Int. J. Plant Sci. 167(3):683–694. 2006.

1058-5893/2006/16703-0029$15.00

STRAMINEOPTERIS AUREOPILOSUS GEN. ET SP. NOV.: REEVALUATING THE ROLE OF VEGETATIVE ANATOMY IN THE RESOLUTION OF LEPTOSPORANGIATE FERN PHYLOGENY

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The discovery of two anatomically preserved rhizomes with attached stipe bases and adventitious roots contributes to our knowledge of filicalean fern diversity and evolution. Specimens are preserved in marine carbonate nodules at the Lower Cretaceous (Valanginian to Hauterivian) Apple Bay locality on Vancouver Island, British Columbia, Canada. They represent a previously unknown filicalean fern with transitional solenostelic-dictyostelic stelar architecture and are described as *Stramineopteris aureopilosus* gen. et sp. nov. Rhizomes range from 2.5 to 5.5 mm in diameter and are amphiphloic. Arc-shaped leaf traces display a slightly asymmetrical divergence pattern and radiate from all sides of the stele. Primary xylem maturation is exarch. Multicellular trichomes are present throughout but are produced in greater numbers at rhizome dichotomies. Both pith and cortex are of a distinctive heterogeneous construction. A comparison of this distinctive combination of characters to previously described fern rhizomes reveals that vegetative anatomy may be more taxonomically diagnostic for a broader range of ferns than is commonly thought. This realization provides the impetus to explore more closely the distribution of several anatomic characters among leptosporangiate ferns and to reexamine the value of vegetative anatomy for developing a clearer understanding of fern systematics.

Keywords: fern, filicalean systematics, fossil, Grammitidaceae, Pteridaceae.

Introduction

The fossil record of anatomically preserved Mesozoic ferns is dominated by large tree ferns (i.e., Cyatheaceae s.l.; Tidwell and Nishida 1993; Tidwell and Ash 1994; Lantz et al. 1999; Smith et al. 2003; Stockey and Rothwell 2004) and by Osmundaceae and its related extinct families (Tidwell and Ash 1994; Serbet and Rothwell 1999; Smith and Stockey 2000; Skog 2001; Rothwell et al. 2002). Relatively large size, distinctive stelar architecture, characteristic frond-trace patterns, sclerotic tissues, persistent leaf bases, and adventitious root mantles of these plants increase preservation potential and provide numerous characters for identification. By contrast, small anatomically preserved leptosporangiate fern rhizomes that represent other filicalean families are underrepresented in the fossil record (Collinson 2001; Skog 2001) and are often much more difficult to place systematically (Serbet and Rothwell 2006).

As a result of explorations for new sources of permineralized fossil plants over the past several years, an expanding body of information about anatomically preserved leptosporangiate ferns is emerging from Mesozoic and Tertiary deposits in western North America (Serbet and Rothwell 1999, 2003, 2006; Stockey et al. 1999, 2006; Smith and Stockey 2000; Pigg and Rothwell 2001; Hernandez-Castillo et al. 2006; Karafit et al. 2006; Mindell et al. 2006; Rothwell and Stockey 2006; Smith et al. 2006; Vavrek et al. 2006), and these studies are providing a growing body of systematic data for addressing questions about the pattern, mode, and tempo of fern evolution.

In this article we describe an additional anatomically preserved rhizomatous filicalean, *Stramineopteris aureopilosus* gen. et sp. nov., from specimens collected at the Lower Cretaceous Apple Bay locality on Vancouver Island, British Columbia, Canada. The distinctive rhizome and stipe anatomy of *Stramineopteris* is compared to that in families of extant Filicales and to the vegetative structure of other fossil and living siphonostelic-dictyostelic ferns. Systematically informative anatomical characters of filicalean vegetative anatomy are reviewed, and the growing role of such characters for addressing familial relationships among the Filicales is elaborated.

Material and Methods

Specimens are preserved in carbonate marine nodules collected from the Apple Bay locality in Quatsino Sound, Vancouver Island, British Columbia (50°36′21″N, 127°39′25″W; UTM 9U WG 951068; Smith et al. 2003, 2004). The nodules are embedded in a fine-grained, carbonate-cemented graywacke matrix and contain both permineralized plants and invertebrate remains. These sediments are Lower Cretaceous Longarm Formation equivalents (Jeletzky 1976; Haggart and Tipper 1994) and correspond to Jeletzky's (1976) Barremian variegated clastic unit (Sweet 2000). Such deposits have been considered to be Valanginian to Barremian based on palynological data (Sweet 2000), but recent isotope stratigraphy of

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Manuscript received June 2005; revised manuscript received January 2006.

the Apple Bay section places the site at the Valanginian-Hauterivian boundary (D. R. Gröcke, personal communication, 2005).

The nodules were cut into slices and prepared using the cellulose acetate peel technique (Joy et al. 1956). Sections of peels were mounted in Eukitt xylene soluble mounting medium (O. Kindler, Freiburg, Germany) on glass slides for light microscopy. Photographs were taken using a Phase One digital scanning camera (Frederiksberg, Denmark) mounted on a Leitz Aristophot bellows camera. Images were processed with Adobe Photoshop. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada. Family circumscriptions follow those of Kramer and Green (1990).

Systematics

Order—Filicales

Family—Incertae sedis (?Pteridaceae s.l.)

*Genus—*Stramineopteris *gen. nov.*

*Species—*Stramineopteris aureopilosus *sp. nov. (Figs. 1–3)*

Generic diagnosis. Transitional solenostelic-dictyostelic fern rhizomes with stipes and adventitious roots diverging from all sides. Stele amphiphloic, exarch, with first-formed metaxylem strands protruding from outer surface of metaxylem; endodermis well differentiated. Frond trace with single arc-shaped xylem strand proximally, dividing into several strands in rachis; partially surrounded by abaxial C-shaped inner cortical zone; epidermis with multicellular trichomes. Roots diarch with thick-walled cortex and smaller-celled hypodermis.

Specific diagnosis. Characters of species as described for genus. Rhizomes 2.5–5.5 mm in diameter. Trichomes uniseriate throughout or with multiseriate bases; some multiseriate bases wide, inflated. Cortex broad, prominently zoned; cells of outer zone thick walled, polygonal with outermost one to three layers forming hypodermal cells with dark contents; inner cortex narrow, cells smaller, thin walled. Metaxylem of stelar cylinder one to three tracheids thick, infrequently interrupted by xylem parenchyma; first-formed metaxylem tracheids smaller, comprising discrete strands up to four cells thick. Stele surrounded by distinct uniseriate outer and inner endodermis with well-differentiated casparian strips; leaf traces also surrounded by endodermis. Outer pith narrow band of thin-walled cells; central pith cells larger, polygonal, with thicker walls. Stipe ground tissue three zoned; C-shaped abaxial zone of thin-walled cells with thickened corners partially surrounding endodermis containing somewhat angular arc-shaped trace; outermost zone with extremely thick, dark walls; cells of remaining ground tissue larger, polygonal, with thick walls.

