-walled parenchyma, and their course of growth through the cortex is oblique. No isolated roots have been identified in the matrix.

Leaf-trace divergence is initiated by the formation of an arc of xylem at the periphery of the stele (fig. 2*a*, top). In slightly more distal transverse sections, a subcircular nodal island of sclerenchyma forms in the space between the xylem of the leaf trace and that of the stele (fig. 2*b*). Continuing distally, the leaf trace and sclerotic bundle grow larger, as does the cortex surrounding them (fig. 2*c*, 2*d*). The trace itself has endarch xylem maturation with metaxylem tracheids that measure up to 200 μm wide; these tracheids having scalariform secondary-wall thickenings and regular septa (fig. 1*g*; fig. 2*e*, 2*f*). Spacing between these planar septa increases with tracheid width.

Associated foliage. Two branching specimens and at least 15 isolated frond segments with gleicheniaceous characters have been found associated with the rhizome (fig. 2*g*, 2*h*; fig. 3). Frond segments show significant variation in size, ranging from 2.5 mm to 8.0 mm in width. All have C-shaped traces with well-developed, infolded adaxial hooks (fig. 2*g*). Protoxylem strands vary (five or more) and show endarch maturation (fig. 2*h*). Xylem at the lateral edges of the trace is constricted, giving the trace an angular shape (fig. 2*g*, arrows). The vascular tissue is surrounded by a narrow sheath of sclerenchymatous tissue (fig. 2*g*). To the outside of this sheath the remaining extraxylary ground tissues are usually thick walled toward the periphery and relatively thin walled near the vascular trace (fig. 2*g*).

At levels of frond branching, the stipe and abaxial arc both widen, and the vascular trace divides to form three separate traces before the frond divides. The changes in xylem configuration that lead to formation of the three traces are similar in each specimen. Proceeding distally through a series of transverse sections in the branching region, both adaxial hooks close to form rings that each enclose ground tissue (fig. 3*a*) and then separate abaxially to form two rings of vascular tissue (fig. 3*b*). Distally, the rings begin to open up on

Fig. 1 *Gleichenia appianensis* Mindell, Stockey, Rothwell et Beard sp. nov. Holotype. *a*, Transverse section of rhizome, showing lobed stele, root traces (arrows), and thick, two-zoned cortex. Note that position of protoxylem strands correlate with subtle lobes of stele (numbered *1*–*5*). AW258 C bot 16, ×28. *b*, Transverse section of rhizome, showing root traces (arrows) and two-zoned cortex. AW 258 C_3 side 5, ×44. *c*, Transverse section of stele, showing tracheary elements in chains surrounded by parenchyma cells. AW 258 C_3 side 5, ×69. *d*, Detail of mixed protostele, showing parenchyma between large metaxylem tracheids. AW 258 C_3 side 5, ×224. *e*, Longitudinal section near stele margin, showing spirally thickened protoxylem (*px*) and scalariform metaxylem tracheids (*mx*). AW 258 C_3 side 9, ×360. *f*, Transverse section, showing stele periphery with marginally mesarch protoxylem strand (*px*) and zone of putative phloem and pericyle (arrow). AW 258 C_3 side 5, ×128. *g*, Oblique transverse section though rhizome, showing diverging leaf trace and internodal island of sclerenchyma. AW 258 D_2 top 2, ×20.

