Int. J. Plant Sci. 167(3):631–637. 2006.

1058-5893/2006/16703-0024$15.00

OSMUNDA VANCOUVERENSIS SP. NOV. (OSMUNDACEAE), PERMINERALIZED FERTILE FROND SEGMENTS FROM THE LOWER CRETACEOUS OF BRITISH COLUMBIA, CANADA

Matthew J. Vavrek,* Ruth A. Stockey,[1,]* and Gar W. Rothwell†

*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and
†Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, U.S.A.

The Lower Cretaceous (Valanginian to Hauterivian) Apple Bay locality on Vancouver Island, British Columbia, has yielded several fragments of fertile permineralized osmundaceous pinnae. Specimens are preserved in calcareous concretions, showing both internal anatomy and allowing for the reconstruction of external morphology. Sporangia are borne laterally and clustered along terete pinna segments. They range from 550 to 650 μm in diameter, with a lateral annulus that is nine to 12 cells wide and two to three cells high and is separated from the stalk by only one or two cells. Spores are spheroidal and trilete, 40-52 μm in diameter, with long laesurae and a coarsely tuberculate exospore. Some tubercles are fused, forming microrugulae. Sporangial structure and spores most closely resemble those of *Osmunda* L. These fossils, described as *Osmunda vancouverensis* sp. nov., add to our growing appreciation for the antiquity of modern Osmundaceae and underscore the potential of the numerous well-preserved fern fossils from Apple Bay to enhance our understanding of the phylogeny of Filicales.

Keywords: Cretaceous, ferns, fossils, *Osmunda*.

Online enhancement: video.

Introduction

The filicalean fern family Osmundaceae is extremely ancient, with possible spores from the Carboniferous onward and permineralized stems occurring as early as the Permian (Phipps et al. 1998). This makes the Osmundaceae one of the oldest known filicalean fern families (Arnold 1964; Miller 1971; Good 1979; Matsumoto and Nishida 2003), with the genus *Osmunda* L. having evolved by the Triassic (Phipps et al. 1998) and at least one modern species appearing as early as the Upper Cretaceous (Serbet and Rothwell 1999). The fossil record is also supported by recent phylogenetic analyses of living species, which imply that the family is an early-diverging clade near the bottom of the leptosporangiate fern tree (Hasebe et al. 1995; Yatabe et al. 1999; Pryer et al. 2004). The diversity of the family was much greater in the past, with 12 extinct genera and more than 150 fossil species (Tidwell and Ash 1994), while today there are only three living genera, with ca. 16–21 species (Hewitson 1962; Kramer 1990). Despite their lower modern diversity, the family and certain species therein have a virtually cosmopolitan, albeit discontinuous, distribution (Hewitson 1962; Tryon and Tryon 1982; Kramer 1990).

While the fossil record for permineralized stems and compressed leaves is abundant (Miller 1967, 1971; Matsumoto and Nishida 2003), fertile material of Osmundaceae is much less common (Van Konijnenburg-van Cittert 1978; Tidwell and Ash 1994; Phipps et al. 1998). Osmundaceous spores have been described *in situ* from a number of Jurassic compressions (Van Konijnenburg-Van Cittert 1978), but permineralized fertile frond parts have not been described. In this study, we examine several permineralized specimens of isolated sporangia and osmundaceous pinnae bearing sporangia that contain well-preserved spores. With these anatomically preserved specimens, we reconstruct a precise three-dimensional image of the sporangia, showing internal and external structure. This fossil material is compared to modern Osmundaceae and is found to most closely correspond to the genus *Osmunda*.

