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EVIDENCE FOR SYMPODIAL VASCULAR ARCHITECTURE IN A FILICALEAN FERN RHIZOME: *DICKWHITEA ALLENBYENSIS* GEN. ET SP. NOV. (ATHYRIACEAE)

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A new genus and species of anatomically preserved fossil filicalean ferns *Dickwhitea allenbyensis* gen. et sp. nov. is described from the Middle Eocene Princeton Chert of southern British Columbia, Canada. Rhizomes have a parenchymatous pith surrounded by a ring of five amphiphloic cauline bundles and pairs of frond traces that diverge from adjacent cauline bundles in a 2/5 phyllotaxis. The cortex is also parenchymatous except at the periphery, where there is a well-developed sclerotic hypodermis. The stipe is characterized by a pair of hippocampiform bundles, and ground tissues are similar to those of the rhizome. Prominent nests of large cells with black contents occur adjacent to the vascular bundles in the ground tissue of the rhizome and stipe. Roots are diarch with cortex that grades from parenchymatous at the interior to sclerotic at the periphery. The vascular architecture of this fern appears to be novel among known Filicales. There are no gaps in the stele that result from the divergence of either frond or root traces, and there is no evidence that cauline bundles anastomose. Rather, the cauline bundles extend through the rhizome independently of each other, with each cauline bundle producing successive frond traces on alternating tangents. Root traces diverge from the outer surface of cauline bundles as is characteristic of solenostelic filicalean species and dictyostelic tree ferns. Examination of the literature reveals that there is a wide range of variation in filicalean vascular architectures that traditionally has not been recognized. Although there is anecdotal evidence that this newly recognized stelar variation is correlated with patterns of systematic diversity, the overall phylogenetic significance of fern vascular architecture has yet to be fully explored.

Keywords: Athyriaceae, dryopterid, Eocene, eustele, fern, fossil.

Introduction

Recent studies of the Middle Eocene Princeton Chert in southern British Columbia, Canada, have documented that the flora includes five filicalean ferns (Basinger 1976, 1981; Pigg and Stockey 1996; Stockey et al. 1999). These are *Osmunda* sp. (Osmundaceae), *Dennstaedtiopsis aerenchymata* Arnold et Daugherty (Dennstaedtiaceae), a blechnoid fern (Blechnaceae) similar to *Woodwardia* spp. (Pigg and Stockey 1996; Smith et al. 2004, 2006), and two dryopterid species (Athyriaceae) with *Onoclea*-type stipe anatomy. One of the dryopterids, *Makotopteris princetonensis* Stockey et al. (1999), is described from both vegetative and fertile organs. The second dryopterid is represented by rhizomes with diverging stipes and adventitious roots and by detached stipes and roots. This last fern is described herein as a morphotaxon, *Dickwhitea allenbyensis* gen. et sp. nov. *Dickwhitea* displays a novel architecture of the cauline vascular system, is more robust than *M. princetonensis*, and has several distinctive histological features that allow for the identification of isolated organs. The unexpected cauline vascular architecture of *D. allenbyensis* is unlike that previously known in leptosporangiate ferns. It further advances our understanding of filicalean evolutionary diversification in the Paleogene and calls to question the completeness with which we understand leptosporangiate fern stelar architecture.

Material and Methods

The current study is based on two permineralized rhizomes with diverging stipes and adventitious roots and additional isolated stipes and adventitious roots that occur in block P1080 of the plant-rich Princeton Chert (Basinger and Rothwell 1977; Pigg and Stockey 1996). The material was collected from one of the numerous chert layers that are interbedded with coal and ash and that crop out on the east bank of the Similkameen River, ca. 8.4 km south of the town of Princeton, British Columbia, Canada. This deposit is located 630 m above the Princeton Black Coal seam and is part of the Princeton Group, Allenby Formation (Boneham 1968). The Princeton Group has been dated as Middle Eocene based on studies of freshwater fishes (Wilson 1977, 1982), mammals (Russell 1935; Gazin 1953), and by K-Ar dates (Hills and Baadsgaard 1967; H. Baadsgaard, personal communication 1999). Chert blocks were cut into slabs and studied using a modified cellulose acetate peel technique wherein the matrix is etched with concentrated (48%) hydrofluoric acid (Basinger and Rothwell 1977). Peel sections were mounted in Eukitt (O. Kindler, Freiburg, Germany), xylene-soluble mounting

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medium for microscopic examination and image capture. Images were captured with a PhotoPhase digital scanning camera (Phase One, Frederiksberg, Denmark), and processed with Adobe Photoshop. Chert slabs, peels, and microscope slides are housed in the University of Alberta Paleobotanical Collections.

