

TRAWETSIA PRINCETONENSIS GEN. ET SP. NOV. (BLECHNACEAE): A PERMINERALIZED FERN FROM THE MIDDLE EOCENE PRINCETON CHERT

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Trawetsia princetonensis Smith, Stockey, Nishida & Rothwell gen. et sp. nov. is described from several permineralized rhizomes, stipes, and higher-order frond members of a blechnoid fern that have been identified from the Middle Eocene Princeton Chert of British Columbia. Rhizomes bear stipes arising from all sides of the stem as well as diarch adventitious roots. The dictyostelic rhizomes are up to 16 mm across and have five to seven amphiphloic cauline bundles that are capped internally and externally by sclerenchyma. Ground tissue, where well preserved, is transitional from arenchymatous to parenchymatous, with abundant small sclerotic nests found throughout the pith and cortex. Multicellular scales are borne on the rhizome but are sparse and do not imbricate. At least three orders of frond material are preserved: stipes, primary pinnae, and laminar pinnules. Stipes have an adaxial groove, two adaxial hippocampiform bundles, and seven or fewer small, circular bundles arranged in an abaxial U-shaped arc. In distal sections of the rachis, the vascular bundles are reduced to three or fewer. Ground tissue of the stipe has sclerenchyma nests near the base but distally becomes completely arenchymatous, further evidence that the Princeton Chert preserves an ancient wetland environment. This fossil material expands our knowledge of fern diversity from the Princeton Chert locality, which also includes osmundaceous, dennstaedtioid, and dryopterid ferns, and it contributes to the understanding of the timing and evolution of derived Filicales. While the vegetative anatomy of this fern allies it with the Blechnaceae, the lack of attached fertile fronds precludes the possible recognition of *T. princetonensis* as a fossil representative of a modern genus or perhaps even a living species.

Keywords: Blechnaceae, Eocene, Filicales, fossil fern, Princeton Chert.

Introduction

The Middle Eocene Princeton Chert locality is well known for its diversity of ferns, conifers, fungi, and flowering plants. To date, one taxodiaceous and two pinaceous conifers, 19 dicots, six monocots, numerous fungi, and several ferns have been recognized (Pigg and Stockey 1996), with additional taxa yet to be described. Many of these are represented by numerous specimens of vegetative and fertile organs, allowing a number of whole-plant reconstructions. Five leptosporangiate ferns representing four families are known from the Princeton Chert: *Dennstaedtiopsis arenchymata* Arnold et Daugherty (Basinger and Rothwell 1977) (Dennstaedtiaceae); *Makopteris princetonensis* Stockey, H. Nishida et Rothwell (Stockey et al. 1999) (Dryopteridaceae); *Dickwhitea allenbyense* Karafit, Rothwell, Stockey et H. Nishida (Karafit et al. 2006) (Dryopteridaceae); *Osmunda* stipes (Osmundaceae); and blechnoid rhizomes and fronds (Blechnaceae; Basinger 1976, 1981; Pigg and Stockey 1996; Stockey et al. 1999).

The family Blechnaceae is composed of nine living genera in two subfamilies (*sensu* Kramer et al. 1990a). The family is found worldwide in many different habitats, with the genus *Blechnum* L. most common in the Southern Hemisphere, *Wood-*