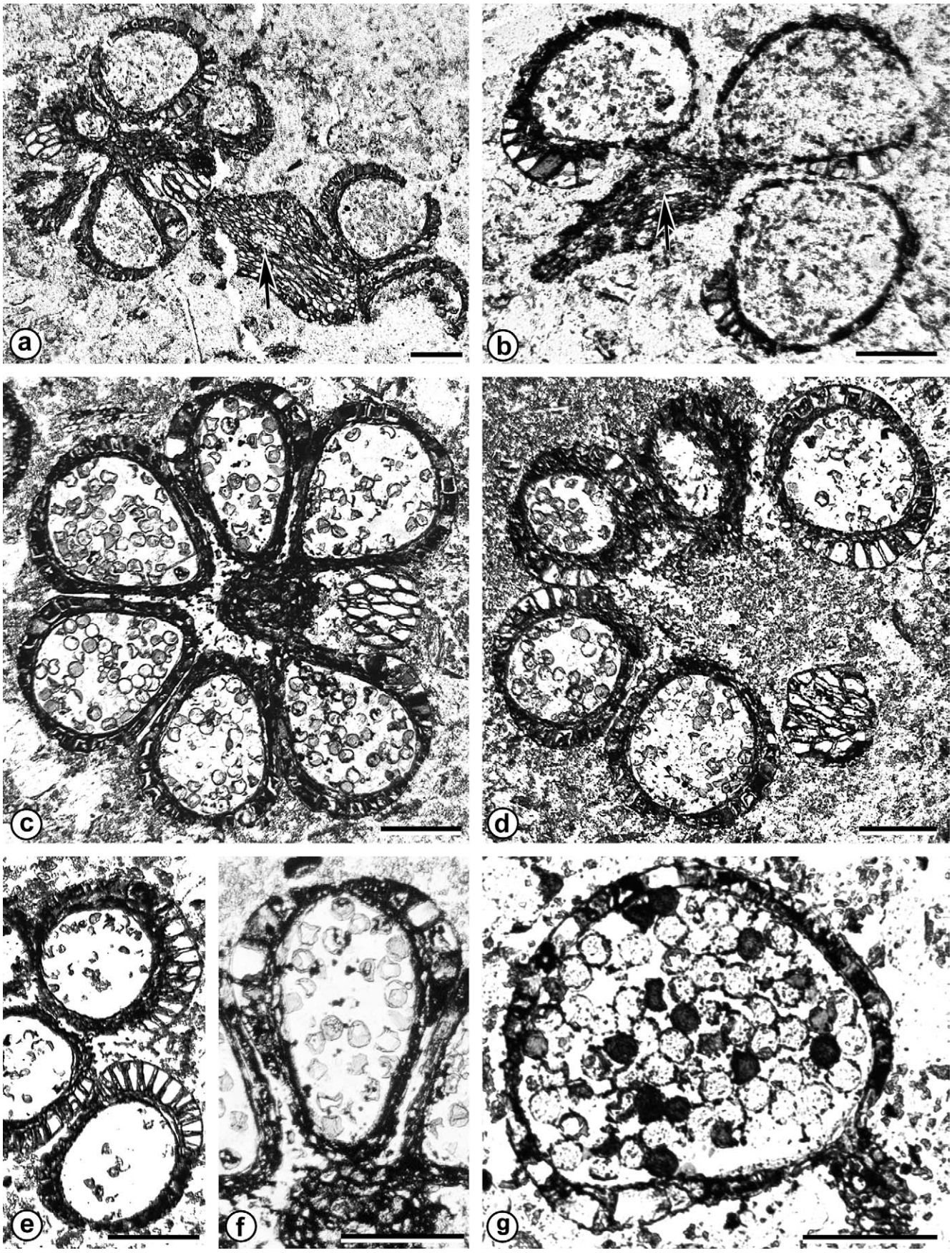
Material and Methods

Nodules containing the specimens were collected from the Apple Bay locality along Quatsino Sound, northern Vancouver Island, British Columbia (50°36′21″N, 127°39′25″W; UTM 9U WG 951068; Smith et al. 2003, 2004). The nodules are small, round, and calcareous and embedded in a sandstone (graywacke) matrix. Sediments have been regarded as Lower Cretaceous (Valanginian-Barremian) in age, Longarm Formation equivalents (Jeletzky 1976; Haggart and Tipper 1994), and they correspond to Jeletzky's (1976) Barremian variegated clastic unit (Sweet 2000). Recent isotope analysis, however, has narrowed the age to the Valanginian-Hauterivian boundary (D. R. Gröcke, McMaster University, personal communication, 2005).

Nodules were cut into slabs 5–10 mm thick, and thin sections were made using the well-known cellulose acetate peel

[1] Author for correspondence; e-mail ruth.stockey@ualberta.canada.

Manuscript received December 2004; revised manuscript received June 2005.


a
b
c
d
e
f
g

technique (Joy et al. 1956). After consecutive sections were made, peels were mounted on slides and photographed using a Phase One digital scanning camera (Phase One, Frederiksberg, Denmark) mounted on a Leitz Aristophot bellows camera. Photos were assembled in AMIRA 3.1, a three-dimensional reconstruction program, for accurate three-dimensional reconstruction of sporangia. Spores were removed from cellulose acetate peels using a modified Daghlian and Taylor (1979) technique under vacuum on a Millipore filter (Millipore, Bedford, MA). Spores 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 deposited in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton.

Systematics

Order—Filicales

Family—Osmundaceae L.

