

COMBINING CHARACTERS OF PTERIDACEAE AND TREE FERNS: *PTERISORUS RADIATA* GEN. ET SP. NOV., A PERMINERALIZED LOWER CRETACEOUS FILICALEAN WITH RADIAL SORI

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An anatomically preserved leptosporangiate filicalean that combines characters of the Pteridaceae and tree ferns has been discovered in the Lower Cretaceous (Valanginian-Hauterivian boundary) Apple Bay flora on Vancouver Island, Canada. Exindusiate sori are radial, with numerous annulate sporangia diverging from a conical receptacle that is positioned below a pinnule vein. No paraphyses or other trichomes are present. Sporangia have a nearly vertical annulus that is not interrupted by the long, quadriseriate stalk. Spores are trilete and angular, with a distinctive equatorial flange and a distal deltoid structure that contacts the rim at the corners of the spore. The suture extends three-fourths of the distance to the margin and is flanked by prominent ridges. Spore walls consist of two dense layers, and the surface is psilate. *Pterisorus radiata* gen. et sp. nov. has characters that are reminiscent of both tree ferns and the most highly derived of modern species, providing direct evidence for the third major radiation of Filicales.

Keywords: Cyatheaceae, filicalean fern, fossil, Pteridaceae.

Introduction

Because extinct species often display novel combinations of characters, fossil plants provide vital data for generating and testing evolutionary and systematic hypotheses and for establishing the minimum ages of clades. The fossil record also reveals that the pattern of leptosporangiate fern phylogeny is punctuated by three major radiations (Rothwell 1987), the last of which produced several highly derived filicalean clades during the Cretaceous and Cenozoic (Lovis 1977). Although there is considerable variation, these highly derived Filicales are commonly grouped as blechnoid, dryopteroid, pteroid, and/or polypodioid lineages in contemporary compilations and classifications (Tryon and Tryon 1982; Kramer and Green 1990; Hasebe et al. 1995; Smith 1995).

By contrast, the overall pattern of fern phylogeny remains a matter of dispute. Whereas some authors consider ferns to be a polyphyletic assemblage comprising several distantly related clades with fernlike characters that have evolved in parallel, others view ferns as a clade that also includes living psilotophytes and equisetophytes (Rothwell 1999; Pryer et al. 2001; Schneider et al. 2004; Rothwell and Nixon 2006). Within this context, one might expect extinct species from the periods of time when the most rapid diversifications were in progress to be attractive candidates for helping to resolve the apparently conflicting data and competing hypotheses.

The Apple Bay assemblage of fossil plants from Vancouver Island in western Canada is particularly well suited for furthering our understanding of fern evolution and phylogeny because of its rich taxonomic diversity, delicate anatomical

preservation, and Early Cretaceous age. Apple Bay fossils were deposited during the Neocomian of the Lower Cretaceous, during the early stages of the third major leptosporangiate radiation (Lovis 1977; Rothwell 1987), before the most highly derived filicalean ferns had become common outside the region that is now Siberia, northeast China, and Korea (Deng 2002). Indeed, the Apple Bay material comprises one of the most diverse fossil assemblages of vascular and non-vascular cryptogams ever discovered, with many specimens displaying details of anatomical preservation that are unknown from other floras of comparable age (Rothwell and Stockey 2003; Stockey 2004).

To date, we have identified nearly two dozen types of leptosporangiate ferns and fern organs that are assignable to the Osmundaceae, Gleicheniaceae, Dipteridaceae, Schizaeaceae, Dicksoniaceae, Cyatheaceae, and Dennstaedtiaceae s.l., as well as some specimens that are more difficult to classify and that could represent evidence for early stages of the third leptosporangiate radiation (Rothwell and Stockey 2003; Stockey 2004). Among the latter are exindusiate radial sori attached below veins on thin pinnule laminae. These sori combine characters of the tree ferns and of taenitoid species of the Pteridaceae and are named *Pterisorus radiata* gen. et sp. nov. The purpose of this article is to describe these soral sporangia and spores and to evaluate their relationships to both the tree fern clade and the Pteridaceae.

Material and Methods

The fertile frond material occurs in a calcareous marine nodule collected at the Apple Bay locality along Quatsino Sound, northern Vancouver Island, British Columbia (50°36'21"N,

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127°39'25"W; UTM 9U WG 951068; Smith et al. 2003). Sediments from which the nodule was collected have been regarded as equivalent to the Lower Cretaceous (Valanginian-Barremian) Longarm Formation (Jeletzky 1976; Haggart and Tipper 1994), corresponding to Jeletzky's (1976) Barremian variegated clastic unit (Sweet 2000). However, a recent isotope analysis has narrowed the age to the Valanginian-Hauterivian boundary (D. R. Gröcke, McMaster University, personal communication, 2005), thus placing the deposits within the Neocomian.