Etymology. Stramineus = "straw colored"; *pteris* = "fern"; *aureo* = "golden"; *pilosus* = "hairy." The ground tissues in the fossils are a yellow, straw color. In addition, the numerous appressed trichomes share this color; thus, "straw colored, golden-haired fern."

Holotype. P13036 G bot, H top; deposited in UAPC-ALTA (fig. 1*a*, 1*b*; figs. 2, 3*g*).

Paratype. P13255 B bot, C top, C bot; deposited in UAPC-ALTA (fig. 1*c*, 1*d*; fig. 3*a*–3*f*).

Locality. Apple Bay, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic occurrence. Longarm Formation equivalent.

Age. Valanginian-Hauterivian boundary, Neocomian epoch, Early Cretaceous.

General description. Rhizomes have a large pith, broad cortex, and thin stelar cylinder. The stele shows no leaf gaps at some levels (fig. 1*b*) and up to three leaf gaps at other levels (fig. 1*a*, 1*d*). Therefore, *Stramineopteris* displays a stelar architecture that is transitional solenostelic-dictyostelic. Stipes and adventitious roots diverge from all sides of the rhizome (fig. 1). The holotype is a dichotomizing rhizome (fig. 1*a*, 1*b*), 5.5 mm in maximum diameter, with abundant multicellular trichomes, particularly at the level of branching (fig. 1*a*, 1*b*; fig. 2*a*). One of the branches is smaller than the other (fig. 1*a*, top) and is quite short. After producing only a few stipes and roots (fig. 1*a*, upper left), this smaller branch terminates in a conical apex covered with dense indument (fig. 1*b*, *B*). The larger branch (fig. 1*a*, 1*b*, bottom) extends distally as a mature rhizome (figs. 1*b*, 2*a*). The paratype is an unbranched segment of rhizome 2.5 mm in diameter at the proximal end (fig. 1*c*) and up to 4.5 mm in diameter distally (fig. 1*d*).

In cross sections, both rhizomes typically have angular outlines with rounded corners (fig. 1). They display radial symmetry by virtue of both stelar architecture and the production of frond and root traces around the entire circumference of the rhizomes (fig. 1). Stipes either are broken off at the periphery of the rhizomes or extend only a short distance into the matrix (fig. 1*a*, 1*b*). However, basal stipe anatomy is often well preserved (fig. 3*a*, 3*d*). Root traces diverge radially from first-formed metaxylem strands of the stelar cylinder, traverse the phloem and endodermis, and extend to the periphery of the cortex. Many roots are broken off at the periphery of the rhizome (fig. 1*d*, arrows), but others extend out into the matrix (fig. 1*a*, arrows), revealing the histology of roots beyond the cortex of the rhizome (fig. 3*g*).

Pith. The pith is differentiated into two zones of compact cells, lacking prominent intercellular spaces. The inner pith consists of uniformly thick-walled polygonal cells (fig. 2*f*). In transverse sections, cells toward the center of the pith sometimes appear different from those toward the periphery (fig. 1). This appearance is the result of more prevalent degradation of the central cells (figs. 1, 2*f*). The outer pith zone is composed of a narrow layer in which the cells are often incompletely preserved (fig. 1; fig. 3*b*, 3*c*). Where preserved, the outer pith cells are smaller and have thinner walls than those in the central region (fig. 2*f*, arrowhead at bottom).

Stele. Stelar organization of the rhizomes varies from solenostelic to dictyostelic (figs. 1, 2*f*). The number of gaps seen in a single cross section ranges from none (fig. 1*a*, top; fig. 1*b*) to one (fig. 1*c*) to two or three (fig. 1*a*, bottom; fig. 1*d*), thus accounting for the transition. The stele is usually represented by tracheids of the xylem that are often surrounded by an empty space that represents the position of phloem and possible pericycle (fig. 1; fig. 2*c*, 2*f*). The latter is enclosed by a distinct endodermis (fig. 1; fig. 2*b*, 2*c*). In transverse sections, the xylem cylinder shows an undulating appearance