Systematics

Order—*Filicales*

Family—Athyriaceae sensu *Pichi-Sermolli (1977)*

Genus—Dickwhitea *gen. nov.*

Species—Dickwhitea allenbyensis *sp. nov.*
(figs. 1, 2)

Combined generic and specific diagnosis. Morphotaxon of permineralized fern rhizomes with diverging stipes and adventitious roots. Rhizomes 6–7 mm wide; radial, with relatively long internodes. Pith and cortex parenchymatous, with clusters of cells containing dark contents immediately to the inside and outside of cauline bundles; sclerotic hypodermis 0.2–0.4 mm wide. Xylem cylinder of five independent amphiphloic cauline bundles; frond traces of two hippocampiform bundles diverging from adjacent cauline bundles. Successive frond traces diverging from margins of cauline bundles that are separated by two intermediate cauline bundles, producing 2/5 phyllotactic helix. True leaf gaps absent. Cauline bundles 5–15 tracheids thick, lacking protoxylem strand; expanding tangentially from alternate sides to produce successive stipe traces. Stipes 2.8–3.0 mm wide, with two hippocampiform bundles; roots diarch with parenchymatous cortex grading to sclerenchyma near epidermis. Frond architecture, pinnules, sporangia, and spores unknown.

Holotype hic designatus. Rhizome with attached stipe bases and adventitious roots, including slabs, slides, and peels from chert block P1080 (figs. 1, 2).

Collecting locality. East bank of the Similkameen River, ca. 8.4 km south of Princeton, British Columbia (Princeton Map Sheet 92 H/7, scale 1 : 50,000, UTM grid ref. 783–724).

Stratigraphic position. Princeton Group. Allenby Formation, 630 m above the Princeton Black Coal seam in the Princeton Basin.

Age. Middle Eocene.

Etymology. The generic name *Dickwhitea* recognizes the contributions by Richard A. White, Duke University, to our understanding of the vascular architecture of ferns. The specific epithet *allenbyensis* signifies the formation from which the material was collected and the nearby abandoned mining town of Allenby, British Columbia, for which the formation was named.

Description

The rhizome of *Dickwhitea allenbyensis* is radial, producing stipes and adventitious roots all the way around the periphery (figs. 1.1, 1.2). The longest specimen can be traced for somewhat over 9.0 cm, but the rhizome is too distorted and incompletely preserved at many levels to determine mean internodal length. Most sections do not show a diverging stipe, and only one stipe is present in those that do (e.g., fig. 1.1, left). Therefore, successive stipes probably are separated by at least 1 cm. Rhizomes are round to oval in cross section, ca. 1 cm in diameter, with the greatest diameter of somewhat flattened or oblique sections measuring 1.6 cm. Diverging stipes are gently angular in cross section with four unequal sides and rounded corners. They lack an adaxial groove (fig. 1.3). In cross section, stipes range 2–3 mm in greatest dimension.

The pith of the rhizome measures 2.9–4.6 mm in diameter and is composed primarily of thin-walled parenchyma cells with no visible internal contents (figs. 1.1, 1.2). The quality of preservation varies considerably, but where well-preserved, the parenchyma cells are tightly packed. Cortical cells are similar to those of the pith except at the periphery, where a sclerotic hypodermis, approximately 0.5 mm thick, is present (figs. 1.1, 1.2, 2.1). Epidermis usually cannot be identified, but where it is preserved, it is represented by thin-walled cells to the outside of the hypodermis (fig. 2.1, top). Frequently, the outer margin of the rhizome shows either a frayed or abraded surface (fig. 1.1). There are often thin patches of dark tissue up to 1 mm wide that are preserved with their long axes parallel to the rhizome surface. It is uncertain whether the latter tissue has been frayed from the surface or whether it represents incompletely preserved epidermal scales.

Multicellular patches of cells, 0.5–1.1 mm in greatest dimension, with prominent dark contents are scattered near the outer margin of the pith, throughout the cortex, and within the mesophyll of the stipes (figs. 1.1–1.3, 2.1–2.5, 2.8). Such patches are comparable to structures typically identified as secretory or sclerotic nests, and these allow the various rhizomes and stipes of *Dickwhitea* (figs. 1.1–1.3, 2.1–2.5, 2.8) to be easily identified in peel preparations.