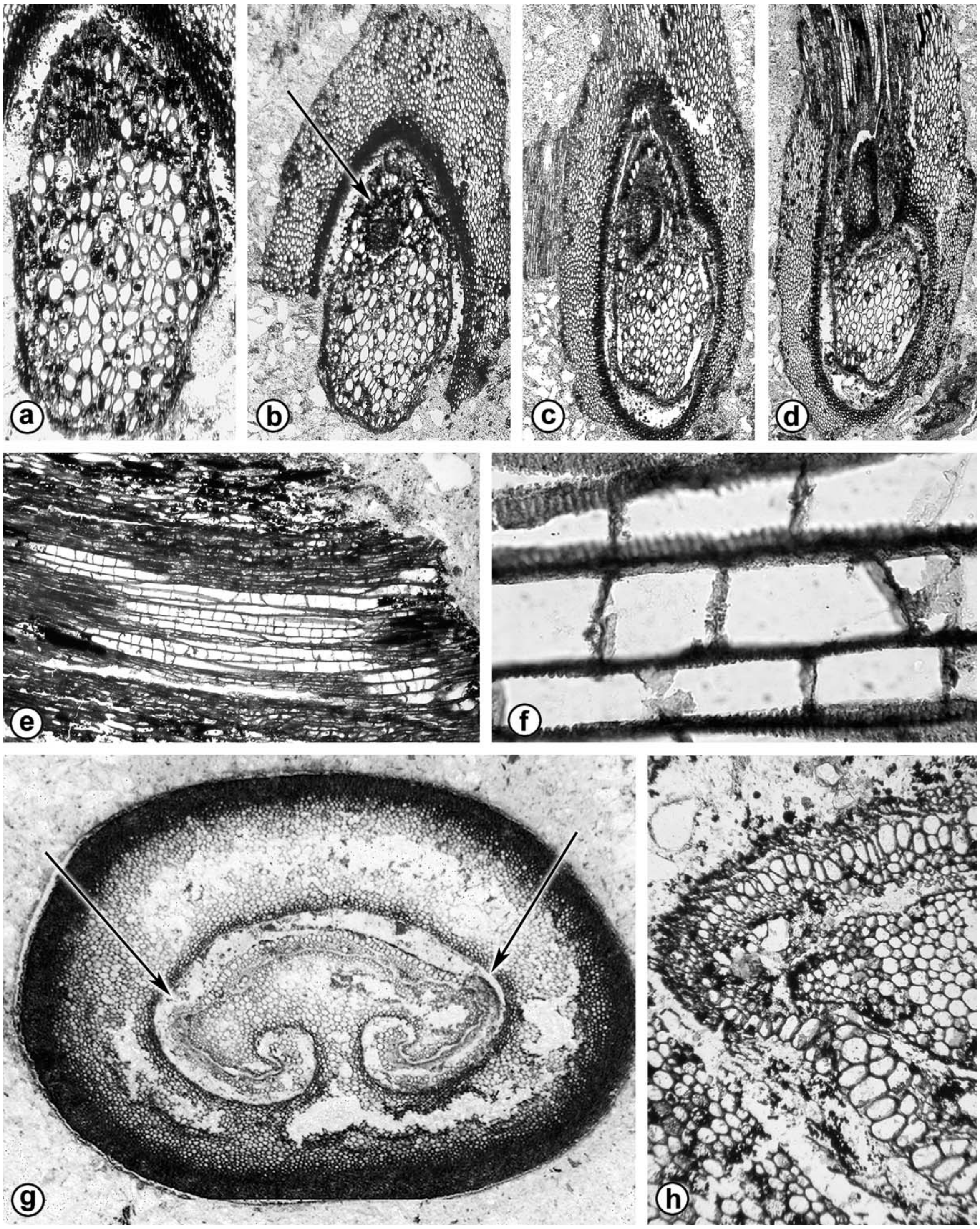

Fig. 2 *a–f*, *Gleichenia appianensis* Mindell, Stockey, Rothwell, Beard sp. nov. Holotype. *g*, *h*, Associated frond segments. *a*, Oblique transverse section of stele at base of stipe divergence. AW 258 D_2 top 50, ×33. *b*, Oblique transverse section of rhizome distal to that in *a*, showing sclerenchymatous internodal island (arrow) developing between arc of xylem and stele. AW 258 D_2 top 39, ×20. *c*, Section distal to *b*, showing well-developed arc of xylem, cortical expansion, and larger internodal island. AW 258 D_2 top 12, ×16. *d*, Transverse section through rhizome at level of leaf-trace departure. AW 258 D_2 top 2, ×16. *e*, Longitudinal section through departing leaf trace, showing elongate metaxylem tracheids with regular septa. AW 258 D_2 top 4, ×40. *f*, Longitudinal section of metaxylem tracheids in stipe base, showing planar septa and scalariform secondary-wall thickenings. AW 258 D_2 top 4, ×360. *g*, Isolated frond segment in transverse section showing angular, C-shaped trace with lateral constrictions (arrows) and adaxial hooks. AW 103 D bot 0, ×23. *h*, Transverse section through isolated frond segment showing lateral constriction and endarch primary-xylem maturation. AW 4 C top 4, ×65.