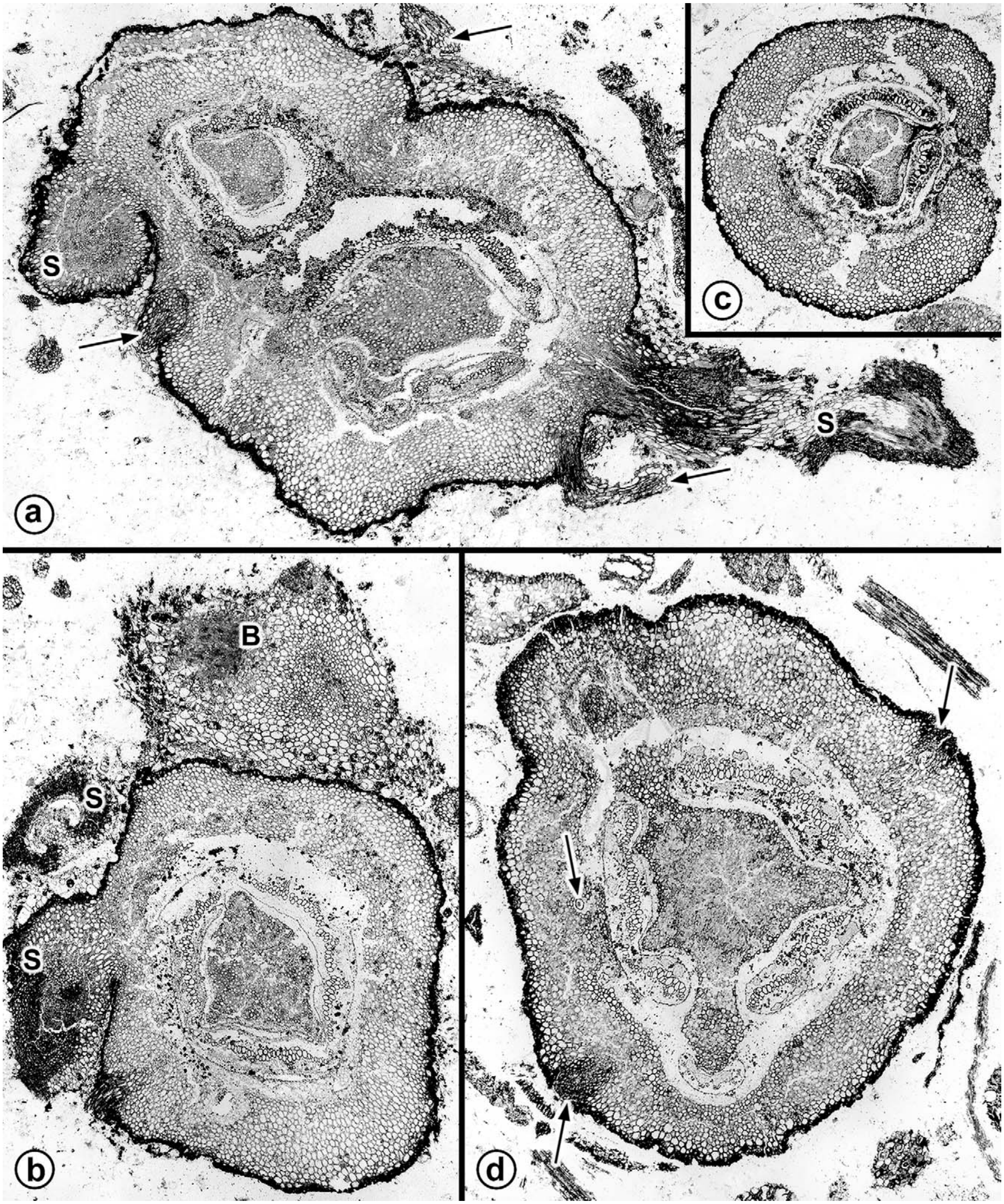
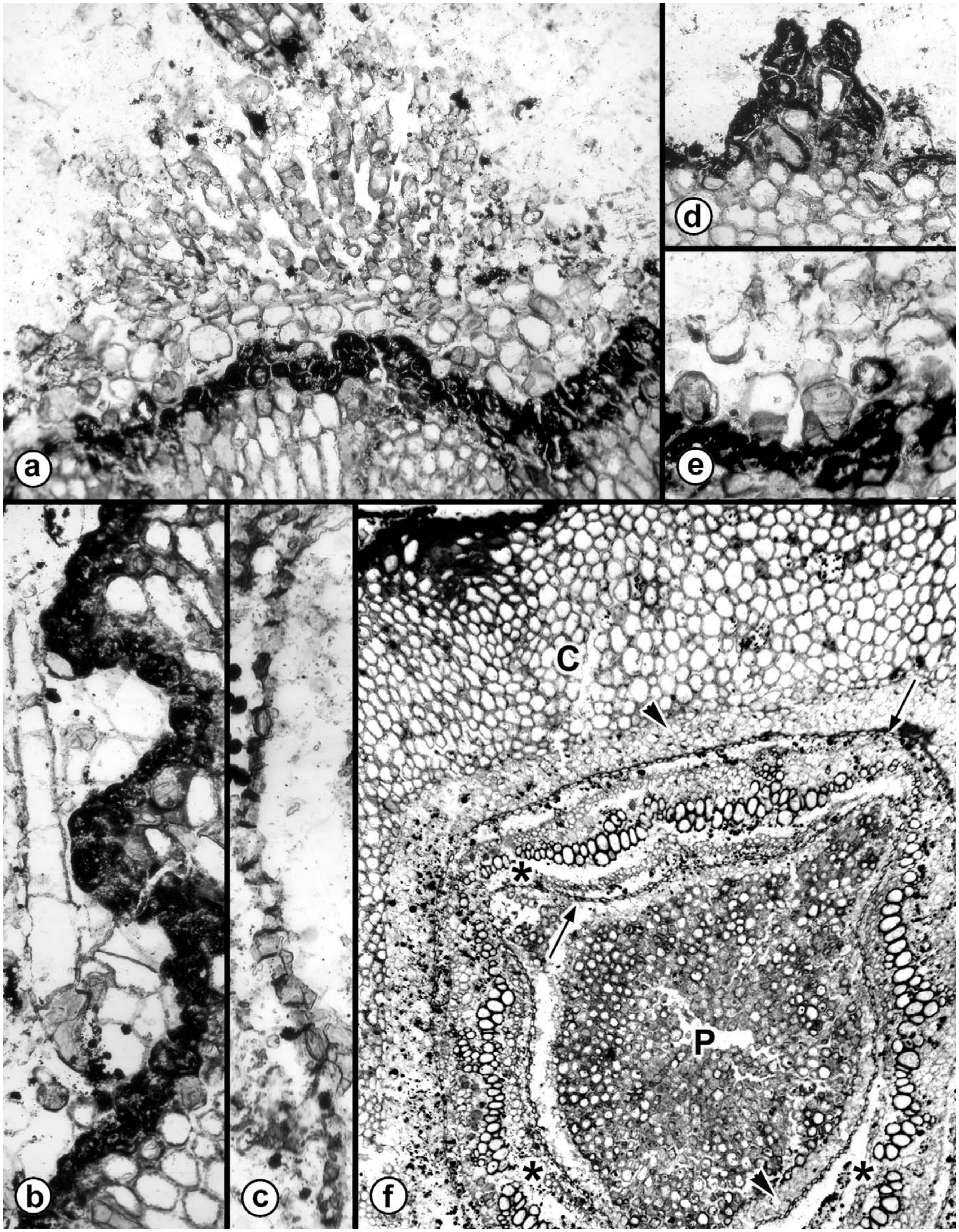


Fig. 1 *Stramineopteris aureopilosus* gen. et sp. nov. All images ×21. *a*, Cross section of branching rhizome showing general features of pith, stele and cortex, and divergence of stipes and roots (arrows). Note that larger branch is dictyostelic, smaller branch (top) solenostelic. Dark region at rhizome periphery represents narrow hypodermis. Holotype P13036 H top 1. *b*, More distal level of branching rhizome, where larger branch forms undulating solenostele and smaller branch (*B*) terminates as apex. Two stipes at left with ramentum of trichomes surrounding branch apex and stipes (*S*). Holotype P13036 G bot 3. *c*, Cross section at proximal end of paratype, showing solenostele with leaf gap, at right. P13255 C bot 50. *d*, Cross section of dictyostelic region of rhizome with diverging stipe traces and root bases (arrows). Paratype P13255 C top 24.


a
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(figs. 1, 2*f*). This results from the divergence of leaf traces, not from the incurving of stele segment margins.

Cauline xylem consists of large-diameter metaxylem tracheids one to four cells thick and peripheral bundles of smaller tracheids (figs. 1, 2*f*; fig. 3*b*, 3*c*). Within the stelar cylinder, the metaxylem tracheids are not fully contiguous. Rather, chains of tracheids (figs. 1, 2*f*) are separated by narrow spaces that represent the positions of thin-walled xylem parenchyma cells (fig. 2*f*, asterisk). Metaxylem tracheids range from 15 to 57 μm in diameter and have scalariform secondary wall thickenings.

The peripheral groups of smaller-diameter tracheids are one to four cells thick (figs. 1, 2*f*) and protrude from the outer surface of the xylem cylinder. These small tracheids are 6–15 μm in diameter and have scalariform wall thickenings. Therefore, they are first-formed metaxylem, rather than protoxylem (Bierhorst 1971). Cauline protoxylem has not been observed and was probably not produced. In some sections, cells of the xylem parenchyma, phloem, and possibly pericycle are also preserved (fig. 2*f*). All of these cells are thin walled and can be differentiated from each other only by their positions within the stele.