Vascular tissue of the rhizome consists of five cauline bundles (figs. 1.1, 1.2, arrows), paired stipe traces at various levels of formation (figs. 1.1, 1.2), and diverging root traces (figs. 2.2, 2.4–2.6, 2.8). The cauline bundles show no evidence of anastomosing from level to level. Rather, frond traces diverge alternately from opposite sides of each cauline bundle (fig. 3). The positions of successive stipe traces around the rhizome are separated by two cauline bundles, producing a 2/5 phyllotactic helix (fig. 3).

Two traces diverge to each stipe, one from each of two adjacent cauline bundles (fig. 1.2). Stipe trace production begins with the tangential elongation of adjacent cauline bundles toward one another (fig. 1.2, bottom left; fig. 2.8). Distally, the end of each elongated bundle expands in thickness and develops a protoxylem strand (figs. 2.2, 2.8, left). Progressing more distally, the expanded end of the bundle extends toward the periphery of the rhizome (fig. 1.2) and opens to form a hook (fig. 2.1) that will become the abaxial end of the stipe trace. Somewhat below the level of stipe divergence, the paired stipe bundles separate from adjacent cauline bundles (fig. 1.2, top). At this level, the separating end of the stipe trace bundles is swollen with a protoxylem strand at the center (fig. 1.2, top). More distally, this end of the stipe bundle opens up to form an adaxial hook (fig. 2.3, top) that is larger than the abaxial hook (fig. 2.3, bottom).