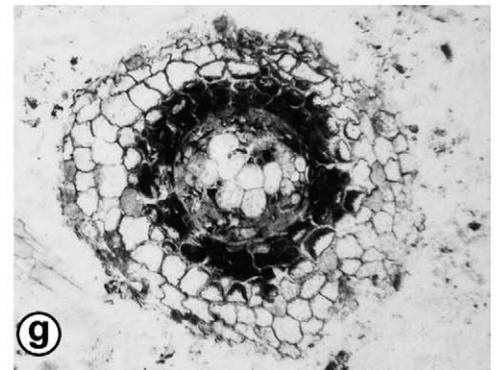
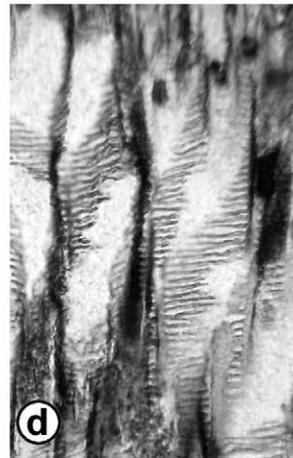
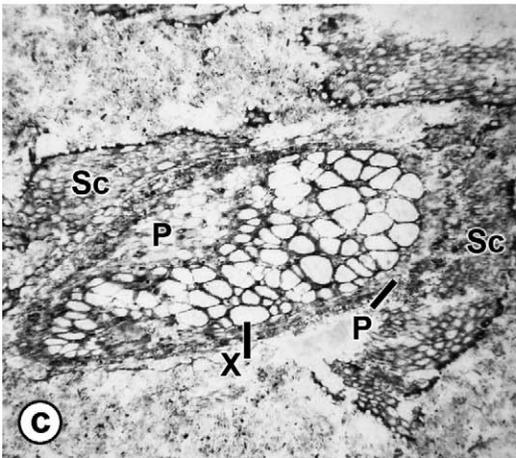
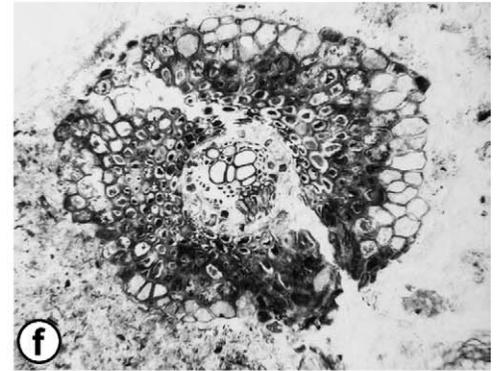
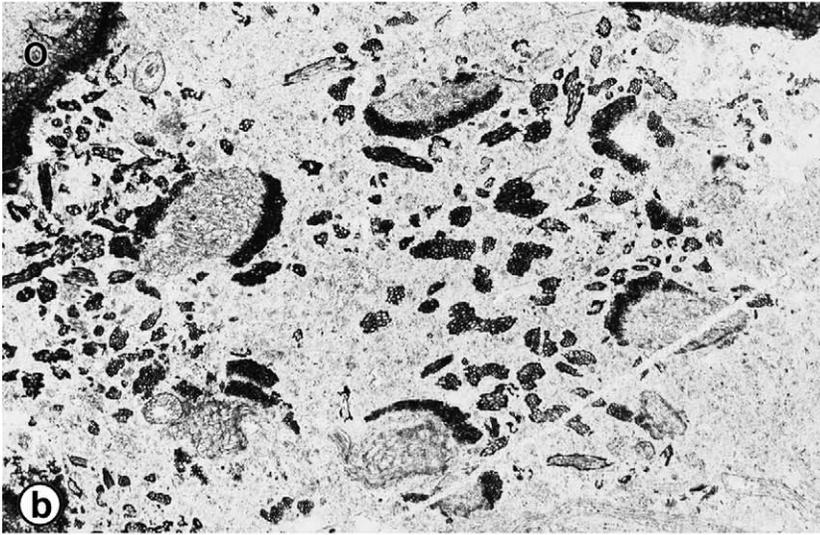
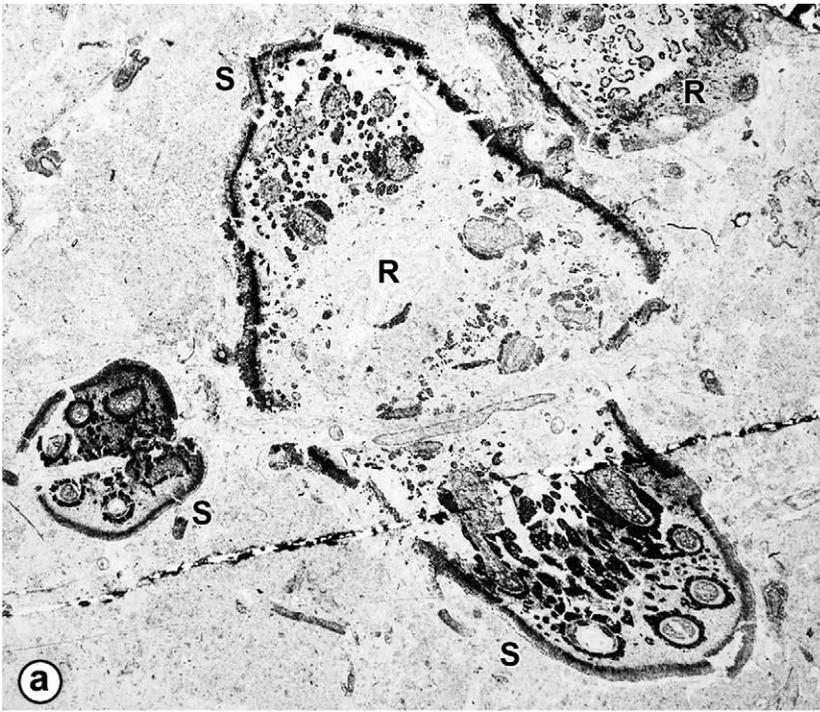
wardia J. E. Smith most common in the Northern Hemisphere, and the seven other genera with an Asiatic-Australasiatic-Pacific distribution (Kramer et al. 1990a). In phylogenetic analyses, Blechnaceae is monophyletic (Hasebe et al. 1995; Cranfill and Kato 2003), but sister group relationships (and indeed all relationships among derived Filicales) remain unresolved. It is probable that a better understanding of the fossil record of ferns will help us unravel these phylogenetic relationships.

In this article, we describe a newly recognized permineralized blechnoid in the Princeton Chert as a new genus and species. *Trawetsia princetonensis* Smith, Stockey, Nishida & Rothwell gen. et sp. nov. is based on interconnected rhizomes, roots, and vegetative frond parts of several orders. This fern has allowed us to gain a better understanding of both the leptosporangiate fern component of the Middle Eocene Princeton Chert biota and the environment of growth for many of the Princeton Chert plants.

Material and Methods

Fossils were collected from the Princeton Chert outcrop, located on the east bank of the Similkameen River, 8.4 km south of the town of Princeton, British Columbia, Canada (Boneham 1968). The outcrop consists of interbedded layers of chert and coal with an occasional ash layer (Stockey 1983). There are ca. 49 chert layers, but these split and

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anastomose to make ca. 70 individual beds ranging in thickness from 1 to 50 cm. The Princeton Chert is part of the Princeton Group, Allenby Formation (Boneham 1968). A Middle Eocene age has been determined based on data from freshwater fish (Wilson 1977, 1982), mammals (Russell 1935; Gazin 1953) and K-Ar dating (Hills and Baadsgaard 1967). The ash of layer 22 is currently dated at 48.7 million years old (H. Baadsgaard, personal communication, 1999).

Fossils of this fern are found in chert collected from disaggregated, loose material at the base of the outcrop (layers unknown). The most abundant co-occurring plant remains are those of *Dennstaedtiopsis aerenchymata* Arnold et Daugherty. More rarely, conifer stems, leaves and roots, *Uhlia allenbyensis* Erwin et Stockey leaf material, *Decodon allenbyensis* Cevallos-Ferriz et Stockey roots, an undescribed type of monocot axis, and/or stems of *Eorhiza arnoldii* Robison et Person are also found in association with the fern described in this article.