A prominent uniseriate endodermis delimits the stele, both to the inside and the outside of the vascular tissues (figs. 1, 2*f*; fig. 3*b*, 3*c*), and surrounds the diverging root and leaf traces (fig. 1*d*, arrow; fig. 3*a*–3*f*). Cells of the endodermis are uniformly contiguous and typically display a distinct dark-colored wall (fig. 2*f*, arrows). Higher magnification reveals that the contiguous anticlinal walls of adjacent endodermal cells are much thicker and darker than the inner and outer cell walls (fig. 2*c*) and represent casparian strips like those that characterize the endodermis in many living pteridophytes.

Cortex. The rhizome cortex is differentiated into two zones that are disrupted at intervals by the divergence of root traces (figs. 1, 2*f*). Cortical cells are tightly packed and show no obvious intercellular spaces (fig. 2*f*). There is a broad outer cortex composed of polygonal thick-walled cells that probably represent sclerenchyma, as well as a narrow inner cortex (fig. 2*f*). Cells of the inner cortex are often degraded or missing (fig. 1*a*–1*d*) but are present in several regions of the rhizomes (fig. 2*f*), where they are nearly identical to those of the outer pith (cf. arrowheads in fig. 2*f*). At the periphery of the outer cortex, two or three layers of cells have their lumens occluded by dark material, forming a distinct hypodermis (fig. 1; fig. 2*a*, 2*b*, 2*d*, 2*e*).

The periphery of the cortex often shows a wavy outline (fig. 1; fig. 2*a*, 2*b*) that is accentuated by the dark color of the hypodermis (fig. 2*a*, 2*b*). In some areas, the hypodermal cells extend from the surface as blunt projections (fig. 2*d*) that look like bumps on the surface of the rhizome (fig. 1). Such cortical projections typically extend through several sections and would appear as ridges or warts in surface view. These structures are most abundant where stipes diverge from the rhizome.

Epidermis and trichomes. Trichomes clothe the rhizome, particularly at the apex, at levels of branching and at levels where stipes diverge (fig. 1*a*, 1*b*). Otherwise, epidermal cells are not well preserved at the surface of the cortex (fig. 2*b*, 2*d*, 2*e*). In cross sections, trichomes are usually oriented obliquely (fig. 2*a*, 2*b*). This probably results from the trichomes being appressed to the surface of the rhizome. Trichomes are multicellular (fig. 2*a*, 2*b*, 2*e*) and either are uniseriate throughout (fig. 2*e*) or have multiseriate bases and are uniseriate distally (fig. 2*b*). Broad-based multicellular trichomes occur most commonly on the rhizome (fig. 2*b*), whereas uniseriate trichomes characterize the stipe bases (fig. 2*a*). Occasionally, trichomes also occur on cortical projections.

Frond bases. Although most fronds are broken off at the periphery of the rhizome, a few extend unbranched for a few centimeters into the matrix (fig. 1*a*, 1*b*) and show relatively well-preserved anatomical features (fig. 3*a*, 3*d*). Stipes consist of an arc-shaped vascular bundle that is surrounded by distinctive cortical tissues. In cross sections, the stipes are oval, wider than high (fig. 1*a*, 1*b*; fig. 3*a*, 3*d*), and ca. 0.9–1.3 mm in maximum dimension. Blunt lateral protrusions extend from one or both sides of some stipes (fig. 1*b*; fig. 3*a*, 3*d*), suggesting that frond bases may have been narrowly winged.

At first glance, the frond trace appears to be C shaped (fig. 1*b*; fig. 3*a*, 3*d*), but closer examination reveals that the “C” (fig. 3*a*) is actually cortical tissue that occurs on the abaxial side of the frond trace and wraps around the lateral margins of the arc-shaped bundle (fig. 3*d*, *Tr*). The xylem bundle of the frond trace is most easily seen in the cortex of the rhizome, where it consists of a thin xylem strand (fig. 3*f*) with up to four apparent protoxylem bundles of small tracheids (fig. 3*e*). However, tracheids of these bundles typically display scalariform wall thickenings, so they actually represent first-formed metaxylem, like the bundles at the exterior of the stele. Within the best-preserved stipes, and sometimes also in the outer cortex, tracheids are differentiated only in the regions of the first-formed metaxylem (fig. 3*e*, arrows). Therefore, the xylem consists of several distinct bundles that are surrounded by thin-walled cells that probably represent phloem (fig. 3*d*, *Tr*). The periphery of the frond trace is delimited by a distinct, uniseriate endodermis (fig. 3*a*) that compares favorably with that of the rhizome.

Fig. 2 *Stramineopteris aureopilosus* gen. et sp. nov. All images show holotype P13036. *a*, Tuft of dense trichomes in oblique cross section, showing crowded bases and uniseriate distal regions. Note lumens of hypodermal cells occluded with dark material. H top 88; ×104. *b*, Longitudinal section through trichome with multicellular base and uniseriate apex; undulations of dark outer cortical cells forming projections, at right. H top 80; ×145. *c*, Closely appressed cells of uniseriate endodermis showing dark, thickened anticlinal walls of casparian strips. G bot 4; ×333. *d*, Longitudinal section through outer cortical projection. Note lumens of hypodermal cells with dark material. G bot 93; ×112. *e*, Dense uniseriate trichome bases attached to dark hypodermal cells at periphery of cortex. H top 103; ×190. *f*, Cross section of rhizome showing amphiphloic, exarch stele. Well-preserved ground tissue zones include wide outer cortex and central pith region of thick-walled cells and narrower zones of thin walled cells (arrowheads) at inner cortex and pith periphery. Uniseriate external and internal endodermis (arrows) define limits of stele. Note xylem parenchyma (asterisk) produces discontinuities in cylinder of tracheids. G bot 51; ×61. C = cortex; *P* = pith.