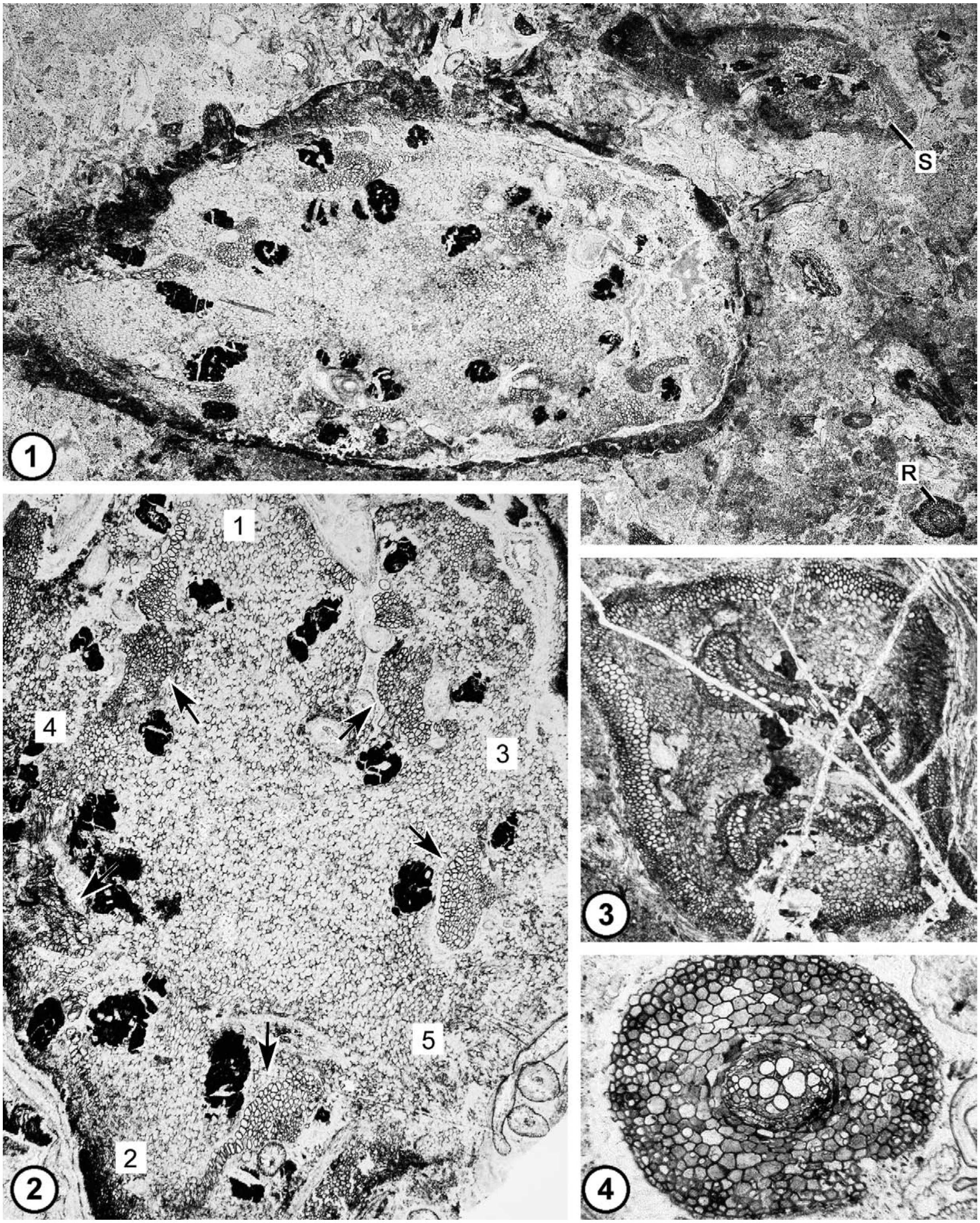

Fig. 1 *Dickwhitea allenbyensis* gen. et sp. nov. Holotype 1.1, Cross section of rhizome with detached stipe (*S*) and root (*R*). P1080 B top, no. 10, ×9. 1.2, Cross section of rhizome showing five cauline meristeles (arrows) surrounding parenchymatous pith. Specimen shows position of five diverging stipe traces that denote a 2/5 phyllotaxis (numbers). Each stipe trace consists of paired hippocampiform bundles. Note lack of anastomoses and presence of clusters of large cells with dark contents. P1080 B top, no. 3, ×16. 1.3, Cross section of stipe somewhat distal to level of divergence from rhizome, showing two hippocampiform bundles, sclerotic nests, and hypodermis. P1080 C_2 side, no. 11, ×21. 1.4, Cross section of adventitious root showing diarch protostele, endodermis, and parenchymatous cortex. Note that the parenchymatous cortex becomes more sclerotic toward periphery. P1080 C_{4a} top, no. 9, ×60.