Genus—Osmunda *L.*

Species—Osmunda vancouverensis *Vavrek, Stockey et Rothwell sp. nov.*

Diagnosis. Frond segments branching, terete, bearing terminal/marginal stalked annulate sporangia. Sporangia 550–650 μm, with lateral annulus adjacent to stalk; annulus nine to 12 cells broad and two to three cells deep; 18–36 cells total. Spores spheroidal, 40–52 μm in diameter, trilete simple with laesurae extending three-fourths of the distance to equator. Surface sculpturing of conate or baculate tubercles, fused, forming microrugulae.

Holotype. Pinnule with nine attached sporangia, eight containing spores; P13032 C top, figure 1*c*, 1*d*, 1*f*, figure 2; deposited in the UAPC-ALTA.

Paratype. Partial pinnule with eight attached dehisced sporangia; P13036 C top, figure 1*a*; deposited in the UAPC-ALTA.

Etymology. The specific epithet *vancouverensis* recognizes the occurrence of the species at the Apple Bay locality, which is located on Vancouver Island, British Columbia.

Locality. Apple Bay, northern Vancouver Island, British Columbia.

Stratigraphic occurrence. Longarm Formation equivalent.

Age. Valanginian to Hauterivian, Early Cretaceous.

Description

Fertile pinnule fragments of *Osmunda vancouverensis* consist of terete pinnule segments that bear clusters of stalked sporangia (fig. 1*a*–1*c*). Segments measure 0.3–1.0 mm in diameter and consist of a terete bundle of tracheids (fig. 1*a*, 1*b*, at arrows) surrounded by a hollow that probably represents the position of phloem. There is parenchymatous mesophyll and an indistinct epidermis at the periphery of each segment (fig. 1*a*–1*c*).

Sporangia are attached all the way around the pinnule segments (fig. 1*a*, 1*c*), forming three-dimensional clusters (fig. 3). Each sporangium has a short stalk three to five cells wide (fig. 1*a*–1*c*, 1*f*) and a subglobose capsule that ranges from 550 to 650 μm in maximum diameter. The capsule wall displays a prominent outer layer with a distinct annulus (fig. 1*a*–1*f*) and vertical dehiscence. Two to three inner layers of smaller, tangentially elongated, and less regularly shaped cells are also present in the best-preserved sporangia (fig. 1*e*, 1*f*; fig. 2*a*).

The annulus is lateral and positioned close to the stalk (fig. 3), being separated from the latter by only one or two cells at the center (fig. 1*a*–1*c*). Each annulus forms a band that is broader than deep and that extends approximately one-third of the way around the capsule (fig. 3). It is typically nine to 13 cells broad and two to three cells deep. In surface views, the cells of the annulus are elongated parallel to the long axis of the sporangium (fig. 1*a*–1*c*), with the total number of annulus cells ranging from 24 to 38 (mean = 27 cells). Some sections (e.g., fig. 1*c*, at top; fig. 1*f*) show the dehiscence slit flanked by cells of the annulus. This indicates that the stomium extends downward between the distal-most cells of the annulus (fig. 1*f*, at arrow), as it does in some living species of *Osmunda* (Hewitson 1962).

Spores occur within several sporangia (figs. 1, 2*a*). They are spheroidal (fig. 2*a*, 2*b*) and trilete, with raised laesurae that are long and thin and that extend nearly to the equator (fig. 2*c*, 2*d*). Spores range from 40 to 52 μm in diameter and have a tuberculate surface ornamentation (fig. 2c–2*f*). The spore wall is approximately 0.5–1.0 μm thick and appears solid and homogeneous in section views of scanning electron micrographs (fig. 2*f*). Exine sculpturing consists of conate and baculate tubercles that are sometimes fused, forming microrugulae (fig. 2*c*–2*f*). Tubercles sometimes show tiny pointed projections (fig. 2*e*), but these are rare in the spores observed.