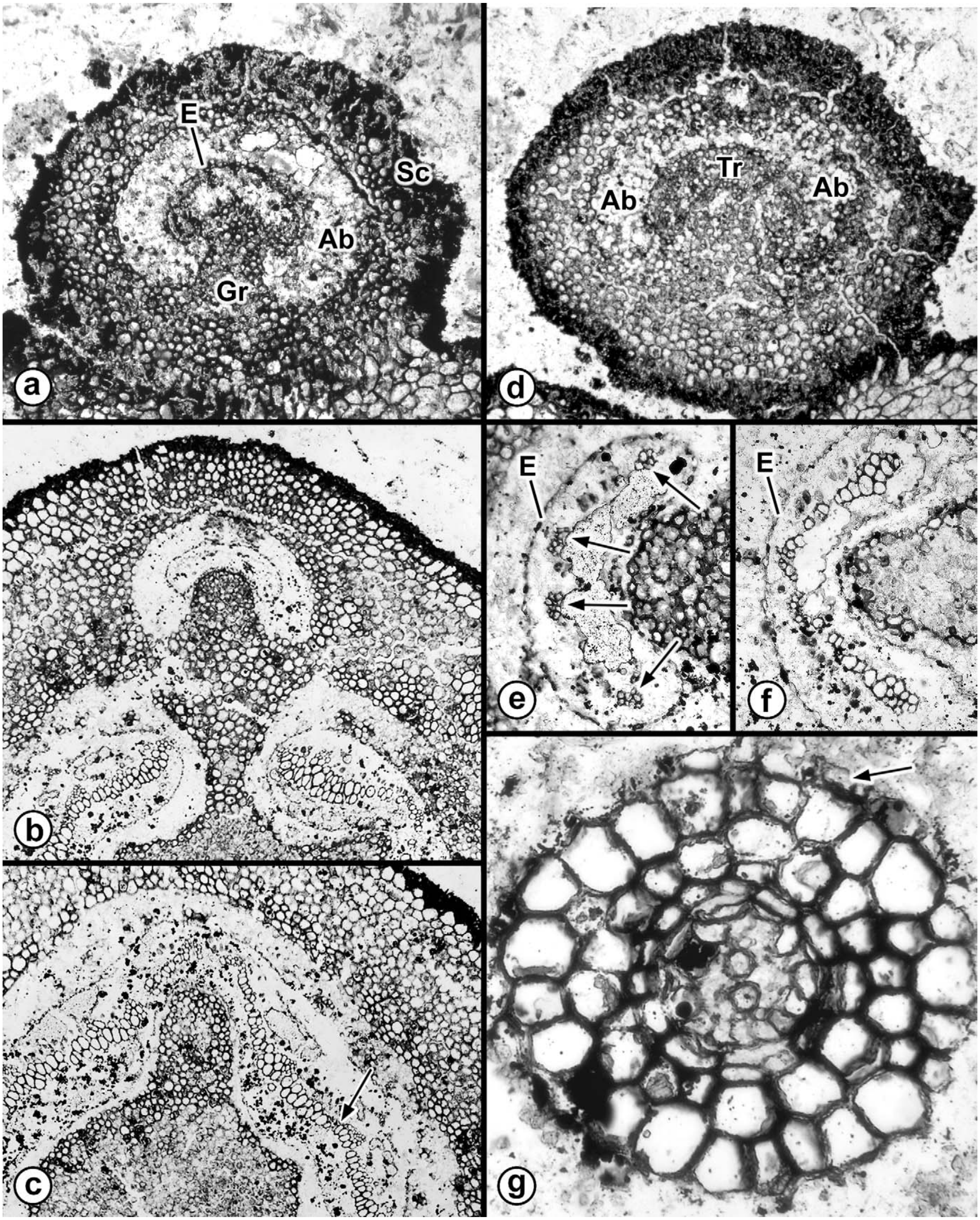


Fig. 3 *Stramineopteris aureopilosus* gen. et sp. nov. *a*, Cross section through stipe proximal to level of separation from rhizome. Note prominent C-shaped zone of inner ground tissue (*Ab*) bending around arc-shaped leaf trace bounded by endodermis (*E*). Zone of sclerotic ground

Ground tissues of the stipe form three zones and lack obvious intercellular spaces. Small-diameter cells with prominently thickened walls and dark internal contents form a peripheral zone that is at least four cells thick (fig. 3*a*, 3*d*). This peripheral zone of sclerenchyma becomes apparent at the level of stipe separation from the rhizome (fig. 1*a*, 1*b*; fig. 3*a*, 3*d*). Internal to the peripheral sclerotic zone is a zone of larger-diameter, uniformly thick-walled cells (fig. 3*a*, 3*d*) that lie adjacent to the frond trace in a narrow region at the center of the adaxial side (fig. 3*a*, *Gr*). A C-shaped zone of thinner-walled cells surrounds the rest of the leaf trace (fig. 3*a*, 3*d*) and is continuous with the thin-walled inner cortical zone of the rhizome (fig. 3*b*). Cells of the latter zone are often absent. However, when preserved, they are filled with dark contents and develop differentially thickened walls at the corners (fig. 3*d*).

Frond-trace divergence. Leaf-trace divergence is first recognized by an outward bulging in the cauline vascular cylinder, with an accompanying reduction in metaxylem thickness to a single layer of tracheids (fig. 1*b*, 1*d*; fig. 3*c*, arrow). Progressing distally, the pith and stele bulge more prominently toward the periphery of the rhizome (fig. 3*c*, top), and then the bulging vascular arc separates to form the frond trace (fig. 1*d*, bottom). One side of the trace often separates from the stele at a slightly lower level than the other side, forming a slight hook. Just distal to separation from the stele, the endodermis defines the shape of the trace. At this level, the arc-shaped bundle of tracheids conforms to the "*Grammitis*-type" trace configuration (Ogura 1972) (fig. 3*c*, 3*f*). More distally, tracheids of the trace become less contiguous (fig. 3*e*), forming three to six terete bundles.

Roots. Root traces diverge from the peripheral strands of small-diameter tracheids in the cauline stele. As the root steles extend toward the cortex, they cause the outer endodermis to bulge outward and then to enclose the root stele. This forms a circular trace that diverges through the cortex (fig. 1*d*) into the adventitious roots that radiate from all sides of the rhizomes (fig. 1*a*, 1*b*; fig. 1*d*, arrows).

Many roots are not preserved beyond the edge of the rhizome because of abrasion (fig. 1*d*). However, several roots do continue out into the rock matrix (fig. 1*a*, bottom arrow). In transverse section, such roots are diarch (fig. 3*g*). Adjacent to the tracheids are spaces that probably represent the positions of phloem cells that are not preserved (fig. 3*g*). At the periphery of the stele is a ring of irregularly shaped cells that may represent endodermis, as well as several layers of larger and somewhat thicker-walled cortical cells (fig. 3*g*). A hypodermal layer consists of incompletely preserved, smaller cells with thinner walls (fig. 3*g*, arrow). Root epidermis is not preserved.

Discussion

Stramineopteris aureopilosus gen. et sp. nov. consists of small, anatomically preserved rhizomes with attached stipe bases and roots. Rhizomes branch dichotomously, are radial and amphiphloic, and display a stelar architecture that is transitional solenostelic-dictyostelic along the axis. Stipe traces diverge from the stele in a slightly asymmetrical fashion to form an arc-shaped trace, as delimited by a distinct endodermis, and contain a *Grammitis*-type xylem bundle (Ogura 1972). Rhizome ground tissues are distinctly zoned, with abundant sclerenchyma. An indument of multicellular trichomes occurs on the rhizome and stipe bases. As the trace extends into the stipe, the xylem arc becomes dissected into several strands that are separated by thin-walled cells. Stipe cortex has three zones, two of which are sclerotic. The sclerotic zones define an outer cortex of thick-walled cells with dark contents and a middle zone of somewhat larger cells that lack the dark contents. The inner cortex wraps around the abaxial side of the trace to form a C-shaped zone of tissue of thinner-walled cells that have thickened corners, similar to angular collenchyma. Diarch roots have several layers of cortical cells with thickened cell walls and an incompletely preserved hypodermis of smaller cells with thinner walls.