Chert blocks were cut into slabs and studied using the cellulose acetate peel technique (Joy et al. 1956) modified for concentrated (48%) hydrofluoric acid (Basinger and Rothwell 1977; Basinger 1981). Peels were mounted on microscope slides using Eukitt (O. Kindler, Freiburg, Germany) xylene-soluble mounting medium. Images were captured with a PowerPhase digital scanning camera (Phase One, Fredriksberg, Denmark) and a MicroLumina digital scanning camera (Leaf Systems, Bedford, MA). Photographs were processed with Adobe Photoshop 6.0.

Systematics

Order—Filicales

Family—Blechnaceae

Genus—*Trawetsia* gen. nov. Smith,
Stockey, H. Nishida et Rothwell

Generic diagnosis. Rhizomes erect, scaly, radial, dictyostelic; pith and cortex with abundant sclerenchyma bundles; five to seven cauline vascular bundles, capped internally and externally by sclerenchyma. Roots diarch. Stipe traces arising from all sides of rhizome; adaxial bundles dividing to produce additional abaxial bundles. Fronds bipinnate; stipe with adaxial groove, two hippocampiform adaxial bundles, round abaxial bundles; abaxial bundles reduced to one distally. Stipe ground tissue with sclerenchyma bundles at base, aerenchymatous distally.

Species—*Trawetsia princetonensis* sp. nov. Smith,
Stockey, Nishida et Rothwell (Figs. 1–4)

Specific diagnosis. Rhizomes 7–16 mm in diameter, amphiphloic, metaxylem tracheids angular in cross section.

Stipes with seven or fewer abaxial bundles. Immature stipes 1 × 2 to 2 × 4 mm in cross section; outer sclerotic zone up to five cells thick; mature stipes 2.5 × 3 to 5.5 × 9 mm in cross section; sclerotic hypodermis up to 10 cells thick. Distal rachides 1.0 × 3.75 to 2.5 × 5.0 mm in cross section, parenchymatous, sclerotic hypodermis four to eight cells thick. Pinnae 0.75 × 1.0 mm in cross section, parenchymatous, sclerotic hypodermis two to four cells thick. Pinnules with two bundles at base. Pinnule lamina 112–192 μm thick. Roots 0.5–0.7 mm in diameter, diarch, inner cortex sclerotic, outer cortex parenchymatous.

Holotype. P1247 A, B₃, B₄, B₅, C.

Paratypes. P1182 C₂, D; P1233 C, D; P1247 D–H; P1330 G; P1345 A, B; P1350 B, C; P1573 A,B; P1645 E; P2793 B; P2917 D; P5110 B, D; P5161 E, F; P5124 A–C; P5125 A; P5126 A₁, B–G; P5129 G, H, I; P6594 A, B₁–D₁, E–I.

Etymology. The generic name *Trawetsia* (namely, “Stewart” spelled backward plus “ia”) is proposed in honor of the late Wilson N. Stewart, University of Alberta, who supervised the first systematic collecting and description of the Princeton Chert and its flora. The specific epithet *princetonensis* recognizes that the material is from Princeton, British Columbia.

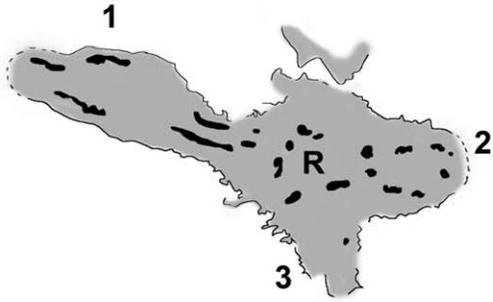
Type locality. Middle Eocene, Princeton Chert, British Columbia.

Description

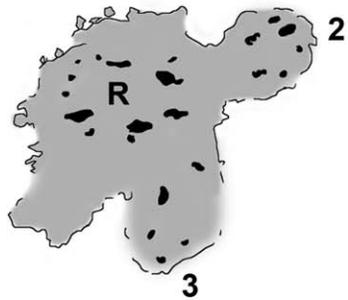
The description of *Trawetsia princetonensis* is based on a combination of interconnected vegetative organs including a total of 12 rhizomes, ca. 35 stipes, and seven groups of additional higher-order frond members (figs. 1, 3, 4). Specimens range from excellently preserved (fig. 3c) to those with only partially preserved tissues (fig. 4a) and to specimens that are torn and fragmented with penetrating roots of other plants (fig. 4a).

Rhizomes. Rhizomes (fig. 1a) are 7–16 mm in diameter and are frequently distorted and broken by preservation processes (fig. 1b). Roots and stipes arise from all sides of the rhizome (fig. 1a; fig. 2a, 2b, 2f, 2h), and the holotype specimen shows the rhizome dichotomizing (fig. 2). Together, these features indicate that the stem was not dorsiventral, but erect. The dictyostele has five to seven amphiphloic cauline vascular bundles (fig. 1a, 1b). These bundles are capped on the inside and the outside by sclerenchyma (fig. 1b, 1c). Metaxylem tracheids are up to 156 μm in diameter and angular in transverse section, with scalariform secondary wall thickenings on radial walls (fig. 1c, 1d). Protoxylem is not typically well differentiated, although the smallest cells are 12 μm in diameter. Phloem is often not well preserved; however, when recognized, it is represented by a region of cells