Anatomical sections were prepared by the cellulose acetate peel technique (Joy et al. 1956), mounted on glass microscope slides with Eukitt (O. Kindler, Freiburg, Germany), and photographed using a Phase One digital studio camera (Phase One, Frederiksberg, Denmark) mounted on a Leitz Aristophot bellows camera. Spores were either examined on inverted peels or were removed from cellulose acetate peels for scanning electron microscopy using a modified Daghlia and Taylor (1979) technique under vacuum on a Millipore filter (Millipore, Bedford, MA). Stubs were coated with 100 Å Au on a Nanotek sputter-coater and examined using a JEOL 6301F scanning electron microscope at 5 kV. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

Systematics

Order—*Filicales*

Family—*Unknown*

Genus—*Pterisorus* Rothwell et Stockey gen. nov.

Diagnosis. Anatomically preserved fertile pinnules of homosporous leptosporangiate ferns with abaxial exindusiate sori positioned below veins. Sori radial, sporangia with elongated stalks, and capsule with oblique to nearly erect annulus not interrupted by stalk; paraphyses absent. Spores radial, trilete, tetrahedral-globose, with prominent equatorial flange; angles projecting, forming distal deltoid structure connected to flange at corners; sporoderm of two compact layers.

Species—*Pterisorus radiata* Rothwell et Stockey sp. nov. (Figs. 1, 2)

Diagnosis. Pinnule lamina with undifferentiated mesophyll, tracheids with scalariform thickenings. Sori radial, ca. 700–800 μm in diameter, with 20–28 sporangia; capsule 260 – 300 \times 145 – 160 μm ; stalk quadriseriate, 140–200 μm long. Annulus with 13–17 cells. Spores 36–48 μm , with coarse ridges flanking arms of trilete; surface psilate, sometimes with minute undulations between ridges and flange. Inner exospore layer 0.3 μm thick, expanding to 2 μm at flange and ridges; outer layer uniformly 0.15 μm thick.

Etymology. The generic name *Pterisorus* (*pteris* = fern + *sorus* = sorus) refers to the fertile structures of this leptosporangiate fern.

Holotype. Pinnule with attached sori on P13135 E top, figures 1, 2; deposited in the UAPC-ALTA.

Etymology. The specific epithet *radiata* reflects the radial shape of the sorus.

Stratigraphic occurrence. Longarm Formation equivalent.

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

Description

Pterisorus radiata is represented by a single anatomically preserved pinnule that bears several superficial exindusiate radial sori (fig. 1a–1c). The pinnule lamina curves gently over each sorus (fig. 1a, 1b) and is 50–60 μm thick with cells that have amber and brown contents. The epidermis is inconspicuous (fig. 1a, 1b), and no trichomes or other idioblasts have been found. Because of the dark contents of the mesophyll cells (fig. 1a, 1b), pinnule histology is somewhat obscured. Nevertheless, preservation is adequate to see that the mesophyll cells are randomly arranged and not differentiated into palisade and spongy zones (fig. 1b, at right). Veins are composed of several tracheids with scalariform secondary wall thickenings (fig. 1e).

Sori are positioned directly below a vein (fig. 1b) that extends to near the pinnule margin. In cross sections of the pinnule, the sori are 700–800 μm wide. Closely spaced serial sections reveal that sori are radial and consist of 20–28 annulate sporangia. The sporangia have narrow, relatively long stalks and ellipsoidal capsules that display a uniseriate wall (fig. 1a, 1d). Each sorus has a small hemispherical receptacle composed of cells with dark walls (fig. 1a, 1b). Sporangial stalks radiate from the receptacle (fig. 1a, 1b). They are 140–200 μm long and ca. 45 μm in diameter and are attached to the proximal end of the oval sporangial capsule (fig. 1a, 1b). Individual stalks are two to three cells long, and cross sections are composed of four cells (fig. 1c at arrow, 1f). No paraphyses or other types of trichomes are preserved (fig. 1a).

Distally, the sporangial stalk expands and attaches to the narrow, proximal end of the capsule. In longitudinal sections, the capsules are oval and vertically elongated (fig. 1a, 1c), measuring 260–300 μm long and 145–160 μm wide. Each sporangium displays a nearly vertical, uniseriate annulus that extends around ca. 70% of the margin of the capsule (fig. 1a, 1d). The annulus is positioned all along one side of the capsule and bends around both ends (fig. 1d); it is not interrupted by the stalk. The annulus consists of 13–17 cells that are larger than all other cells of the sporangial wall and that display thickened interior and lateral cell walls. By contrast, the outer-facing cell wall is quite thin (fig. 1d). The stomium is located on one side of the sporangium near the base of the capsule (fig. 1c, 1d) and is not particularly well differentiated. However, cells of the stomium are recognizable by their small size and shortness in longitudinal sections (fig. 1d, at center), as compared to other thin-walled cells of the capsule that are longitudinally elongated (fig. 1b, at arrow).