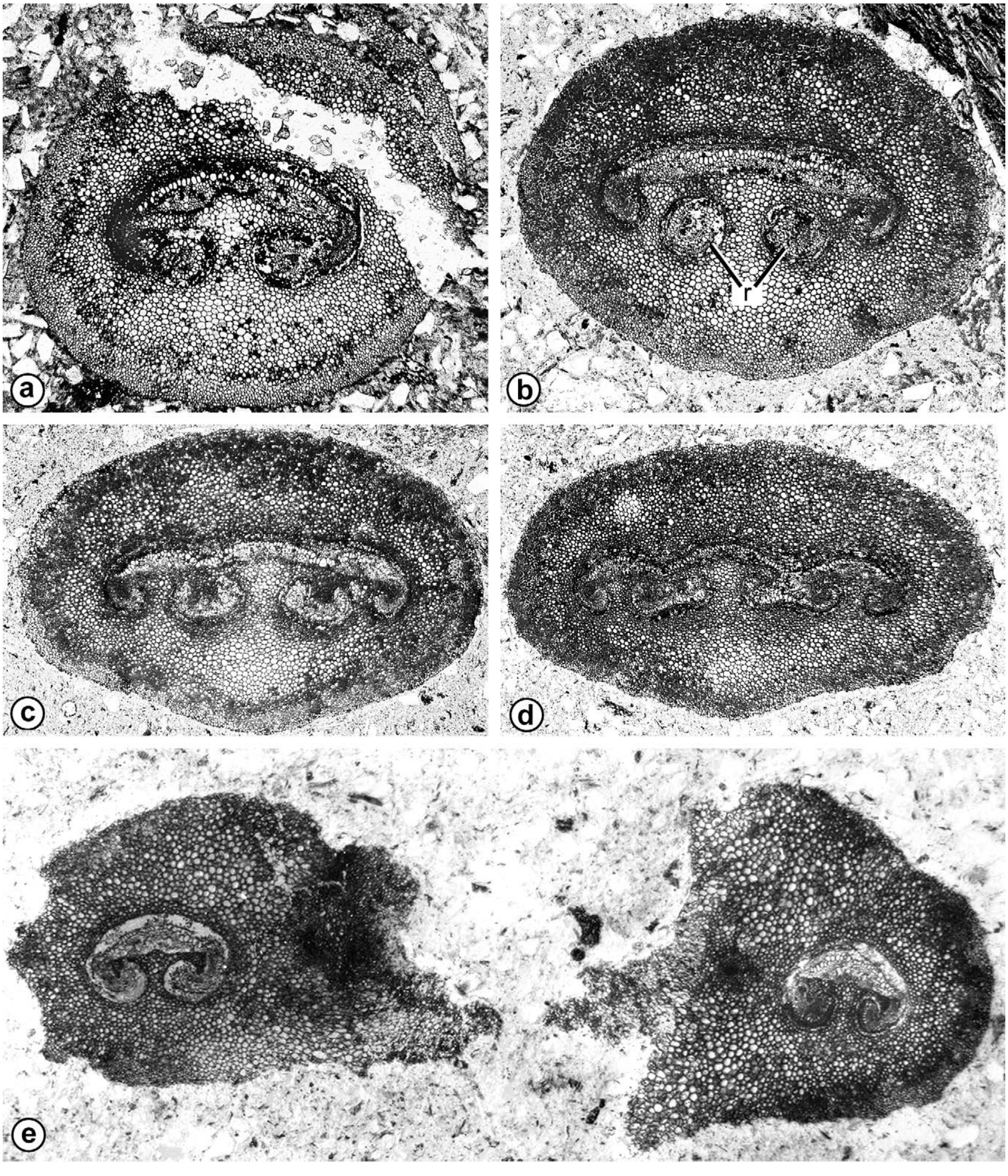

Fig. 3 Transverse sections showing branching of gleicheniaceous fronds. *a*, Base of frond segment, showing single trace with adaxial rings of vascular tissue forming at hooks of C-shaped trace. AW 503 C2 top 7, ×30. *b*, Frond segment distal to *a* with two free adaxial rings (*r*) and abaxial arc with adaxial hooks. AW 503 C top 171, ×33. *c*, Adaxial rings of vascular tissue open on abaxial side, coincident with indentations of abaxial arc. AW 503 C top 42, ×21. *d*, Section distal to *c*, showing fusion of three-lobed abaxial arc with tissue of flattened remnants of adaxial rings and proximal to the level shown in fig. 2*h*. AW 503 C top 2, 18. *e,* Transverse section through frond at point above bifurcation, showing two separate axes both with angular C-shaped trace. AW 503 B bot 0, ×24.

their abaxial side, coincident with the development of two constrictions on the abaxial arc (fig. 3*c*). At the level of constriction, the xylem of the abaxial arc unites with the abaxial side of the xylem of the remnant rings (fig. 3*d*). Distal to this level, the trace divides to produce three separate bundles (fig. 3*d*). In both branching specimens, only two of the resulting pinnae persist (fig. 3*e*). In each specimen, the central segment truncates and terminates as incompletely preserved tissue.

Discussion