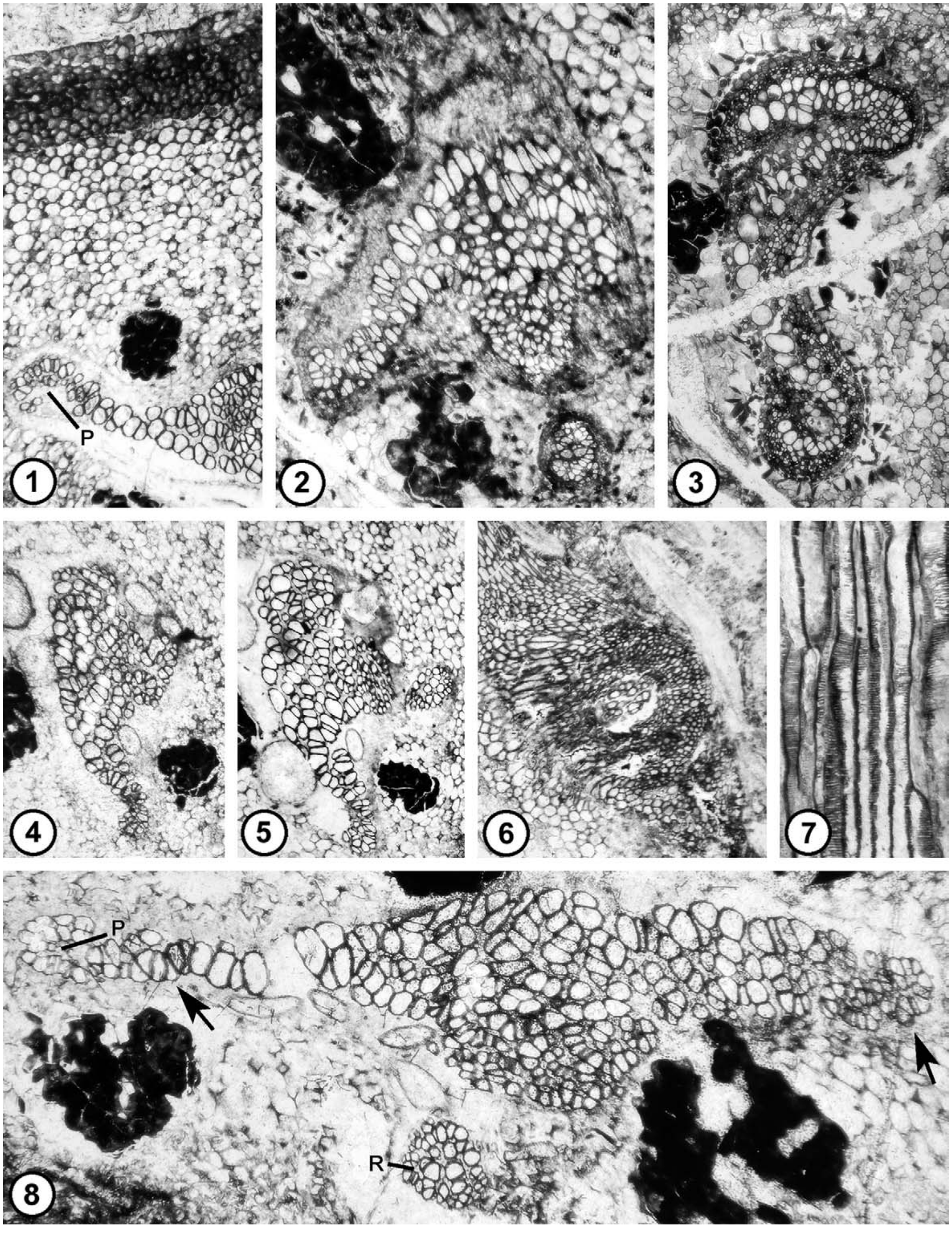

Fig. 2 *Dickwhitea allenbyensis* gen. et sp. nov. 2.1, Rhizome showing diverging leaf trace, large cells with black contents, parenchymatous pith, and cortex and sclerotic hypodermis. P1080 C_{4a} top, no. 10, ×9. 2.2, Amphiphloic meristele showing diverging leaf and root traces. P1080 C_{4b} bot, no. 5, ×40. 2.3, Frond trace in stipe showing metaxylem, phloem, and two strands of protoxylem. P1080 C_2 side, no. 11, ×60. 2.4, Cauline meristele showing root-trace bulge. P1080 B bot, no. 10, ×30. 2.5, Cauline meristele pictured in 2.4 at more distal level, showing root trace diverging toward periphery of rhizome. Note no root gap is formed. P1080 B bot, no. 9, ×30. 2.6, Root trace pictured in 2.4 and 2.6 at more distal level, forming sclerotic cortex. P1080 B bot, no. 7, ×28. 2.7, Longitudinal section of cauline bundle showing metaxylem tracheids with uniseriate, scalariform wall thickenings. P1080 D_{4a} top, no. 4, ×120. 2.8, Cauline bundle with developing root (*R*) and frond traces (arrows). Note leaf trace diverging to left of meristele while another frond trace is developing that will diverge to more distal frond, at right. P1080 B top, no. 10, ×57. *P*, protoxylem.

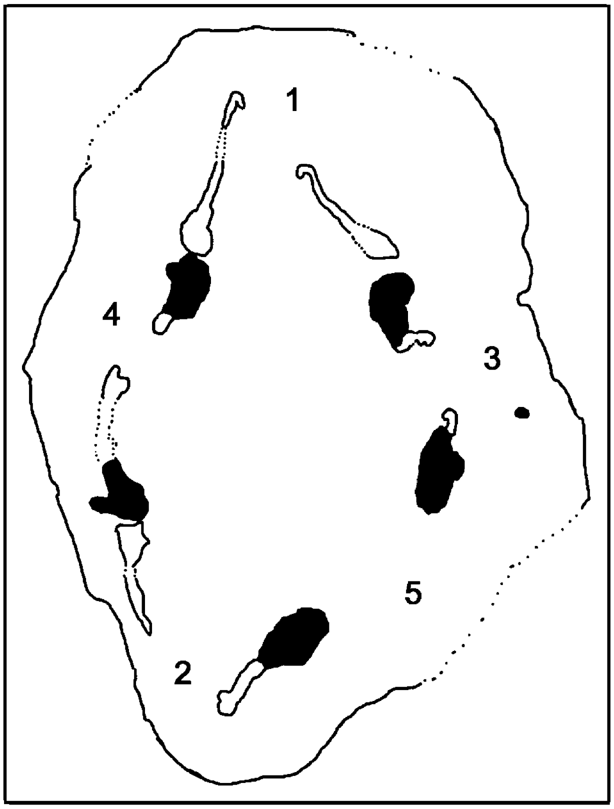

Fig. 3 *Dickwhitea allenbyensis* gen. et sp. nov. Diagram of cross section of rhizome showing vascular architecture. Cauline bundles and a root trace are black, and the paired hippocampiform stipe traces are white. Numbers indicate the order of successive stipe divergence.