Spores fill nearly all of the sporangia (fig. 1a–1d, 1g). There are about 15 spores in a midlongitudinal section of the sporangium (fig. 1a–1d), and counts from serial sections through entire capsules indicate that the number of spores per sporangium is in the range of 64. Individual spores are radial, trilete, and angular (fig. 2a–2c), measuring 36–48 μm (mean of 100 spores = 44.4 μm), with a prominent equatorial flange (fig. 2a–2d). The laesurae are long and thin, and they are flanked by conspicuous ridges 1 μm wide. Laesurae extend about three-fourths of the distance to the equator (fig. 2a, 2b, 2d). On the distal surface, there is a raised deltoid structure with corners that connect to the equatorial flange (fig. 2c), providing an angular appearance to spores (fig. 2a–2c).

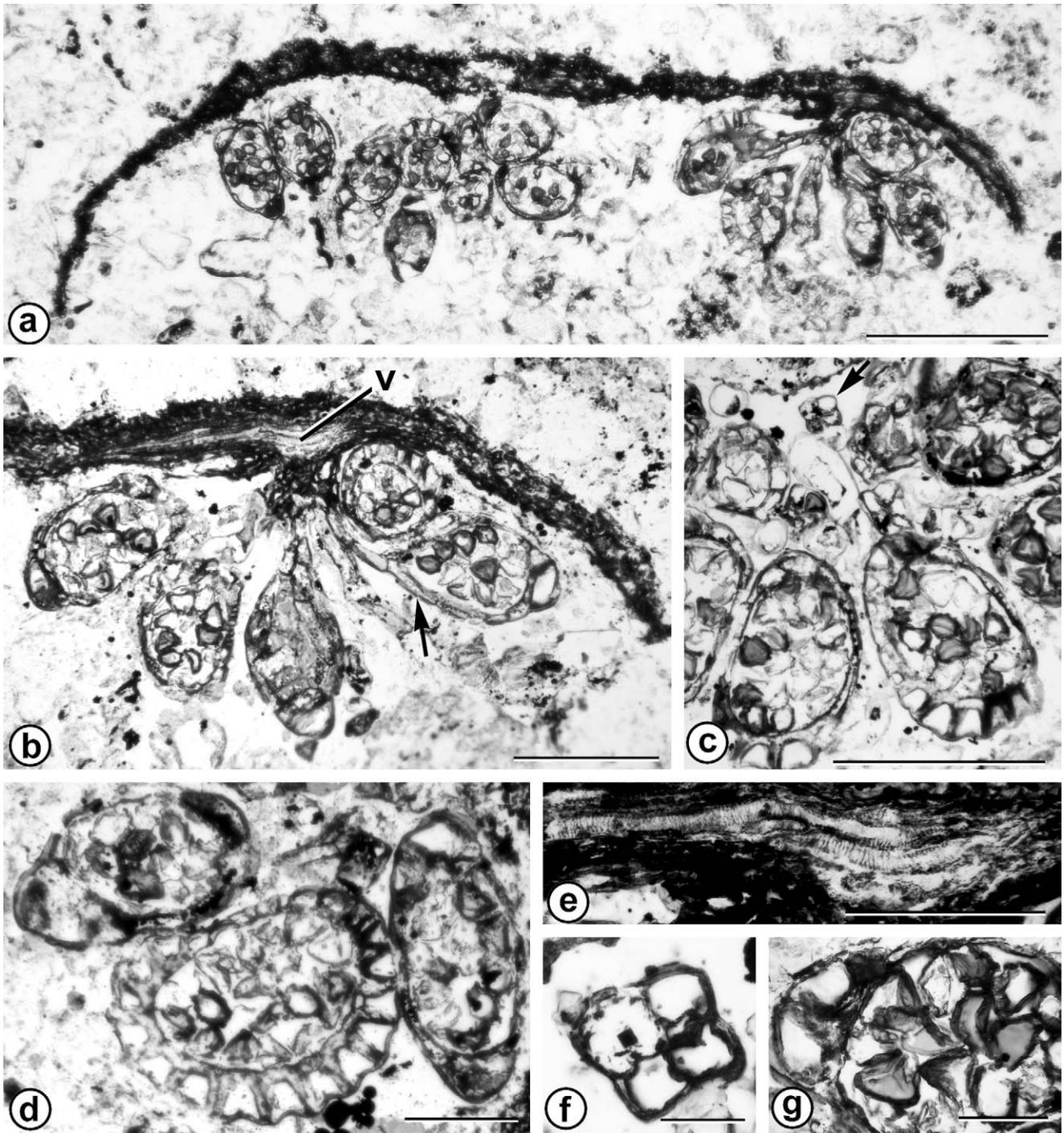


Fig. 1 *Pterisorus radiata* gen. et sp. nov. Holotype P13135 E top. *a*, Cross section of pinnule showing parts of three sori. Sorus at right attached. Peel 5 \times 60. Scale bar = 500 μ m. *b*, Sorus attached below vein (*v*), showing conical receptacle and several radiating sporangia with long, narrow stalks. Peel 25 \times 96. Scale bar = 250 μ m. *c*, Section of sorus showing sporangia in several planes of section. Note quadriseriate stalk in cross section (arrow). Peel 1 \times 145. Scale bar = 250 μ m. *d*, Sporangial capsules in longitudinal (at center) and cross (at sides) sections. Note short cells and position of stomium on sporangial wall (at center) and wall thickenings on interior and lateral walls of annulus cells. Peel 12 \times 190. Scale bar = 100 μ m. *e*, Pinnule vein immediately above receptacle of sorus, showing scalariform thickenings of tracheid walls. Peel 25 \times 330. Scale bar = 100 μ m. *f*, Cross section of sporangial stalk. Peel 25 \times 570. Scale bar = 25 μ m. *g*, Cross section of sporangial capsule with tightly packed trilete spores. Peel 13 \times 290. Scale bar = 50 μ m.