Rhizomes with vitalized protosteles occur in several fern families, most notably in the basal leptosporangiate ferns (Bower 1926; Ogura 1972). Anatomical studies of Gleicheniaceae (Boodle 1901*b*), Schizaeaceae (Boodle 1901*a*), Hymenophyllaceae (Boodle 1900), and Cheiropleuriaceae (Bower 1915) have revealed protosteles that differ from family to family. *Lygodium* Sw., the only protostelic genus in Schizaeaceae, shows a round cylinder of xylem with exarch maturation and indistinct protoxylem strands (table 1). By contrast, the Appian Way rhizome shows distinct marginally mesarch protoxylem strands. The leaf trace in *Lygodium* diverges as a solid cylinder (Boodle 1901*a*) as opposed to the arc of xylem-enclosing sclerenchyma that characterizes the frond trace in the Appian Way rhizome.

The Hymenophyllaceae has several protostelic genera that were formerly grouped in the genus *Trichomanes* L. (Ogura 1972; Dubuisson 1997). Like those of *Lygodium*, the rhizomes of these taxa are characterized by exarch primary-xylem maturation, but the leaf trace diverges as a hollow cylinder of xylem that encloses sclerenchyma (table 1; Boodle 1900). In the Appian Way fern, the leaf trace appears as an arc of xylem with a nodal island that opens up into the characteristic C-shaped trace as it diverges from the stele (table 1). Like the Appian Way rhizome, *Cheiropleuria* Nakai has mesarch primary-xylem maturation, but the protoxylem strands are indistinct, and the leaf trace diverges as a solid cylinder that rapidly dichotomizes as it leaves the stele (Bower 1915).