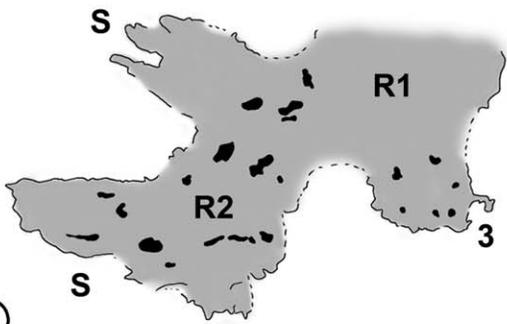
Fig. 1 Rhizomes and roots of *Trawetsia princetonensis* gen. et sp. nov. *a*, Cross section of rhizome (R) showing central stele and one free and two departing stipes (S). Holotype P1247 C top #14 × 6. *b*, Cross section of central dictyostele showing six cauline vascular bundles capped by sclerenchyma, abundant sclerenchyma bundles in pith and cortex, and outer heterogeneous zone (O). Holotype P1247 B top #15 × 14. *c*, Cauline vascular bundle showing sclerenchyma caps (Sc), amphiphloic phloem (P), and xylem (X). Paratype P6594 A #10 × 38. *d*, Scalariform pitting on xylem. Paratype P6594 A #10 × 310. *e*, Outer heterogeneous zone of rhizome with scales (arrows). Holotype P1247 B₃ top #1 × 21. *f*, Cross section of root near divergence point showing conspicuous sclerotic inner cortex. Paratype P6594 A #14 × 66. *g*, Distal cross section of root showing inner sclerotic cortex and outer parenchymatous cortex. Holotype P1247 B₃ bot #14 × 104.



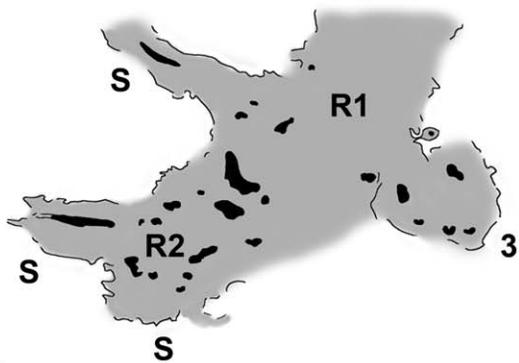
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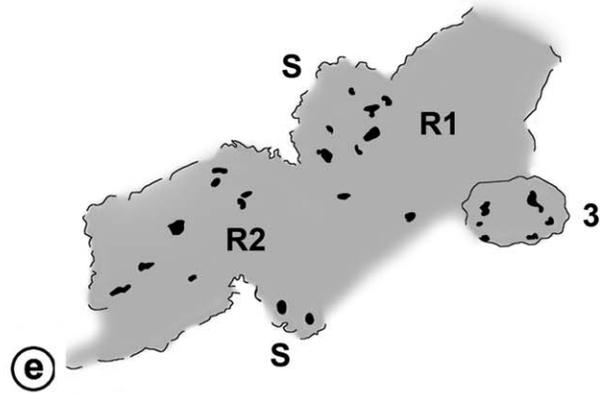
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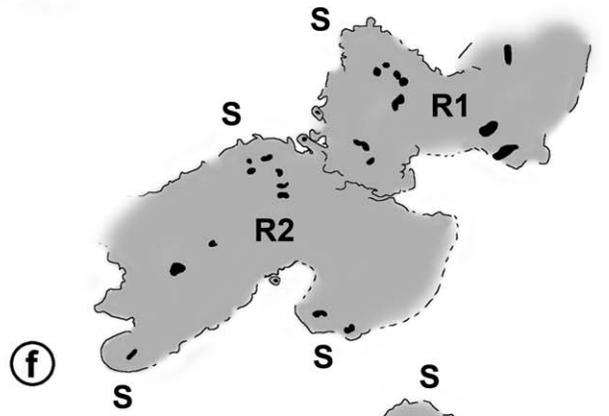
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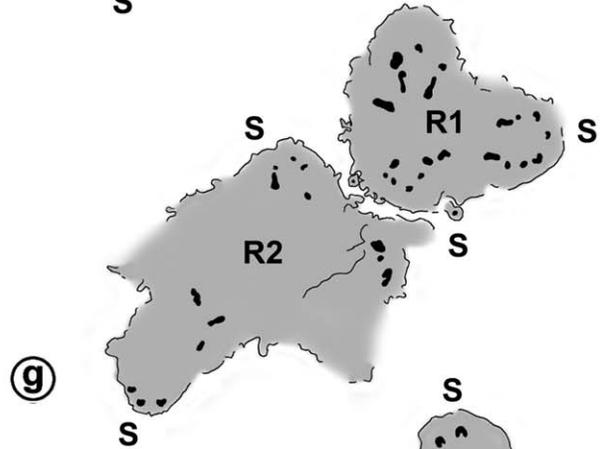
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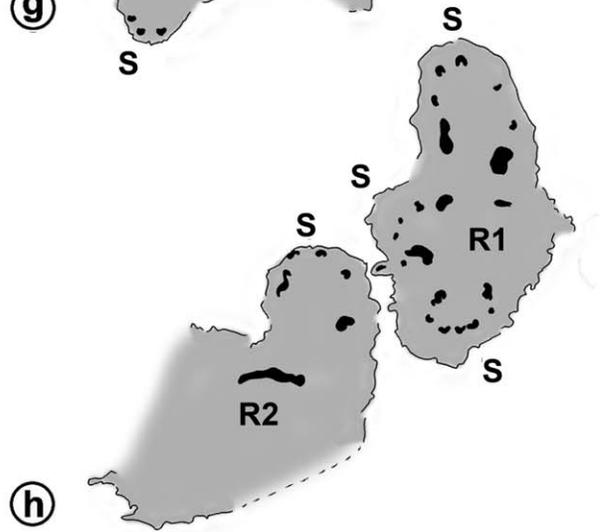
(e)



(f)



(g)



(h)

ca. 60 μm thick adjacent to the metaxylem (fig. 1c). Ground tissue in the rhizome is incompletely preserved. The pith has many fiber bundles that extend into the cortex distally (fig. 1a, 1b). The cortex of the rhizome is characterized by a sclerotic hypodermis, four to six cells thick, and an incompletely preserved epidermis of thin-walled cells, three to four cells thick, from which multicellular scales arise (fig. 1e). Roots are 0.5–0.7 mm in diameter. They are diarch and show a sclerotic inner cortex and parenchymatous outer cortex that corresponds to the “*Dennstaedtia* type” of Schneider (1996) (fig. 1f, 1g).