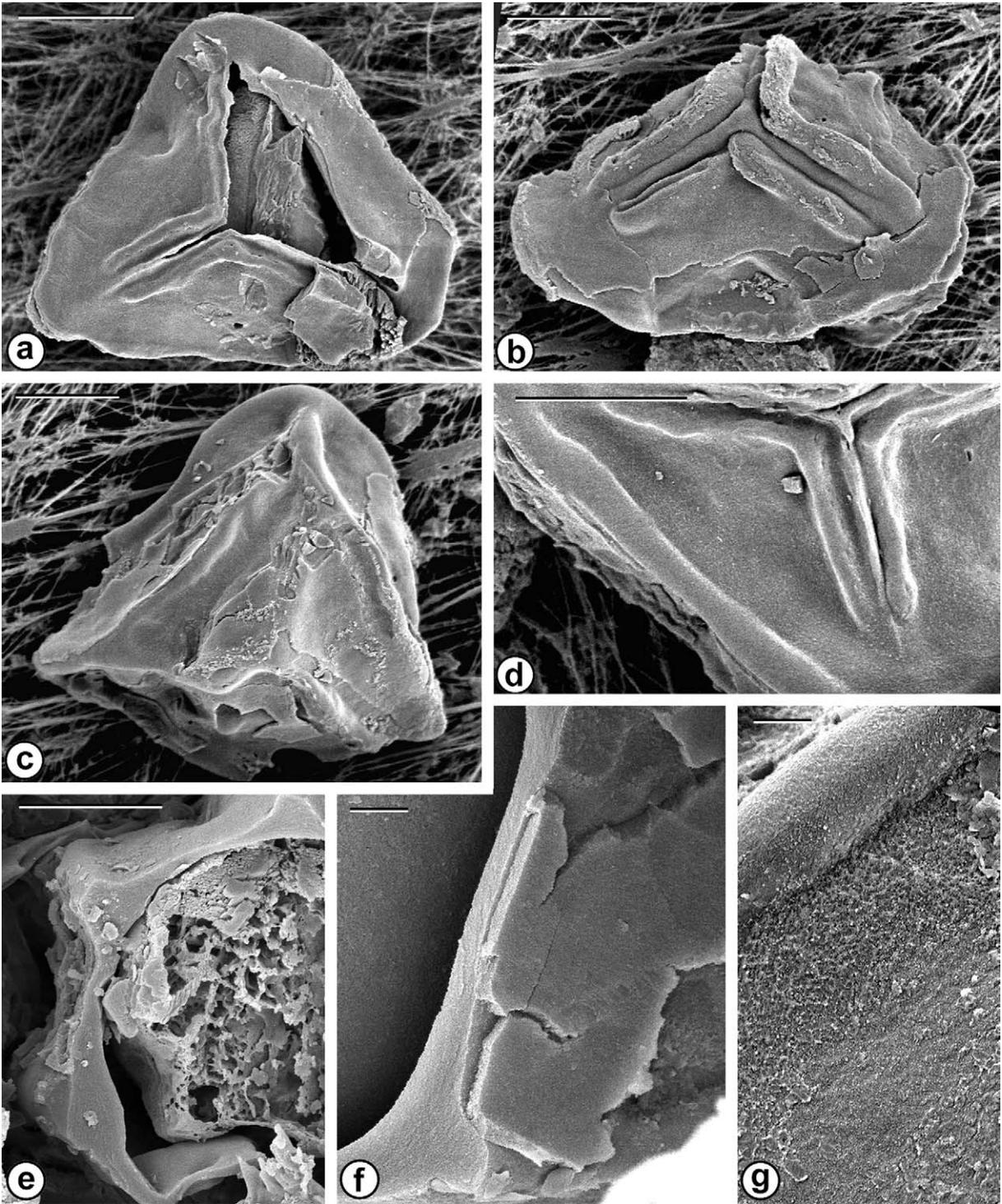


Fig. 2 *Pterisorus radiata* gen. et sp. nov. Scanning electron micrographs of spores, all of holotype P13235 E top. *a*, Proximal view of angular spore with partly detached outer wall layer. $\times 2000$. Scale bar = $10\ \mu\text{m}$. *b*, Proximal/lateral view of spore showing trilete and wide ridges flanking trilete, with outer wall detached from several areas of equatorial ridge. $\times 1800$. Scale bar = $10\ \mu\text{m}$. *c*, Proximal surface of spore showing deltoid structure connecting to equatorial flange. Note partly detached outer wall layer. $\times 1800$. Scale bar = $10\ \mu\text{m}$. *d*, Proximal surface showing features of equatorial rim, trilete, and ridges flanking trilete. Note psilate surface of spore. $\times 3000$. Scale bar = $10\ \mu\text{m}$. *e*, Cross section of spore showing dense sporoderm that is thickened in regions of equatorial flange and at angles of distal deltoid structure. $\times 5000$. Scale bar = $5\ \mu\text{m}$. *f*, Cross section of spore wall at juncture of proximal surface and equatorial flange, showing partly detached outer layer and psilate surfaces. $\times 10,000$. Scale bar = $10\ \mu\text{m}$. *g*, Spore surface at juncture of proximal surface and equatorial flange, showing surface sculpturing in these regions. $\times 10,000$. Scale bar = $10\ \mu\text{m}$.

The spore surface is psilate (fig. 2*a–2f*) and often appears homogeneous on fractured surfaces (fig. 2*f*). However, other spores show what appears to be a thin layer of spore wall that is loosely attached and/or partly broken away from some areas of the spore surface (fig. 2*a–2c, 2f*). In section views of such spores, both layers are compact and closely spaced (fig. 2*f*), with the inner layer ranging from 2.0 μm thick at the rim and ridges to 0.3 μm in the thinnest areas between the rim and ridges (fig. 2*e*). The outer layer has a uniform thickness of 0.15 μm .

Discussion

Permineralized sori of leptosporangiate ferns that can be compared to *Pterisorus radiata* are rare in the fossil record. Except for species of the Paleozoic Filicales (Rothwell 1999 and references cited therein) and the more basal families with living representatives (Nishida 1991; Yao et al. 1991; Yoshida et al. 1996; Trivett et al. 2002; Klavins et al. 2004; Vavrek et al. 2006), the sporangia of very few anatomically preserved fossil ferns have been described previously. Among these, sori of the middle Eocene *Makotopteris princetonensis* Stockey, Nishida & Rothwell (Stockey et al. 1999) and the Miocene *Woodwardia virginica* (L.) J.E. Smith (Pigg and Rothwell 2001) are indusiate. Both species have monolete spores rather than the distinctive trilete spores of *P. radiata*. Sporangia of the Eocene *Acrostichum preaureum* Arnold & Daugherty (1963) are not attached to the frond, but if they were arranged in the same way as in the living species of *Acrostichum*, one would expect them to have been distributed across much of the pinnule surface and to be interspersed with distinctive trichomes (Tryon and Tryon 1982; Kramer and Green 1990). Sporangia of *A. preaureum* differ from *P. radiata* by having an annulus that is interrupted by the stalk and a larger number of

cells of the annulus (i.e., 20+) and by the absence of a distinctive equatorial flange on the spores (Arnold and Daugherty 1963).

Additional isolated permineralized filiclean sori and annulate sporangia from the Nipania Rajmahal Series of India have been described but not named (Jacob 1938; Vishnu-Mittre 1958). The isolated sori and sporangia are of several types. Some sporangia have a terminal annulus and are most similar to the Schizaeaceae (Vishnu-Mittre 1958). Others have an oblique or nearly vertical annulus, and some contain trilete spores. Sporangia identified as Type I by Vishnu-Mittre (1958) are most similar to those of *P. radiata*. Like *P. radiata*, the Type I sporangia have a nearly vertical annulus and a stalk that is four-celled in cross section, but the capsule is at least twice as large (i.e., 350 – 550 \times 150 – 400 μm ; Vishnu-Mittre 1958) as that of *P. radiata*. Moreover, the spores of the Indian sporangia are smaller (i.e., 25–35 μm) than those of *P. radiata*, and they lack both the distinctive equatorial flange and distal deltoid structure of *P. radiata* spores.

Anatomical preservation of *P. radiata* allows for the delineation of more characters and more detailed comparisons with living species (table 1) than are available for fertile ferns preserved by other modes of fossilization. The radial sori of *Pterisorus* are superficial below a vein and have a small hemispherical receptacle from which long quadriseriate sporangial stalks radiate. No paraphyses are present. The ellipsoidal sporangial capsules are vertically elongated and have a uniseriate wall and a nearly vertical annulus. The annulus is not interrupted by the stalk, but the stomium is located closer to the base than to the apex of the capsule. Spores are radial, trilete, and angular and have a distinct equatorial flange, proximal ridges that parallel the arms of the trilete, and a distal deltoid structure that contacts the flange at the corners.