Roots of *Stramineopteris* are similar to the *Lonchitis* type in having cortical cells of uniform shape and size, to the *Notholaena* type in having moderately thickened cortical cell walls, and to the *Cyclosorus* type in having a hypodermis of one to two thin-walled cells (Schneider 1996*a*, 1996*b*). However, *Stramineopteris* roots lack the parenchymatous cortical cells of the *Lonchitis* type and do not have the innermost triangular cells of the *Notholaena* type or the zoned cortex of the *Cyclosorus* type (Schneider 1996*a*, 1996*b*). As a result, *Stramineopteris* roots do not conform to any of Schneider's (1996*b*) types, but their diarch nature supports the placement of *Stramineopteris* among the Filicales.

Comparison to Fossil Taxa

There are several previously described small fossil fern rhizomes that show a wide variety of structural features and that are easily distinguished from *Stramineopteris*. These

tissue (*Gr*) adjacent to trace on adaxial side and sclerotic hypodermal cells (*Sc*) form stipe periphery. Paratype P13255 B bot 5; ×65. *b*, Cross section of rhizome at level where leaf trace traverses cortex. Sclerotic central pith region continuous with outer cortex and adjacent to adaxial side of leaf trace. C-shaped inner cortical region wraps around arc-shaped leaf trace, and endodermis surrounds both leaf trace and cauline vascular tissue. Note outer pith zone has thin- and thick-walled cells of combined pith and outer cortex nearly adjacent to leaf trace. Paratype P13255 C top 14; ×43. *c*, Cross section of rhizome showing leaf-trace divergence at two levels. Most proximal level at right, where trace divergence is first evident (arrow). Early trace divergence recognized by outward bulging of pith and reduction of metaxylem thickness to one layer in incipient trace. More distal level of trace divergence (top) shows prominent outward bulging of pith and vascular tissue below leaf gap opening. Paratype P13255 C top 14; ×40. *d*, Cross section through stipe immediately proximal to level of separation from rhizome, showing preservation of cells in C-shaped abaxial inner cortical zone (*Ab*) and stipe trace (*Tr*). Paratype P13255 B bot 5; ×70. *e*, Cross section through stipe trace immediately distal to separation from stele, showing small groups of tracheids (arrows). Note only first-formed metaxylem tracheids are differentiated. Paratype P13255 C top 24; ×100. *f*, Cross section showing stipe trace with differentiated metaxylem immediately distal to opening of leaf gap. Note *Grammitis*-type xylem configuration. Paratype P13255 C top 46; ×91. *g*, Cross section of diarch root with uniformly thick-walled cortical cells distal to divergence from rhizome. Holotype P13036 G bot 48; ×296.

include species with distinctive protosteles, highly dissected dictyosteles, polycyclic steles, or endarch or mesarch solenosteles (Millay and Taylor 1990; Tidwell and Skog 1992; Stockey et al. 1999; Collinson 2001; Pigg and Rothwell 2001; Skog 2001; Serbet and Rothwell 2003, 2006; Bonde and Kumaran 2005; Hernandez-Castillo et al. 2006; Karafit et al. 2006; Mindell et al. 2006). Exarch solenostelic fossil rhizomes that most closely resemble *Stramineopteris* are produced by species of *Solenostelopteris* Kershaw (1910), *Dictyostelopteris* Vishnu-Mittre (1958), *Loxsomopteris* Skog (1976), and *Dennstaedtiopsis* Arnold and Daugherty (1964). However, none of these has a stele that displays the solenostele-dictyostele transition seen in *Stramineopteris*. Likewise, none of these genera has a stipe trace that is dissected into several strands distal to the rhizome cortex. Species of *Solenostelopteris* and *Dictyostelopteris* agree with *Stramineopteris* in having peripheral strands of first-formed metaxylem (or protoxylem) that occur outside the rest of the metaxylem. Similar protruding strands of tiny tracheids are not produced by *Dennstaedtiopsis* (Arnold and Daugherty 1964) or *Loxsomopteris* (Nishida and Nishida 1982). *Dictyostelopteris* is designated for poorly preserved dictyostelic rhizome fragments that have few additional characters for identification (Vishnu-Mittre 1958).

Stramineopteris has discontinuities in the tracheal cylinder of the stele that are occupied by xylem parenchyma cells, and in this respect it is unlike species of *Solenostelopteris* and *Dictyostelopteris*, which lack such discontinuities, although xylem parenchyma does occur in some of these species (Kershaw 1910; Ogura 1930; Vishnu-Mittre 1958; Sharma and Bohra 1976; Bohra and Sharma 1979; Nishida and Nishida 1982; Tidwell and Skog 1999). The distinct C-shaped zone of thin-walled cells with thickened corners, similar to angular collenchyma, that surrounds the stipe traces of *Stramineopteris* is not produced by any of the species of *Solenostelopteris*, *Dictyostelopteris*, *Loxsomopteris*, or *Dennstaedtiopsis*. In addition, *Dennstaedtiopsis* has distinctive aerenchymatous ground tissues that contrast with the thick-walled, closely spaced cortical cells of *Stramineopteris* (Arnold and Daugherty 1964). *Loxsomopteris* is characterized by conical and bristle hairs, which are not seen in *Stramineopteris*. In the rare cases where trichomes are preserved in species of *Solenostelopteris*, *Dictyostelopteris*, and *Dennstaedtiopsis*, such trichomes lack the broad multicellular bases seen in *Stramineopteris*.