The Appian Way rhizome is most similar to species of Gleicheniaceae. This family is composed exclusively of protostelic forms except for one solenostelic species, *Dicranopteris pectinata* (Willd.) Underw. (Boodle and Hiley 1909; Ogura 1972). All other described gleicheniaceous species also have characters in common with the Appian fern. In the subfamily Stromatopteroideae, *Stromatopteris monofilaformis* Mett. (the sole representative of the genus) is similar in stelar construction to the Appian Way fern except that tracheid chains are significantly longer (≥ 5), and in this species there are no obvious protoxylem strands (table 1; Bierhorst 1969, 1971).

The remaining four gleicheniaceous genera, *Diplopterygium* Nakai, *Sticherus* C. Presl, *Gleichenia* J.E. Smith, and *Dicranopteris* Bernhardi (subfamily Gleichenioideae), have been subject to substantial taxonomic revision (Holttum 1957; Tryon and Tryon 1982; Kramer 1990), with most authors recognizing *Diplopterygium* and *Sticherus* as subgenera within *Gleichenia*. Rhizomes of these protostelic taxa have an inner cortex of thick-walled cells and relatively thin-walled cells in the outer cortex. Like those of *Gleichenia appianensis*, steles of these species are small, with obvious protoxylem strands, marginally mesarch xylem maturation, and protoxylem strands varying in number from 5 to 15 (table 1; Ogura 1972).

Dicranopteris has similar stelar construction to *G. appianensis*, but the frond trace diverges as a hollow cylinder rather than an arc (table 1; Boodle 1901*b*; Ogura 1972). There has been some confusion about this, because *Dicranopteris dichotoma* (Thunb. ex Murray) Willd. is a synonym of *Dicranopteris pedata* (Houtt.) Nakaike, which Boodle originally figured as *Gleichenia dichotoma* Willd. and Ogura figured as *D. dichotoma*. In *Diplopterygium* the stele is unlobed, and Ogura (1972) shows 11 protoxylem strands, a number far greater than the five to six observed in *G. appianensis* (table 1). In *Sticherus flabellatus* (R. Br.) H. St. John (figured by Boodle as *Gleichenia flabellata* Br.; table 1), the frond trace diverges as an arc of xylem enclosing a nodal island, as in *G. appianensis* (Boodle 1901*b*; Bierhorst 1971). However, the stele is unlobed, and Boodle (1901*b*) shows 14 protoxylem strands.

Table 1

Comparison of Appian Rhizome Stelar Anatomy and Leaf-Trace Divergence to Extant Fern Genera with Ectophloic, Protostelic Rhizomes

Family and genus	Primary-xylem maturation	Protoxylem groups	Stele lobed	Leaf-trace divergence
Schizaeaceae:				
Lygodium	Exarch	Indistinct	No	Solid cylinder of xylem
Hymenophyllaceae:				
Trichomanes s.l.	Exarch	Indistinct	No	Hollow cylinder of xylem
Dipteridaceae:				
Cheiropleuria	Mesarch	Indistinct	No	Dichotomizing solid cylinder of xylem
Gleicheniaceae:				
Stromatopteris	Marginally mesarch	Indistinct	Yes	Solid cylinder of xylem
Dicranopteris	Marginally mesarch	Distinct (5–15)	Yes	Hollow cylinder of xylem
Diplopterygium	Marginally mesarch	Distinct (11)	No	Arc of xylem enclosing sclerenchyma
Sticherus	Marginally mesarch	Distinct (14)	No	Arc of xylem enclosing sclerenchyma
Gleichenia	Marginally mesarch	Distinct (5–15)	Yes	Arc of xylem enclosing parenchyma
Appian Rhizome	Marginally mesarch	Distinct (5–6)	Yes	Arc of xylem enclosing sclerenchyma

Sources. Data from Boodle (1900, 1901*a*, 1901*b*); Bower (1915); Chrysler (1943); Bierhorst (1969, 1971); Ogura (1972).