Discussion

The permineralized remains from Apple Bay consist of nonlaminar pinnule segments with terminal/lateral annulate sporangia that contain spores. Individual sporangia have a short, wide stalk, a large globose capsule with a wall that is two to three cell layers thick, a lateral annulus, vertical

Fig. 1 *Osmunda vancouverensis* sp. nov. *a*, Fertile pinnule showing branching pattern, vascular bundle (arrow), attachment of sporangia, and position of annulus. Note dehisced sporangium at right. Paratype P13036 C top #21 ×37. *b*, Cross section of attached sporangia showing short broad stalk with vascular bundle (arrow) and position of annulus. P13129 C top #12 ×55. *c*, Several sporangia showing attachment to nonlaminate pinnules, histology of sporangial wall, annulus, and spores. Holotype P13032 C top #8 ×57. *d*, Several sporangia showing histology of sporangial wall, annulus, and spores. Holotype P13032 C top #15 ×57. *e*, Sporangia in section view showing multicellular wall with prominent annulus. P13033 D top #15 ×57. *f*, Oblique section near base of attached sporangium showing stomium (at arrow) with annulus on both sides, and multicellular sporangial wall. Holotype P 13032 C top #8 ×90. *g*, Sporangium showing spherical spores. P13380 D bot #5 ×100. All scale bars = 250 μm.

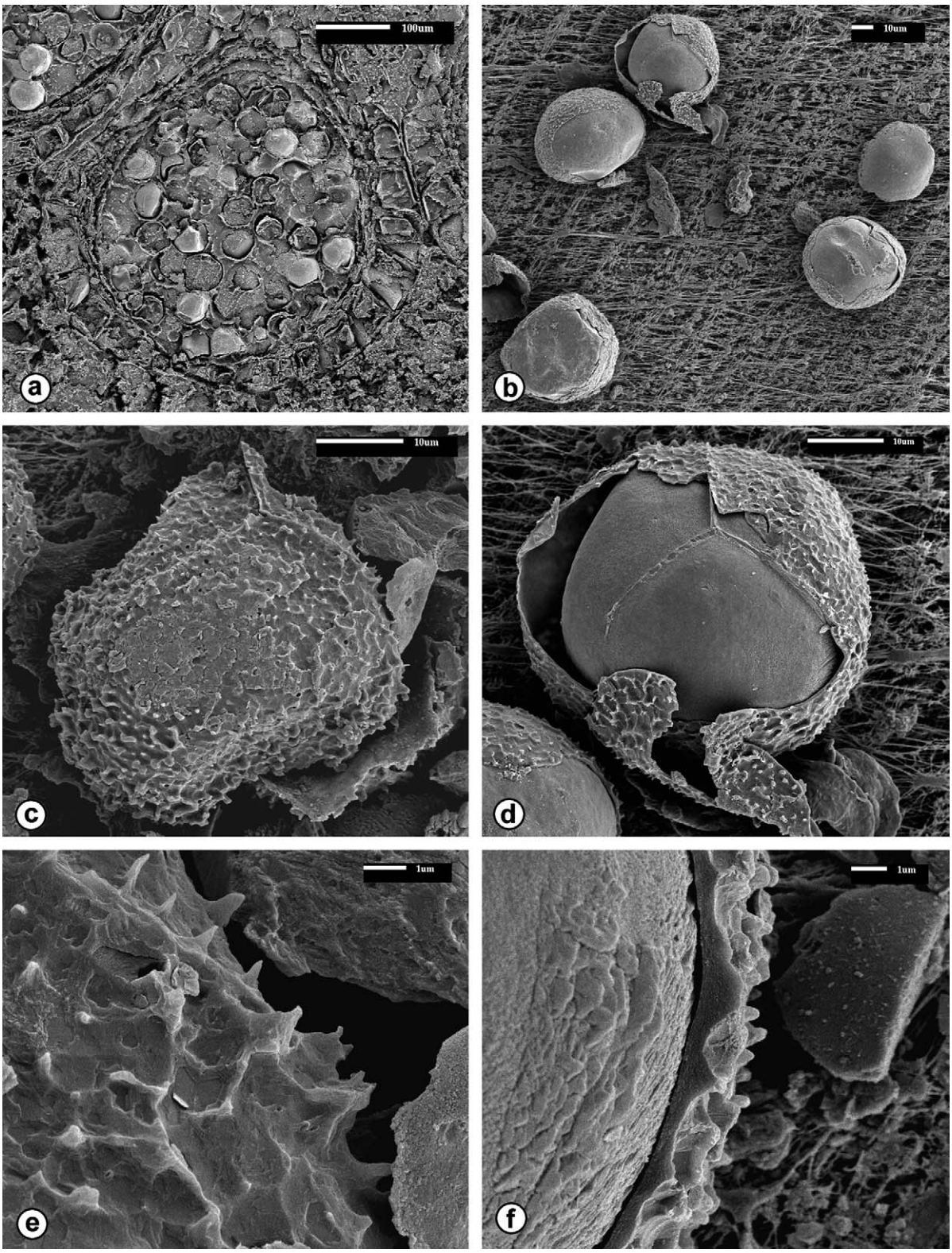


Fig. 2 Scanning electron micrographs of sporangium and spores of *Osmunda vancouverensis* sp. nov. all from holotype P13032 C top. *a*, Cross section of sporangium with spores showing features of annulus and internal wall layers. *b*, Several spores showing overall shape and ornamentation. *c*, Proximal view showing trilete spore and ornamentation. *d*, Proximal view with wall broken away to show trilete mark on endocast. *e*, Spore wall showing sculpturing of interspersed tubercles and spines, which are more or less interconnected, forming rugulae. Note echinae at tips of tubercles at right. *f*, Section of spore showing homogenous, dense wall structure.