This combination of characters is suggestive of both highly derived filicleans of the Pteridaceae and of species of the

Table 1

Characters of Selected Ferns with Exindusiate Sori and Stalked Sporangia

Fern character	<i>Pterisorus radiata</i> gen. et sp. nov.	<i>Lophosoria quadripinnata</i>	<i>Sphaeropteris elongata</i>	<i>Pterozonium cyclosorum</i>
Major group	Cretaceous fossil	Tree fern clade of second radiation	Tree fern clade of second radiation	Derived clade of third radiation
Family	?	Lophosoriaceae	Cyatheaceae s.s.	Pteridaceae
Sorus position	Abaxial; under vein	Abaxial; under vein	Abaxial; under vein	Abaxial; under vein
Sorus shape	Round	Round	Round	Oval-elongate
Indusium	Absent	Absent	Absent	Absent
Receptacle	Hemispherical	Low	Globose-elongate	Low
Paraphyses	Absent	Present	Present	Absent
Stalk	Long; 4-seriate	Short; 6-seriate	Short; 4-seriate	Long; 2–3-seriate
Annulus	Subvertical; passing stalk	Oblique; passing stalk	Oblique; passing stalk	Subvertical; interrupted by stalk
Spore number	~64	64	64	64
Spores	Trilete; tetrahedral-globose, angular; equatorial flange; proximal ridges flanking arms of trilete; distal deltoid structure	Trilete; spheroidal; flange toward proximal face; proximal ridges and tubercles not flanking arms of trilete; no distal structure	Trilete; tetrahedral-globose; no flange; proximal ridges absent; no distal structure	Trilete; tetrahedral-globose, angular; equatorial flange; proximal ridges flanking arms of trilete; distal deltoid structure
Aperture	3/4 to margin	To near margin	To flange	3/4 to margin
Spore surface	Psilate	Tuberculate-perforate	Coarsely echinate	Slightly rugose
Sporoderm	Two dense layers	Blechnoid with detached outer layer and thin perispore	Dense with complex perispore	Two dense layers; outer layer = compact perispore?

Sources. Characters from Eames (1936); Tryon and Tryon (1982); Kramer and Green (1990); and Tryon and Lugardon (1991).

tree fern clade (i.e., Plagiogyriaceae, Metaxyaceae, Loxomataceae, Dicksoniaceae, and Cyatheaceae = Cyatheaceae s.l. *sensu* Lantz et al. 1999; table 1; Bower 1926, 1928; Kramer and Green 1990). In contrast to the round exindusiate sori of *P. radiata* and many species of Cyatheaceae s.s., most species of other tree ferns and Pteridaceae have sori that have other combinations of characters (Tryon et al. 1990). Those species of tree ferns that do have round exindusiate sori (Conant et al. 1996) also have numerous paraphyses among the sporangia (Tryon and Tryon 1982). Paraphyses are absent from the sori of *P. radiata* as well as from the subfamily Taenitidoideae of the Pteridaceae (*sensu* Tryon et al. 1990; table 1). In addition, most Pteridaceae have either false indusia and elongate sori or sporangia that are diffusely arranged (Tryon and Tryon 1982). Short, nearly round, exindusiate sori, however, have been illustrated for *Pterozonium cyclosorum* A.C. Sm. (Tryon and Tryon 1982).

The sporangial stalk of *P. radiata* is relatively long and therefore compares favorably with many species of the Pteridaceae (Kramer and Green 1990). Sporangial stalks are typically shorter in the tree ferns, except in *Plagiogyria* and species of the Dicksoniaceae (Bower 1926; Tryon and Tryon 1982), where they may be as long as those of *P. radiata* (Bower 1926; Tryon and Tryon 1982; table 1). The four-celled stalk of *P. radiata* is comparable to the "tree fern" *Metaxya* (Bower 1928). Otherwise, it is intermediate between the two- to three-celled stalks of most Pteridaceae and the five- to six-celled stalks of most other tree ferns (Bower 1926; table 1). In tree ferns, the annulus is typically oriented obliquely on the sporangium (Bower 1926). However, in *Metaxya*, it is nearly as vertical as it is in *P. radiata* and species of the Pteridaceae. Whereas the annulus is interrupted by the sporangial stalk in Pteridaceae, those of *P. radiata* and species of the tree fern clade are not (Tryon and Tryon 1982; Kramer and Green 1990; table 1).

Although *P. radiata*, tree ferns, and species in the Pteridaceae all produce trilete spores, details of spore structure are perhaps the most distinctly "pteridaceous" of all *P. radiata* characters (table 1). In both *P. radiata* and species of Pteridaceae, subfamily Taenitidoideae, the spores are angular with a distinctive equatorial flange, and many species also display both a distal deltoid structure that contacts the equatorial flange at the corners and proximal flanges flanking the arms of the trilete (fig. 2a–2d; table 1; Tryon and Lugardon 1991). The "tree fern" *Lophosoria* C. Presl also has a flange and proximal ridges or tubercles, but the flange is displaced proximally from the equator of the spores (Tryon and Lugardon 1991). Also, the proximal ridges and tubercles of *Lophosoria* spores do not flank the arms of the trilete as they do in *P. radiata* and taenitidoid species of the Pteridaceae (Tryon and Lugardon 1991; table 1).