Stipes. Stipes measure from 1×2 to 5.5×9.0 mm in diameter. Stipe traces originate as two hippocampiform bundles that each divide again several times to give rise to five to seven smaller, circular abaxial bundles (fig. 3a). Ground tissue of the diverging stipes contains abundant nests of sclerenchyma (fig. 3a). Stipes lack stipules and arise from all sides of the rhizome (fig. 1a; fig. 2a, 2b, 2f, 2h). Distal to the level of divergence from the rhizome, stipes are aerenchymatous with an adaxial groove, a pair of pneumatophores on the lateral sides, two adaxial hippocampiform bundles, and a U-shaped string of abaxial bundles (fig. 3b). Each leaf trace is surrounded by a sheath of cells with dark contents.

Several different ontogenetic stages and taphonomic states of stipes are preserved in the chert matrix. Immature stipes, or stipe tips, have an almost uniformly aerenchymatous ground tissue, lack sclerenchyma (fig. 3c), and measure 1×2 to 2×4 mm in cross section. Metaxylem tracheids are angular in cross section. Vascular bundles are surrounded by a sclerenchymatous sheath with dark cell contents (fig. 3d). The sclerotic hypodermis measures up to five cells thick. In contrast, more mature stipes, or stipe bases, are larger in size, measuring 2.5×3.0 to 5.5×9.0 mm in cross section, with a well-developed sclerotic hypodermis up to 10 cells thick (fig. 3b). Cells of the vascular bundle sheath have more internal dark contents than in the immature stipes, giving them a darker, thicker appearance (fig. 3d, 3e). At the level where stipe bases diverge from the rhizome, the ground tissue has abundant sclerenchyma (fig. 3a). At more distal levels, the stipe is entirely aerenchymatous (fig. 3b), but there is a transition area where the aerenchyma has interspersed sclerenchyma bundles (fig. 3f). Other stipes found in the chert have mature vascular bundles, and the cortex has a shrunken, spiky outline in cross sections (fig. 3g). These latter specimens probably represent old, dried-up stipes that have remained near the plant.

Stipe preservation is remarkably varied in the chert. Often they are cracked, distorted, fragmented; sometimes dramatically so (fig. 4a). The immature stipes, lacking well-developed sclerenchyma, are simply mildly distorted (figs. 3c, 4a). However, stipes with a thick outer sclerotic zone are

often cracked and broken open (figs. 3b, 4a). Tissue preservation is variable; sometimes all the cells in a stipe are preserved, while a neighboring stipe will be lacking much of the ground tissue and cellular details of the vascular bundles.

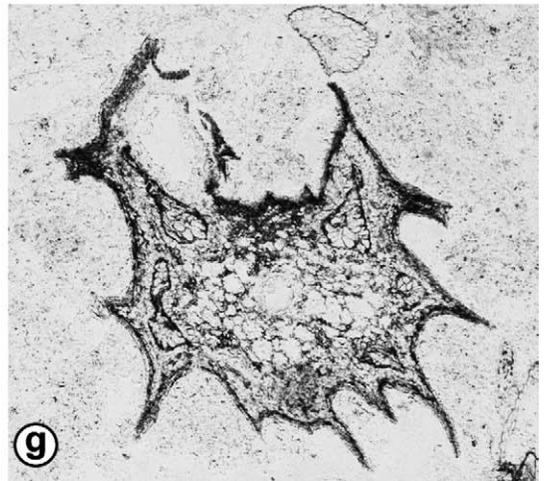
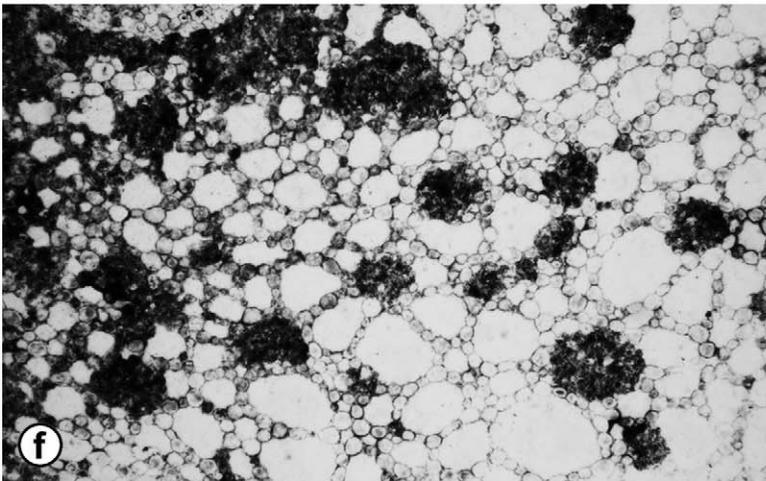
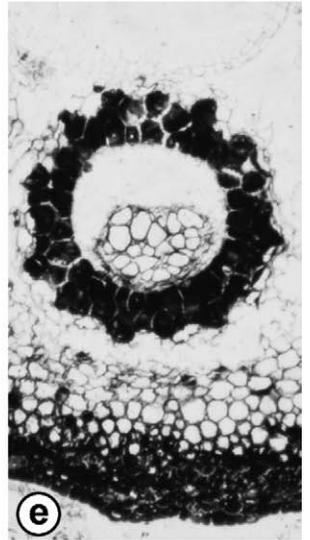
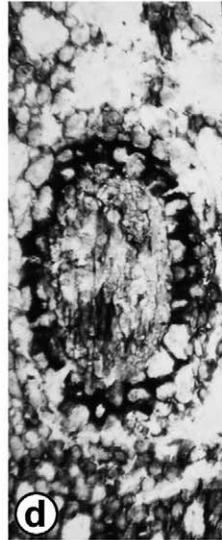
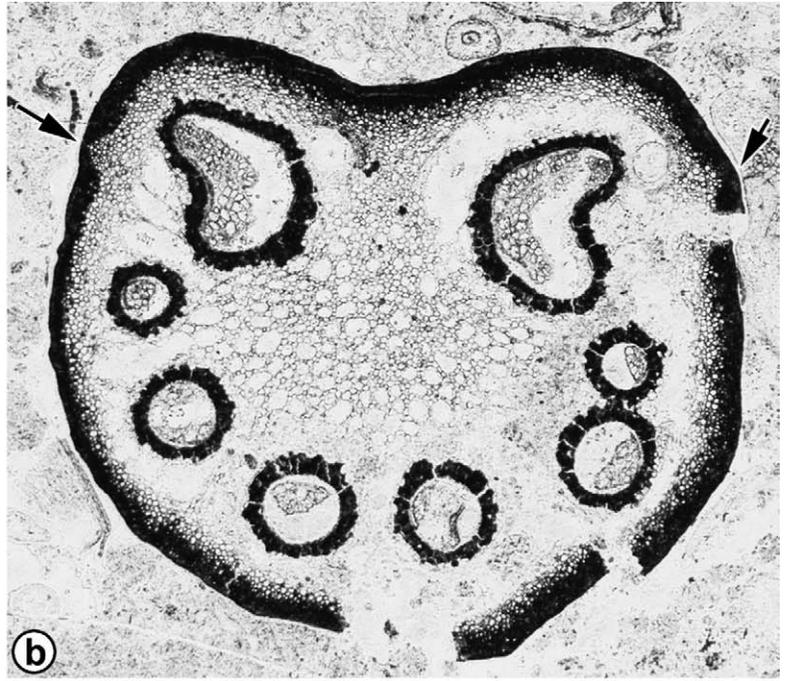
Higher frond members. Distal sections through rachides and primary pinnae show a reduced number of vascular bundles: two hippocampiform and one (occasionally two) abaxial bundle(s) (fig. 4b). At this level, the frond members measure 1.0×3.75 to 2.5×5.0 mm in cross section. A prominent groove is present on the adaxial side of the stipe/rachis, and inner ground tissue is completely parenchymatous, grading to an outer layer of thick-walled cells four to eight cells thick (fig. 4c). Some chert blocks preserve primary pinnae with secondary pinnae next to them. These smaller secondary pinnae are 0.75×1.0 mm in cross section (fig. 4b, arrows). They have two hippocampiform bundles, an adaxial groove, and parenchymatous ground tissue, with only two to four thicker-walled cells to the periphery. Laminae arise from the edges of the smaller pinnae (fig. 4d). Pinnules are 112–192 μm thick and composed of indistinct cells with dark contents.