The diverging stipe traces are somewhat angular (figs. 1.1, 1.3), with the two hippocampiform bundles (fig. 1.3) embedded in parenchymatous ground tissue (fig. 2.3). Stipe bundles display two protoxylem strands, one at the center of the hook at each end (fig. 2.3). Xylem is surrounded by phloem and by a bundle sheath of large cells with prominent radial walls (fig. 2.3, upper left). Nests of secretory/sclerotic cells with dark contents and a sclerotic hypodermis, like those of the rhizome, characterize the ground tissue of the stipes (figs. 1.1, 1.2, 2.3), and allow them to be easily identified as *Dickwhitea*. Trichomes or scales have not been identified at the periphery of stipes, but this may be due to incomplete preservation of the epidermis.

Roots of *Dickwhitea* are consistently diarch. Well-preserved specimens show phloem, pericycle, and endodermis at the center, and a uniseriate epidermis at the periphery (fig. 1.4). The cortex consists of thin-walled parenchyma toward the center, grading to somewhat smaller and thicker-walled sclerenchyma toward the epidermis (fig. 1.4).

Discussion

Of the five filicalean ferns that have been identified in the Middle Eocene Princeton Chert of southern British Columbia, two have highly dissected steles with *Onoclea*-type stipe traces (Ogura 1972) that consist of paired hippocampiform bundles, and these characters allow for their assignment to the Athyriaceae *sensu* Pichi-Sermolli (1977) or Dryopteridaceae *sensu* Kramer and Green (1990; Hasebe et al. 1995). The first of these to be described, *Makotopteris princetonensis* Stockey et al. (1999), is represented by the entire vegetative and fertile sporophyte. The second, described herein as *Dickwhitea allenbyensis,* is known from two permineralized rhizomes with attached stipe bases and adventitious roots and isolated stipe and root segments. The rhizome of *Dickwhitea* is three to five times as large as that of *M. princetonensis*. It also has distinctive nests of dark sclerotic or secretory cells in the ground tissues that are consistently located immediately to the inside and to the outside of the cauline bundles of the rhizome (figs. 1.1, 1.2) and vascular bundles in the stipe (fig. 1.3), and that allow the rhizomes and stipes of *D. allenbyensis* to be easily identified in section views.

Although *D. allenbyensis* and *M. princetonensis* are both characterized by rhizomes with a prominent pith, a highly dissected stele, helical phyllotaxis, and stipe traces that consist of two hippocampiform bundles, the stelar architecture appears to be fundamentally different in these two ferns. Whereas *M. princetonensis* displays a typical dryopterid dictyostele (Bower 1928; Ogura 1972; Kato 1977; White and Weidlich 1995) with gaps that are formed in the cauline vascular cylinder by the divergence of root traces and that close by the fusion of cauline bundles, no gaps are produced by the divergence of either root or stipe traces in *Dickwhitea*. In *D. allenbyensis*, root traces diverge from the outer margin of cauline bundles without forming a gap, and stipe traces diverge from a lateral margin of the cauline bundles. Cauline bundles have not been observed to either divide or fuse throughout the several centimeters of rhizome that are preserved, and the number of cauline bundles is consistently five in all sections that are both complete and well enough preserved to allow for this determination to be made. Therefore, we are forced to conclude that the vascular architecture of *D. allenbyensis* is unlike that previously described for any other leptosporangiate fern.

If correctly interpreted, cauline bundles of *D. allenbyensis* extend through the rhizome independently of each other. Frond traces diverge alternately from the lateral margins of a cauline bundle to produce one of the two traces that enter the base of a stipe (fig. 3). Together, the five cauline bundles constitute a sympodial system that is the structural equivalent of the eustele in seed plants (Namboodiri and Beck 1968*b*). Because each stipe has paired traces that are derived from adjacent cauline bundles, the vascular architecture of *D. allenbyensis* is particularly comparable to *Ginkgo biloba* (Gunckel and Wetmore 1946), *Sequoia sempervirens* (Namboodiri and Beck 1968*a*), and many other species of nonflowering seed plants with paired leaf traces (Rothwell 1976). Before the discovery of *D. allenbyensis*, this architecture of the cauline vascular system was thought to be restricted almost exclusively to seed plants and their progymnospermous sister groups (Namboodiri and Beck 1968*b*; Rothwell 1976; Beck et al. 1982). However, it is now evident that such an architecture has been derived independently in lignophytes and leptosporangiate ferns.