The two-layered wall of *P. radiata* compares closely to that in the Pteridaceae, where the outer layer of the sporoderm

consists of perispore (Tryon and Lugardon 1991). In contrast, the exospore of *Lophosoria* is of the blechnoid type, with a largely detached outer layer that is similar to the underlying exospore (Tryon and Lugardon 1991). There are thin deposits of perispore both below and covering the detached outer layer of *Lophosoria* spores (Tryon and Lugardon 1991) that are absent from spores of *P. radiata* and the Pteridaceae. Perispore material of the Cyatheaceae (including species of *Sphaeropteris* Bernhardtii) is typically complex, often forming the surface sculpture (Tryon and Lugardon 1991).

Pterisorus radiata spores are strikingly similar to species of the genus *Pterozonium* Fée (Tryon and Lugardon 1991; table 1). Except for a larger size range for species of *Pterozonium* (i.e., 63–78 μm ; Tryon et al. 1990), as compared with *P. radiata* (i.e., 36–48 μm), spores of all are extremely similar. All have a tetrahedral-globose shape and an equatorial flange with prominent angles connected to a projecting deltoid structure on the distal surface. Also, all have thin trilete arms that project about three-fourths of the distance to the margin of the spore and are flanked by ridges (Tryon and Lugardon 1991). The spore wall of *P. radiata* and some species of the Pteridaceae, subfamily Taenitidoideae, is relatively smooth, whereas other living species show various combinations of tuberculae or rugulae as well as granulose deposits (Tryon and Lugardon 1991).

The novel combination of characters displayed by *P. radiata* as compared to living ferns (table 1) emphasizes that the fossil does not conform to either the Pteridaceae or to the Cyatheaceae s.l. (*sensu* Lantz et al. 1999). Rather, it shares a combination of characters that are reminiscent of both (table 1). Given the Lower Cretaceous (Valanginian-Hauterivian) occurrence of the fossil, i.e., during the early stages of the third major radiation of filicaleans (including the family Pteridaceae), it is not surprising that extinct genera such as *Pterisorus* would display combinations of characters that are intermediate between families of the second (including Cyatheaceae s.l.) and third (including Pteridaceae) radiations (Rothwell 1999). In this regard, diverse fossil assemblages of pteridophytes like that at Apple Bay provide some of the most vital evidence for understanding fern evolution, with the promise of ultimately developing an in-depth understanding of the overall pattern of fern phylogeny.

Acknowledgments

We thank George Braybrook, University of Alberta, for technical assistance; A. R. Sweet, Geological Survey of Canada, for data on pollen analysis; and D. R. Gröcke, McMaster University, for isotope analysis. This work was supported in part by Natural Sciences and Engineering Research Council of Canada grant A-6908 to R. A. Stockey.

Literature Cited

- Arnold CA, LY Daugherty 1963 The fern genus *Acrostichum* in the Eocene Clarno Formation of Oregon. *Contrib Mus Paleontol Univ Mich* 18:205–227.
- Bower FO 1926 The ferns. Vol 2. Cambridge University Press, Cambridge. 344 pp.
- 1928 The ferns. Vol 3. Cambridge University Press, Cambridge. 306 pp.
- Conant DS, LA Raubeson, DK Attwood, S Perera, EA Zimmer, JA Sweere, DB Stein 1996 Phylogenetic and evolutionary implications of combined analysis of DNA and morphology in the Cyatheaceae.