As in *G. appianensis*, living species of *Gleichenia* s.s. have a lobed stele with 5 to 15 protoxylem strands and a frond trace that diverges as an arc of xylem enclosing a nodal island (table 1; Boodle 1901*b*; Ogura 1972). Our specimen is most similar to *Gleichenia dicarpa* R. Br. (=*Gleichenia circinnata* Sw.) as illustrated by Boodle (1901*b*) and Ogura (1972). This species has five protoxylem strands, a lobed stele, and a similar mode of leaf-trace divergence (Ogura 1972). The nodal island formed in *G. dicarpa* is parenchymatous (Ogura 1972), while that of the Appian Way rhizome is sclerenchymatous.

The presence of planar septa in the long metaxylem tracheids of the frond trace of *G. appianensis* is a feature unknown in extant *Gleichenia*. However, such septa probably represent tyloses, which have been observed in the stipes of numerous fern families (Ogura 1972) and specifically in the protoxylem of *Gleichenia* (Chrysler 1943).

The fossil record of Gleicheniaceae has been reviewed by several authors (Tidwell and Ash 1994; Collinson 1996, 2001, 2002; Skog 2001). Remains are predominantly compression/impressions and are described from as far back as the Permian (Yao and Taylor 1988). The fossil record of North American Gleicheniaceae begins in the Triassic, with spores from eastern North America (Cornet and Traverse 1975), fertile frond compressions and spores from New Mexico (Ash 1969), and fronds from Virginia (Cornet and Olsen 1990). While Cretaceous compression records are abundant (Andrews and Pearsall 1941; Rushforth 1971; Crabtree 1988; Wing et al. 1993; Skog and Dilcher 1994), Tertiary remains of any sort are scarce worldwide (Tidwell and Ash 1994; Collinson 2001).

Anatomically preserved rhizomes of Gleicheniaceae are rare in the fossil record. *Antarctipteris sclericaulis* Millay and Taylor (1990), a rhizome from the Triassic of Antarctica, was suggested to have gleicheniaceous affinities based on its mixed protostele, simple frond trace, and scalariform tracheids. Unlike *G. appianensis*, the Antarctic specimens lack any clear protoxylem strands in the stele (Millay and Taylor 1990). *Antarctipteris sclericaulis* also has axially elongate sclerenchyma strands surrounding the stele and bar-shaped leaf traces (Millay and Taylor 1990) that do not occur in *G. appianensis*.

Gandolfo et al. (1997) described the charcoalified remains assignable to Gleicheniaceae from the Turonian (Late Cretaceous) of New Jersey. Rhizomes with attached frond bases of *Boodlepteris turoniana* Gandolfo have a dorsiventral protostele without distinguishable protoxylem strands (Gandolfo et al. 1997), while the protoxylem strands in *G. appianensis* are distinct and there is no evidence of dorsiventrality.

Thus, we have placed the Appian rhizome in a new species, *G. appianensis* Mindell, Stockey, Rothwell et Beard sp. nov. Of those extant species of *Gleichenia* studied anatomically, *G. appianensis* is most similar to *G. dicarpa*. It should be noted that while a few species of all gleicheniaceous genera have been studied in anatomical detail, there are a large number of species that have not been sectioned. Nevertheless, with the current body of literature, the anatomical distinctions between the gleicheniaceous genera seem to be clear (table 1).

The numerous associated frond segments known from the Appian Way could be those of *G. appianensis*; however, they have not been found in attachment. The infolded, angular C-shaped traces with characteristic constrictions are indicative of the Gleicheniaceae, as is the pseudodichotomous branching (Chrysler 1943, 1944; Ogura 1972). The latter clearly represent fronds that follow the same branching sequence as that described for *Sticherus intermedius* (Bak.) Chrysler (Chrysler 1943, 1944). While the bifurcating frond in Gleicheniaceae appears superficially to be an even dichtomomy, a central terminal or dormant bud occurs between the lateral axes. Histological studies through this region show that the lateral traces diverge from the margins of the central trace, the latter persisting in the form of a bud and, thus, the pseudodichotomy (Chrysler 1943).