The ophioglossalean eusporangiate ferns *Botrychium* and *Ophioglossum* are the only other nonseed plants in which a comparable cauline architecture has been suggested (White

1984). Both *Botrychium* and *Ophioglossum* display ectophloic solenosteles (Bower 1926; Eames 1936; Bierhorst 1971), but the protoxylem architecture of the rhizomes of these genera is equivalent to the vascular architecture of the metaxylem and phloem in *Dickwhitea* (White 1984). In all three ferns, as well as in many seed plants, there are cauline strands (i.e., protoxylem strands in *Botrychium* and *Ophioglossum* and primary bundles in *Dickwhitea* and most seed plants) that extend through the stem independently with adjacent strands dividing to produce two bundles for each frond.

Going back to the classic studies of Jeffrey (1902) and others (Gwynne-Vaughan 1901, 1903; Tansley 1907; Bower 1928), the steles of fern rhizomes typically have been stereotyped as consisting of a cylinder of vascular tissue in which the wall of the cylinder is perforated by leaf gaps that are formed by the divergence of leaf traces. In solenostelic ferns, only one leaf gap appears in a single cross section. However, in dictyostelic ferns, the gaps are long enough and/or the internodes are short enough that two or more gaps overlap and are present in a single cross section. Solenosteles occur in many species of the basal families of leptosporangiate ferns (e.g., Botryopteridaceae, Schizaeaceae, Gleicheniaceae, Hymenophyllaceae, Dennstaedtiaceae, etc.; Gwynne-Vaughan 1903; Bower 1926; Ogura 1972; White 1984; Rothwell 1999) as well as in some species of more highly derived leptosporangiate ferns (Bower 1928; Ogura 1972; White 1984). Dictyosteles characterize many species of tree ferns and other leptosporangiate ferns, particularly the more highly derived families (Bower 1928; Ogura 1972; White 1984). However, the dictyosteles in some families of ferns are structurally quite different from those in other families. For example, in the Osmundaceae the xylem is typically dissected by numerous leaf gaps, but there are no gaps in the phloem (Bierhorst 1971). Therefore, typical living species of Osmundaceae have a vascular architecture that is more accurately referred to as dictyoxylic rather than dictyostelic (Serbet and Rothwell 1999; Smith and Stockey 2000; Rothwell et al. 2003). Likewise, the stelar cylinders of many derived ferns in the Athyriaceae (e.g., Blechnaceae) have gaps in the wall of the vascular cylinder that are formed by the divergence of root traces rather than frond traces (Kato 1977; White and Weidlich 1995). Whereas the dissected steles of Osmundaceae clearly have evolved from a protostele independently of other families that have leaf gaps in both the xylem and phloem, we do not yet know if "dictyosteles" with root gaps (e.g., Blechnaceae and Athryiaceae) have evolved independently of dictyosteles with leaf gaps (e.g., Cyatheaceae s.l.).

Since the landmark recognition by Namboodiri and Beck (1968*b*; Beck 1970) that the eustele of lignophytes is both architecturally dissimilar and evolutionarily independent of the dictyostele of leptosporangiate ferns, this feature has been one of the most reliable vegetative characters for distinguishing ferns from seed plants. However, the discovery of an essentially eustelic architecture in the rhizome of *Dickwhitea* now calls to question the universality of this distinction. It is unclear whether the dissected stele of *Dickwhitea* is unique among leptosporangiate ferns or if this distinctive stelar architecture has simply been overlooked previously among the inadequately surveyed rhizome anatomy of ferns. Likewise, we do not know whether the stelar architecture of *Dickwhitea* has arisen by a modification of a more common architecture of dissected leptosporangiate fern steles (i.e., dictyosteles) or if it has an independent origin from the protostele. In either case, however, the characterization of *D. allenbyensis* reaffirms that the rhizome vascular architecture is systematically informative. Since only a small fraction of the ferns have been studied anatomically, a much more comprehensive survey of fern structure will be required (White 1984) before we can fully appreciate the architectural diversity and phylogenetic utility of fern steles.

Acknowledgments

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