Vegetative Anatomy and the Familial Systematics of Filicales

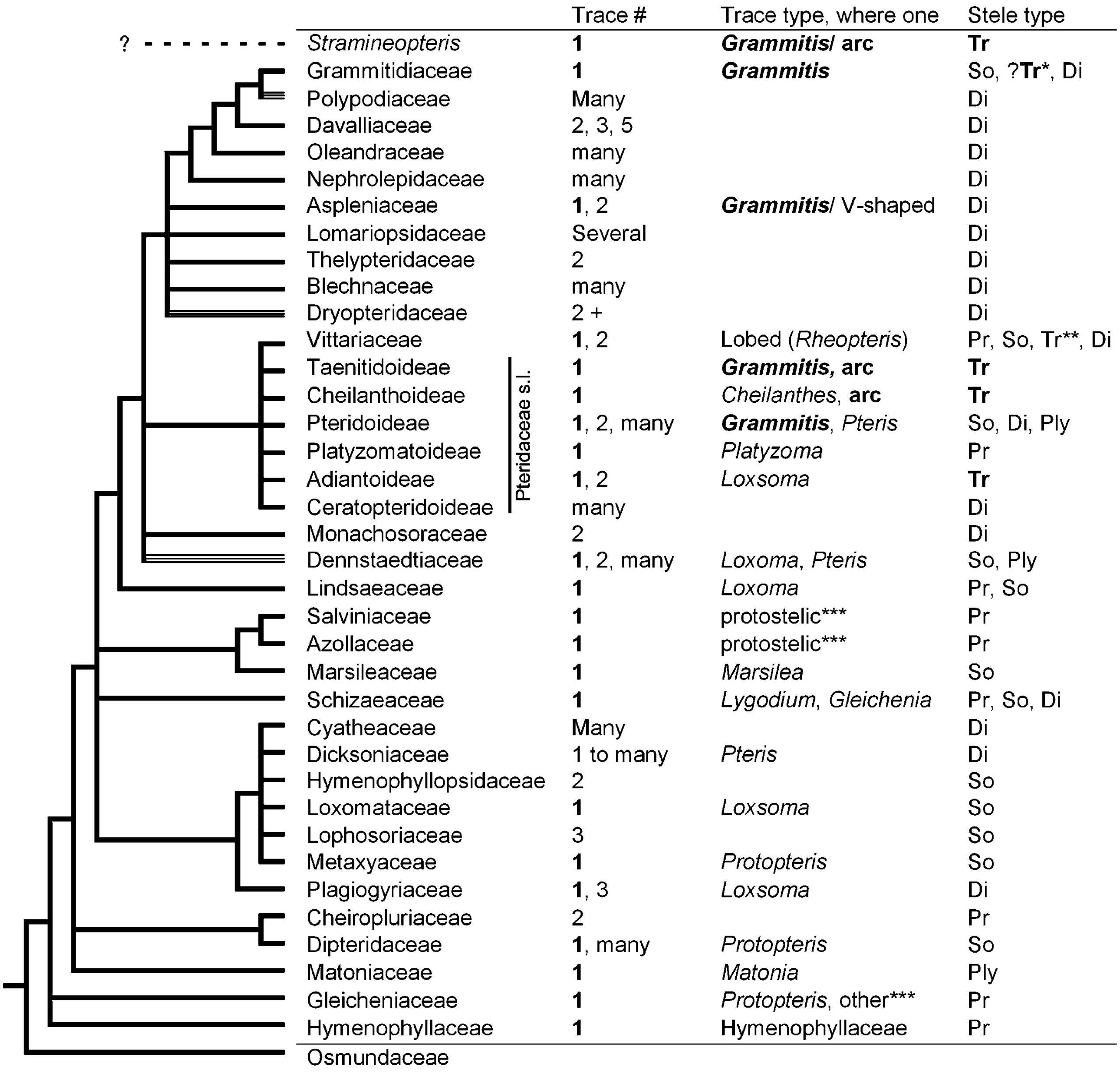
Relatively early summaries of classical anatomical studies (Bower 1923, 1926, 1928; Eames 1936) have demonstrated that there is a wide variety of structural diversity among the few living filicalean species that have been investigated in detail and have provided data for recognizing general trends that are considered to reflect evolutionary changes from primitive to derived. Examples of these are transitions from protosteles to solenosteles to dictyosteles, from exarch to mesarch to endarch xylem maturation, and from ectophloic to amphiphloic phloem distribution. While such characters distinguish some relatively basal families with living species (e.g., Osmundaceae; Hewitson 1962) and may be more or less consistent within other extant filicalean families (Kramer and Green 1990), many vegetative anatomical features are basically similar among a large number of fern families (Bower 1923, 1926, 1928; Tryon and Tryon 1982; Kramer and Green 1990). Where known, others tend to vary within families, appear to be homoplasious (Ranker et al. 2004), and are not heavily used in broad systematic treatments (Holttum 1947; Smith 1995).

Together, these factors have fostered the widely held belief that vegetative anatomical characters are of little systematic value for determining most familial relationships, particularly in comparison to gene sequence characters that have produced robust phylogenies within genera and families (Wolf 1995; Cranfill and Kato 2003; Ranker et al. 2004) and have provided at least preliminary hypotheses of relationships among filicalean families with living species (Hasebe et al. 1995; Pryer et al. 2004). Against this backdrop, it is easy to understand why even the most comprehensive contemporary systematic investigations of living filicalean families (Cranfill and Kato 2003) do not include detailed anatomical surveys of all included species, particularly since such anatomical surveys are extremely labor intensive and time consuming. Up to the present, the anatomy of only a small minority of living ferns has been studied in detail (we estimate <3%). However, when such surveys have been conducted, they have almost always resulted in the development of reliable characters for identifying species, for recognizing related species, and even for determining familial affinities (Hewitson 1962; Kato 1977; Nishida 1984).

Anatomically preserved remains of fossil Gleicheniaceae sometimes are recognizable (Gandolfo et al. 1997; Mindell et al. 2006), but small vegetative organs of many other families are much more difficult to classify with certainty. For example, Millay and Taylor (1990) described several extinct genera and species based on small anatomically preserved Antarctic ferns from the Triassic Fremouw Peak Locality for which familial affinities have been suggested: *Antarctipteris sclericaulis* (?Gleicheniaceae), *Schopfiopteris repens* (?Cyatheaceae, ?Pteridaceae), and *Soloropteris rupex* (?Matoniaceae). However, other ferns from the same study, *Fremouwa inaffecta* and *Schleporia incarcerata*, were described as filicalean species of unknown affinity (Millay and Taylor 1990). Up to the present, only a few small anatomically preserved vegetative fern shoots have been assigned to families with more confidence. These include *Tasmanopteris* Tidwell and Skog and *Heweria* Tidwell and Skog (Matoniaceae; Tidwell and Skog 1992), *Dennstaedtiopsis* Arnold and Daugherty and *Microlepiopsis* Serbet and Rothwell (Dennstaedtiaceae; Arnold and Daugherty 1964; Serbet and Rothwell 2003), *Loxsomopteris* Skog (Loxomataceae; Skog 1976), and *Acrostichum* (Pteridaceae s.l.; Arnold and Daugherty 1963; Bonde and Kumaran 2005).

When evaluating possible relationships of *Stramineopteris*, particularly to extant leptosporangiate fern families, an in-depth assessment is limited by the paucity of comparative anatomical data emphasized above. Nevertheless, a preliminary assessment of the systematic distribution of anatomical characters reveals intriguing patterns with the suggestion of at least some broad family-level correlations. Whereas many species of the more highly derived families are typified by having dictyosteles and several traces entering the stipe (fig. 4), only a few of the subfamilies of the Pteridaceae s.l. (i.e., Cheilanthoideae, Taenitidoideae, and Adiantoideae) are known to include species with the transitional solenostelic-dictyostelic architecture (Ogura 1972; Tryon et al. 1990) that characterizes *Stramineopteris* (fig. 4).