Permineralized frond segments are known from the Mesozoic. These are all placed in Gleicheniaceae based on the characteristic C-shaped trace and, sometimes, the fertile structures that are present. Phipps et al. (2000) assign *Gleichenipteris antarcticus* to the family based on sporangial shape and arrangement and point to a close association with rachides of *Antarctipteris sclericaulis* (Millay and Taylor 1990). It should be noted, however, that *A. sclericaulis* lacks the characteristic C-shaped trace near the level of stipe divergence from the rhizome.

Sharma and Bohra (1977) describe gleicheniaceous stipes from the Jurassic Rajmahal Hills of India. These show the constricted, infolded, C-shaped trace observed in many extant species of *Gleichenia* (Chrysler 1944). Gandolfo et al. (1997) described charcoalified fertile frond remains that gave enough characters to place *Boodlepteris turoniana* within the Gleicheniaceae as a sister group to *Stromatopteris* in a cladistic analysis based on morphological and anatomical characters. The trace in these fossil fronds is C-shaped with two visible endarch protoxylem strands and is surrounded by a cortex of thick-walled sclerenchyma. The stipe traces associated with *G. appianensis* are superficially similar to those of *Boodlepteris* in that they have endarch xylem maturation and scalariform metaxylem tracheids, but they differ from the Appian Way stipes in having numerous protoxylem strands and a cortex that is typically parenchymatous toward the trace and sclerenchymatous toward the periphery of the stipe. Branching of the fronds in *Boodlepteris turoniana* was observed only externally and suggests that branching was either dichotomous or pseudodichotomous (Gandolfo et al. 1997). Branching in *G. appianensis* fronds is preserved anatomically and clearly shows a pseudodichotomous pattern, as illustrated by Chrysler (1943) for a living gleicheniaceous species.

Gleichenia chaloneri Herendeen et Skog (1998) has been described from fusainized frond segments from the early Cretaceous (Albian) of Bedfordshire, England. These frond fragments have a C-shaped trace with incurved arms and 7–8 protoxylem strands. Like the Appian Way frond remains, sclerenchyma immediately surrounds the vascular tissue. Histology of the branching regions is not known in the branching specimens described by Herendeen and Skog (1998), but they are similar in most respects to our isolated stipes and rachides.

The specimens described in this article are the only Tertiary macrofossils of the Gleicheniaceae thus far described from the New World, and they provide direct evidence for Gleicheniaceae in the Eocene of North America. In addition to the vegetative remains described in this article, spores of *Gleicheniidites* Ross have also been identified from the Appian Way locality by Sweet (1997). Biogeographic reviews of the ferns (Tidwell and Ash 1994; Collinson 2001, 2002; Skog 2001) all point to the poor worldwide record of Gleicheniaceae in the Tertiary. The family is well represented in North America in the Triassic (Tidwell and Ash 1994) and Cretaceous (Berry 1922; Andrews and Pearsall 1941; Rushforth 1971; Crabtree 1988; Skog and Dilcher 1994; Gandolfo et al. 1997). However, in addition to some spore records and ambiguous compressions known from Europe and South America (Collinson 2001), clear Tertiary records are known only from the Eocene of southeast England (Holttum 1957) and the Oligocene of Australia (Blackburn and Sluiter 1994). Today, the family's Northern Hemisphere distribution is restricted to tropical and subtropical latitudes (Tryon and Tryon 1982).

The branching frond segments described here from Appian Way represent the first anatomically preserved bifurcating leaves of Gleicheniaceae in the fossil record, and they demonstrate that the pseudodichotomous branching pattern of Gleicheniaceae was established by at least the early Tertiary. The presence of anatomically preserved rhizomes, fronds, and spores confirms that this long-lived family persisted at the northwestern margin of the North American continent at least until the Eocene.

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