- Pages 231–248 in JM Camus, M Gibby, RJ Johns, eds. Pteridology in perspective. Royal Botanic Gardens, Kew.
- Daghlian CP, TN Taylor 1979 A new method for isolating pollen and spores from acetate peels for scanning electron microscopy. *Rev Palaeobot Palynol* 27:85–89.
- Deng S 2002 Ecology of the Early Cretaceous ferns of northeast China. *Rev Palaeobot Palynol* 119:93–112.
- Eames A 1936 Morphology of vascular plants, lower groups. McGraw-Hill, New York. 433 pp.
- Haggart JW, HW Tipper 1994 New results in Jura-Cretaceous stratigraphy, northern Vancouver Island, British Columbia. *Geol Surv Can Curr Res* 1994E:59–66.
- Hasebe M, PG Wolf, KM Pryer, K Ueda, M Ito, R Sano, GJ Gastony, et al 1995 Fern phylogeny based on *rbcL* nucleotide sequences. *Am Fern J* 85:134–181.
- Jacob K 1938 Fossil plants. DSc thesis. Lucknow University, Uttar Pradesh, India.
- Jeletzky JA 1976 Mesozoic and Tertiary rocks of Quatsino Sound, Vancouver Island, British Columbia. *Geol Surv Can Bull* 242:1–243.
- Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in paleobotany. *Ann Bot, NS*, 20:635–637.
- Klavins SD, TN Taylor, EL Taylor 2004 Matoniaceae ferns (Gleicheniales) from the Middle Triassic of Antarctica. *J Paleontol* 78: 211–217.
- Kramer KU, PS Green 1990 The families and genera of vascular plants. Vol 1. Pteridophytes and gymnosperms. Springer, Berlin. 404 pp.
- Lantz TC, GW Rothwell, RA Stockey 1999 *Conantiopteris schuchmanii*, gen. et sp. nov. and the role of fossils in resolving the phylogeny of Cyatheaaceae s.l. *J Plant Res* 112:361–381.
- Lovis JD 1977 Evolutionary patterns and processes in ferns. *Adv Bot Res* 4:229–415.
- Nishida H 1991 Diversity and significance of Late Cretaceous permineralized plant remains from Hokkaido, Japan. *Bot Mag Tokyo* 104:253–273.
- Pigg KB, GW Rothwell 2001 Anatomically preserved *Woodwardia virginica* (Blechnaceae) and a new filicalean fern from the middle Miocene Yakima Canyon flora of central Washington, USA. *Am J Bot* 88:777–787.
- Pryer KM, H Schneider, AR Smith, R Cranfill, PG Wolf, JS Hunt, SD Sipes 2001 Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409:618–622.
- Rothwell GW 1987 Complex Paleozoic Filicales in the evolutionary radiation of ferns. *Am J Bot* 74:458–461.
- 1999 Fossils and ferns in the resolution of land plant phylogeny. *Bot Rev* 65:188–218.
- Rothwell GW, KC Nixon 2006 How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *Int J Plant Sci* 167:737–749.
- Rothwell GW, RA Stockey 2003 Anatomically preserved vascular and nonvascular cryptogams from the Lower Cretaceous of western North America. Botany 2003, Botanical Society of America 98th annual meeting, Mobile, AL. Abstracts 232:62.
- Schneider H, E Schuettpelz, KM Pryer, R Cranfill, S Magallón, R Lupia 2004 Ferns diversified in the shadow of angiosperms. *Nature* 428:553–557.
- Smith A 1995 Non-molecular phylogenetic hypotheses for ferns. *Am Fern J* 85:104–122.
- Smith SY, GW Rothwell, RA Stockey 2003 *Cyathea cranhamii* sp. nov. (Cyatheaaceae), anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. *Am J Bot* 90:755–760.
- Stockey RA 2004 Anatomically preserved pteridophytes: unexpected diversity for the early Cretaceous. Pages 25–26 in Abstracts of Ferns for the 21st Century, an International Symposium on Pteridophytes. Royal Botanic Garden, Edinburgh. Symposium 4: Fossils.
- Stockey RA, H Nishida, GW Rothwell 1999 Permineralized ferns from the Middle Eocene Princeton Chert. I. *Makotopteris princetonensis* gen. et sp. nov. (Athyraceae). *Int J Plant Sci* 160: 1047–1055.
- Sweet AR 2000 Applied research report on two samples of Cretaceous age from Vancouver Island, British Columbia as requested J. Haggart (GSC Pacific, Vancouver). *Geol Surv Can Paleontol Rep ARS-2000-02:1–3*.
- Trivett ML, GW Rothwell, RA Stockey 2002 A permineralized schizaeaceous fern from the Late Eocene of Vancouver Island, British Columbia, Canada. Botany 2002. Madison, WI. Abstracts 248:63.
- Tryon AF, B Lugardon 1991 Spores of the Pteridophyta. Springer, New York. 648 pp.
- Tryon RM, AF Tryon 1982 Ferns and allied plants with special reference to tropical America. Springer, New York. 857 pp.
- Tryon RM, AF Tryon, KU Kramer 1990 Pteridaceae. Pages 230–255 in KU Kramer, PS Green, eds. The families and genera of vascular plants. Vol 1. Pteridophytes and Gymnosperms. Springer, Berlin.
- Vavrek MJ, RA Stockey, GW Rothwell 2006 *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. *Int J Plant Sci* 167:631–637.
- Vishnu-Mittre 1958 Studies on the fossil flora of Nipania Rajmahal Series, India: Pteridophyta, and general observations on Nipania fossil flora. *Palaeobotanist* 7:47–66.
- Yao X, TN Taylor, EL Taylor 1991 Silicified dipterid ferns from the Jurassic of Antarctica. *Rev Palaeobot Palynol* 67:353–362.
- Yoshida A, H Nishida, M Nishida 1996 Permineralized schizaeaceous fertile pinnules from the Upper Cretaceous of Hokkaido, Japan. I. *Schizaeopteris*. *Res Inst Evol Biol Sci Rep* 8:85–94.