Among the families that contain species that agree with *Stramineopteris* by having leaf traces that diverge from the stele as a single bundle, most have distinctive trace configurations that have been defined and named by Ogura (1972). Of these, many have incurved adaxial xylem, such as the *Loxsoma* type (Ogura 1972), but *Stramineopteris* does not. Within the rhizome cortex, *Stramineopteris* stipe traces are most similar to *Cryptogramma stelleri* (Gmel.) Prantl of the Cheilanthoideae and to *Onychium siliculosum*



	Trace #	Trace type, where one	Stele type
Stramineopteris	**1**	***Grammitis*/ arc**	**Tr**
Grammitidiaceae	**1**	***Grammitis***	So, ?**Tr***, Di
Polypodiaceae	Many		Di
Davalliaceae	2, 3, 5		Di
Oleandraceae	many		Di
Nephrolepidaceae	many		Di
Aspleniaceae	**1**, 2	***Grammitis***/ V-shaped	Di
Lomariopsidaceae	Several		Di
Thelypteridaceae	2		Di
Blechnaceae	many		Di
Dryopteridaceae	2 +		Di
Vittariaceae	**1**, 2	Lobed (*Rheopteris*)	Pr, So, Tr**, Di
Taenitidoideae	**1**	***Grammitis*, arc**	**Tr**
Cheilanthoideae	**1**	*Cheilanthes*, **arc**	**Tr**
Pteridoideae	**1**, 2, many	***Grammitis***, *Pteris*	So, Di, Ply
Platyzomatoideae	**1**	*Platyzoma*	Pr
Adiantoideae	**1**, 2	*Loxsoma*	**Tr**
Ceratopteridoideae	many		Di
Monachosoraceae	2		Di
Dennstaedtiaceae	**1**, 2, many	*Loxoma*, *Pteris*	So, Ply
Lindsaeaceae	**1**	*Loxoma*	Pr, So
Salviniaceae	**1**	protostelic***	Pr
Azollaceae	**1**	protostelic***	Pr
Marsileaceae	**1**	*Marsilea*	So
Schizaeaceae	**1**	*Lygodium*, *Gleichenia*	Pr, So, Di
Cyatheaceae	Many		Di
Dicksoniaceae	1 to many	*Pteris*	Di
Hymenophyllopsidaceae	2		So
Loxomataceae	**1**	*Loxsoma*	So
Lophosoriaceae	3		So
Metaxyaceae	**1**	*Protopteris*	So
Plagiogyriaceae	**1**, 3	*Loxsoma*	Di
Cheiropluriaceae	2		Pr
Dipteridaceae	**1**, many	*Protopteris*	So
Matoniaceae	**1**	*Matonia*	Ply
Gleicheniaceae	**1**	*Protopteris*, other***	Pr
Hymenophyllaceae	**1**	Hymenophyllaceae	Pr
Osmundaceae			

Fig. 4 Distribution of three anatomical characters of potentially informative systematic significance. Characters are plotted on phylogeny of filicalean families with living representatives and rooted with Osmundaceae. Characters are stelar architecture (stele type), number of bundles entering stipe (trace number), and named rachial configuraton types (trace type) for stipes with single bundle (*sensu* Ogura 1972); they are scored primarily from Ogura (1972), Tryon and Tryon (1982), Nishida (1984), and Kramer and Green (1990). Phylogeny based on "Tree of Life" (http://tolweb.org/tree/phylogeny.html; May 2005) and modified based on Wolf (1995) and Wolf et al. (1998). Note that *Pteris* type is often referred to as inverted Omega or dennstaedtioid-type trace. * = Ogura (1972) describes dictyostelic *Grammitis*; thus, the transitional type is probably present (see "Discussion"). ** = Vittariaceae considered typically ectophloic and lacking sclerenchyma (Kramer 1990). * * * = See Ogura (1972) for finer distinctions; all trace types have incurved adaxial ends in Gleicheniaceae.

(Desv.) C. Chr. of the Taenitidoideae (Ogata 1929, 1930). Therefore, *Stramineopteris* displays a *Grammitis*-type trace (fig. 4).

By mapping a data set that includes only these three characters of vegetative anatomy (i.e., transitional solenostelic-dictyostelic stele architecture, a single bundle entering the stipe, and configuration of the rachis xylem) onto a tentative filicalean phylogeny, we have been able to relate *Stramineopteris* to a relatively restricted range of filicalean diversity (fig. 4). One or two of the pertinent characters occur in a somewhat wider range of living Filicales (fig. 4), but the combination of all three characters is known to occur in only one subfamily of the Pteridaceae s.l. (i.e., Taenitidoideae *sensu* Tryon et al. 1990) and possibly also in the Grammitidaceae *sensu* Parris (1990) (fig. 4). *Grammitis* Swartz, although widely regarded as having solenostelic rhizomes (Parris 1990; Ranker et al. 2004), has been reported to have dictyostelic species as well (Ogura 1972). Therefore, the family Grammitidaceae warrants further study to determine whether it includes species with transitional solenosteles-dictyosteles similar to those of *Stramineopteris*. In addition, the small plant size, divergence of stipe traces as a single bundle, and trichomes that often occur in living species of *Grammitis* are all similar to comparable characters of *Stramineopteris* (Ogata 1931, 1933; Ogura 1972).

Stramineopteris aureopilosus expands our knowledge of extinct fern diversity and contributes new information about filicalean radiations during the Lower Cretaceous. Although *S. aureopilosus* is known only from vegetative organs, the distinctive combination of anatomical characters elaborated above suggests that it represents a highly derived filicalean, possibly Pteridoideae, Cheilanthoideae, or Taenitidoideae of the Pteridaceae s.l., or Grammitidaceae (fig. 4). Such relationships are also suggested by the presence of potentially pteridaceous fertile material at the same locality (i.e., *Pterisorus* Rothwell and Stockey 2006) and are supported by the occurrence of highly derived filicaleans in Lower Cretaceous deposits of China (Deng 2002). Together, these occurrences imply that the third radiation of Filicales may have begun earlier than widely recognized (Pryer et al. 2004; Schneider et al. 2004).

Stramineopteris aureopilosus highlights a pressing need for developing comprehensive detailed anatomical data to help build an accurate framework for filicalean systematics. Despite the fact that many pteridologists have come to regard anatomical characters as relatively uninformative for resolving broad-scale patterns of fern systematics, studies of extinct species such as *Stramineopteris* indicate this opinion may reflect a paucity of anatomical data, rather than the inapplicability of such data. Most important, anatomical characters provide a bridge for incorporating additional extinct species into broad-scale phylogenetic analyses of ferns and for ultimately reconciling the disparate patterns of fern phylogeny implied by analyses that either include or exclude extinct species (cf. Rothwell 1999; Pryer et al. 2001).

Acknowledgments

We thank Joe Morin, Mike Trask, Gerald Cranham, Sharon Hubbard, Thor Henrich, Graham Beard, Dan Bowen, and Pat Trask of the Vancouver Island Paleontological Society for help in the field and for calling this site to our attention. We also thank Dr. Harufumi Nishida, Chuo University, for specimens and bibliographic information; A. R. Sweet, Geological Survey of Canada, for data on pollen analysis; Dr. Elizabeth Gierlowski-Kordesch, Ohio University, for sedimentological and depositional information; and D. R. Gröcke, McMaster University, for isotope analysis. This research was supported in part by grant A-6908 from the Natural Sciences and Engineering Research Council of Canada to R. A. Stockey.

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