Discussion

Trawetsia princetonensis from the Princeton Chert locality has rhizomes and vegetative frond parts with well-preserved internal anatomy similar to that of several living species of dryopteroid Dryopteridaceae and Blechnaceae (Ogata 1928–1933; Ogura 1972; Kramer et al. 1990a, 1990b). While the stipes of some dryopteroids have multiple bundles in an abaxial petiolar arc like *Trawetsia*, these stipes tend to have small adaxial hippocampiform bundles with a reduced hook in the xylem, and they lack the prominent adaxial groove at the stipe base (Ogata 1928–1933; Ogura 1972; Kramer et al. 1990b) that are characteristic of *Trawetsia* and living blechnoids. However, because we have yet to find reproductive material that can be compared to extant genera, we cannot more precisely place the fossil material within family Blechnaceae.

Anatomical features of most living species of *Blechnum* have not been studied in detail; however, a few have been examined by Bower (1914, 1928). Among those, the vascular system of *Trawetsia* is most similar in general appearance to *Blechnum tabulare* (Thunb.) Kuhn., although there is no mention of the sclerenchyma bundles that are so prominent in *T. princetonensis*. White and Weidlich (1995), during their study of vascular system organization, included illustrations of cross sections of *Blechnum discolor* (Forst. f.) Keys and *Blechnum binervatum* (Poiret) C. Morton & Lellinger ssp. *acutum* (Desv.) R. M. Tryon & Stolze (= *Blechnum kunthianum* C. Chr.). However, these species both show 13 cauline

Fig. 2 Camera lucida drawings of select serial sections through 2.5 cm of the dichotomizing rhizome of the holotype P1247. a, Cross section showing stipe divergence to left and formation of stipe traces to right. A bot. b, Two stipes diverging. B₃ top. c, Rhizome, beginning to widen. B₃ bot. d, Widening rhizome with stipe diverging at bottom right. B₄ top. e, Large-diameter rhizome with stipe diverging at bottom right. B₄ bot. f, Two rhizomes as result of dichotomy. B₅ top. g, Two rhizomes producing roots toward the area of divergence; rhizome on right showing formation of three stipes. B₅ bot. h, Two distinct rhizomes, with production of stipes from all sides. C top. Black outlines represent camera lucida drawings of rhizome edge; dashed areas are inferred. Black areas inside rhizomes represent xylem. The basal three stipes (1–3) are numbered in the order of divergence for clarity, more distal stipes are labeled S, and rhizomes are labeled R (R1 and R2 to denote the dichotomizing axis). All $\times 3$.



meristeles, in contrast to five to seven in *Trawetsia*. No sclerenchyma is associated with meristeles of these two living species, and *B. discolor* has a central core of sclerenchyma in the pith instead of numerous distinct strands as in *Trawetsia*. In addition, *B. binervatum* ssp. *acutum* appears to lack sclerenchyma in the ground tissue.

In comparison to other extant genera of the Blechnaceae, *Trawetsia* shares some similarities with rhizomes of *Woodwardia virginica* (L.) J. E. Smith but differs in having cauline bundle sheaths, more cauline bundles, and sclerenchyma in the pith and cortex. *Woodwardia areolata* (L.) T. Moore and *Woodwardia radicans* (L.) Smith differ in the distribution of sclerenchyma in the ground tissue (Lucansky 1981). *Woodwardia radicans* has a very small rhizome, up to 5 mm (Lucansky 1981), unlike *Trawetsia*, which is up to 16 mm. Rhizomes of the three species examined by Lucansky (1981) all show some degree of aerenchymatous ground tissue. Determination of possible ground tissue in *Trawetsia* will have to await the discovery of rhizomes with well-preserved ground tissue. Finally, rhizomes of *Trawetsia* are clearly unlike those of *Stenochlaena* J. Smith, which have numerous smaller bundles in their cortex (Mehra and Chopra 1951).

Stipes of *W. virginica* as figured by Lucansky (1981) are very similar to those of *Trawetsia*, showing aerenchyma, two hippocampiform bundles, five abaxial bundles, and an adaxial groove and sclerotic hypodermis. Stipes of *W. areolata* are aerenchymatous like those of *Trawetsia*, but *W. areolata* only has a total of two (to four) vascular bundles (Lucansky 1981), unlike our fossil with a total of seven to nine vascular bundles. Lucansky's (1981) examination of stipes of *W. radicans* showed no aerenchyma in the ground tissue, and there are only two to three abaxial bundles, in contrast to five to seven in *Trawetsia*. Because of lack of detailed anatomical information for the rhizomes and stipes of other living blechnoid ferns, further comparisons cannot be made at this time.

Fossils assigned to Blechnaceae are found throughout Europe and North America, the most abundant of which are compression fossils from the Paleocene to Miocene and include both vegetative and fertile pinnae (Smith 1938; Hurnick 1976; Collinson 2001). The only previously described permineralized blechnoid fossils are from western North America. Whole plants identical to *W. virginica* are known from the Miocene Yakima Canyon (Pigg and Rothwell 2001). Those fossils are virtually identical to living plants of *W. virginica* and differ from *Trawetsia* in the same features discussed above. An additional blechnoid or dryopteroid rhizome with attached stipes, *Midlandia nishidaei*, occurs in late Cretaceous sediments near Drumheller, Alberta (Serbet 1997; Serbet and Rothwell 2006). Stipes of *Midlandia* have two hippocampiform bundles and one to four abaxial bundles (Serbet and

Rothwell 2005), in contrast to the stipes of *Trawetsia*, which have up to seven abaxial bundles. These two genera also differ in the mode of leaf trace production: *Midlandia* produces all stipe bundles directly from the cauline bundles like *Woodwardia* (Serbet and Rothwell 2006), but *Trawetsia* produces hippocampiform bundles from the cauline vasculature that subsequently divide to form the smaller abaxial stipe traces, as do some species of *Blechnum* (Bower 1914). In addition, *Midlandia* lacks the prominent sclerotic nests and bundle sheaths found in rhizomes and frond parts of *Trawetsia*.

Higher-order frond parts of *Trawetsia* also show typical blechnoid characters. They are adaxially grooved and have several abaxial bundles arranged in a U-shaped arc (Ogura 1972; Kramer et al. 1990a). The adaxial bundles conform to the hippocampiform shape that is shared by dryopterid and blechnoid ferns, but smaller bundles located between the hippocampiform traces are found only in Blechnaceae (Ogura 1972). Anatomy of the fronds of other blechnoids has not yet been investigated, so detailed comparison is not currently possible.

Variation in anatomical structure of these fossils has allowed us to detail some of the developmental changes that occur in the fronds (fig. 4a). Immature stipes have a weakly sclerotic hypodermis, and bundle sheath cells lack dense contents. In mature stipes, the hypodermis is distinct, thick, and sclerotic, and bundle sheath cells have very dark contents.

In addition, the mode of preservation will help us to understand the taphonomy of the Princeton site as a whole. While some misshapen stipes are simply old and dried up, other younger, less sclerotic tissues are somewhat distorted, and some stipes have been cracked and deformed after burial. This indicates that there was a range of factors affecting the preservation of various types of organs. Penetrating roots in the fern stipes and rhizomes indicate that some of the ferns represent earlier vegetation that underwent a period of decomposition before fossilization. Secondary quartz infiltration is apparent in the matrix and in the fern remains, indicating that the chert and fossils within were also affected by post-diagenetic processes.

Aerenchyma characterizes stipes of *Trawetsia*, and we await discovery of well-preserved rhizomes of *Trawetsia* to determine whether the rhizome ground tissue was aerenchymatous, as in some species of *Woodwardia* (Lucansky 1981). The presence of aerenchyma in *Trawetsia* provides further evidence that the Princeton Chert represents an aquatic or semiaquatic habitat (Cevallos-Ferriz et al. 1991). Aerenchymatous ground tissues are also known in several previously described aquatic to semiaquatic plants from the Princeton Chert (e.g., *Dennstaedtiopsis aerenchymata* Arnold et Daugherty, *Eorhiza arnoldii* Robison et Person; *Heleophyton helobiaeoides* Erwin et Stockey;

Fig. 3 Frond members of *Trawetsia princetonensis* gen. et sp. nov. *a*, Diverging stipe in cross section. Note abundant sclerenchyma in ground tissue and hippocampiform bundle dividing to produce fifth abaxial bundle (arrow). Holotype P1247 C top #14 \times 10. *b*, Mature stipe in cross section showing typical blechnoid anatomy: adaxial groove, pair of pneumatophores (arrows), two adaxial hippocampiform bundles, six abaxial bundles, aerenchymatous ground tissue, and well-developed outer sclerotic zone. Holotype P1247 B₅ top #10 \times 19. *c*, Immature stipe in cross section. Paratype P5126 C bot #13 \times 24. *d*, Abaxial bundle of immature stipe showing sheath. Holotype P1247 B₃ bot #14 \times 72. *e*, Abaxial bundle of mature stipe showing well-developed bundle sheath with dark cellular contents. Holotype P1247 B₃ bot #14 \times 58. *f*, Ground tissue of stipe showing transition zone: aerenchymatous with sclerenchyma bundles. Paratype P6594 D₁ bot #5 \times 63. *g*, Older, desiccated stipe in cross section. Holotype P1247 B₃ top #9 \times 22.

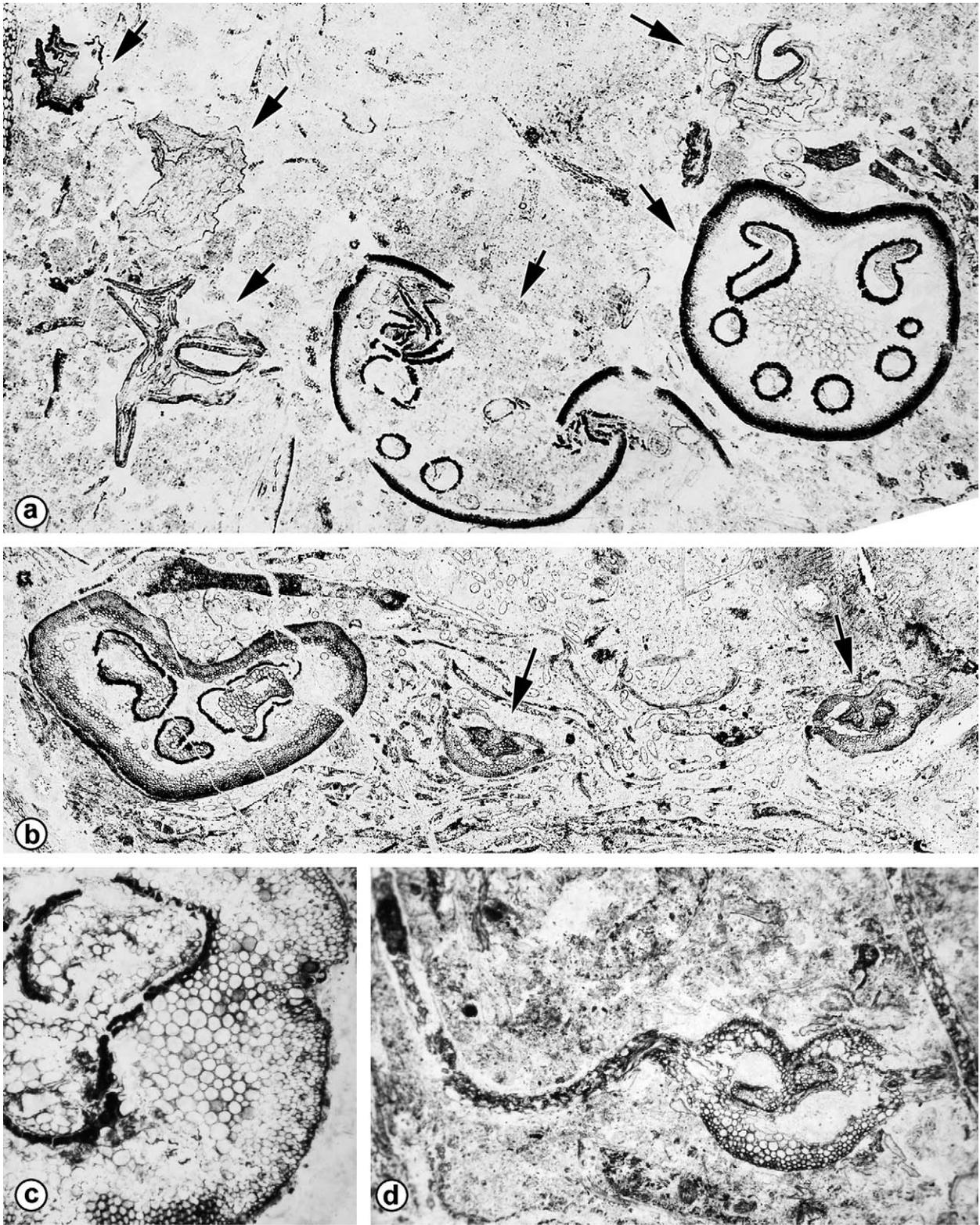


Fig. 4 Frond members of *Trawetsia princetonensis* gen. et sp. nov. *a*, Differential preservation of six stipes (arrows) in one slab. Holotype P1247 C bot #6 $\times 10$. *b*, Cross sections through distal frond members; primary pinna showing two adaxial hippocampiform bundles and one abaxial bundle with prominent outer sclerotic zone and two smaller secondary pinnae (arrows), each with two hippocampiform bundles and traces to laminae. Paratype P 5129 I top #17 $\times 14$. *c*, Cross section of pinna showing parenchymatous ground tissue. Paratype P5129 H top #11 $\times 45$. *d*, Pinna with lamina. Paratype P5129 G bot #11 $\times 40$.

Ublia allenbyensis) and the habitats of growth known for closely related living species. In this regard, the rhizomes of *Trawetsia* were probably buried in growth position.

While *T. princetonensis* is not the oldest or most complete fossil blechnoid known, these specimens represent an important contribution to the Eocene fossil record of derived Filicales and add to our ever-growing understanding of the environment represented by the Princeton Chert. *Trawetsia* provides additional evidence that the family Blechnaceae was well developed in western North America by the early Tertiary. Whether *T. princetonensis* is an extinct member of Blechnaceae showing a mosaic of characters or an extant species awaits the discovery of its reproductive structures. In ei-

ther case, *Trawetsia* enriches our knowledge of the enigmatic fossil record for highly derived filicalean ferns in the Tertiary and provides additional evidence to ultimately resolve the overall pattern of phylogeny for leptosporangiate ferns.

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