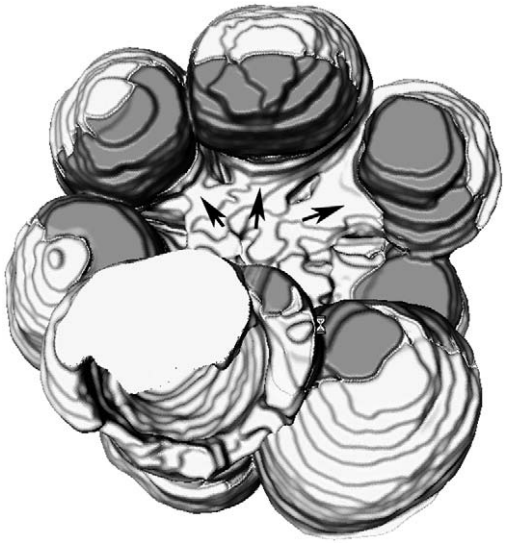


Fig. 3 Image from a three-dimensional reconstruction that shows the external surface of a sporangial cluster (holotype P13032 C top). Arrows are placed on sporangial stalks with point at base of sporangium. Position of annulus indicated by dark areas. A video based on 30 serial sections (using Amira 3.1 software; TGS, San Diego, CA) is available in the online edition of the *International Journal of Plant Sciences*.

dehiscence, and globose trilete spores with tuberculate ornamentation. Mesozoic and Cenozoic filicaleans with such features conform to the family Osmundaceae (Eames 1936; Hewitson 1962; Tryon and Lugardon 1991). Among extant genera of Osmundaceae, only *Osmunda* has nonlaminate fertile pinnules with sporangia that form three-dimensional clusters (Eames 1936). By contrast, *Todea* Willdenow in Bernhardi and *Leptopteris* C. Presl have species with sporangia that are borne abaxially on laminate pinnules (Hewitson 1962). In all of these characters, the Apple Bay ferns clearly conform to the genus *Osmunda* of the family Osmundaceae but can be distinguished from all living species of *Osmunda* and the other genera of Osmundaceae by a novel combination of characters (table 1). The most obvious of these are nonlaminate fertile pinnules like the genus *Osmunda* combined with an annulus that is positioned close to the stalk like that of *Leptopteris* species (Hewitson 1962). Therefore, we have assigned the specimens to the genus *Osmunda* and described a new species *O. vancouverensis* based on the fossil material.

Three subgenera of the genus *Osmunda* (i.e., *Osmunda*, *Osmundastrum*, *Plenasium*) traditionally have been recognized primarily by gross frond morphology and by several anatomical characters of the rhizome and stipe (Hewitson 1962). However, there is disagreement about the subgeneric placement of *Osmunda claytoniana* L. Whereas Miller (1967) places *O. claytoniana* in the subgenus *Osmunda* and considers *Osmunda cinnamomea* L. to be the only member of subgenus *Osmundastrum*, Kramer (1990) places both species in subgenus *Osmundastrum*. The results of a recent molecular analysis of *rbc*L nucleotide sequences resolves the genus *Osmunda* as a paraphyletic grade, wherein *O. cinnomomea* is basal within the clade, and *Todea barbara* (L.) Moore and *Leptopteris* spp. are sister taxa of a clade that is the sister group to the remainder of the *Osmunda* species (Yatabe et al. 1999).

Since gross frond morphology, internal anatomy of the rhizome and stipes, and molecular characters all are unknown for *Osmunda vancouverensis*, it is difficult to place this fossil species more precisely among the modern Osmundaceae. Systematic placement of *O. vancouverensis* is further complicated because sporangial characters are somewhat variable and overlapping among living osmundaceous species and are not considered to be specifically diagnostic (Hewitson 1962). Nevertheless, there are some sporangial characters that appear to be useful in distinguishing among the various species of the three osmundaceous genera. Position of the annulus ranges from near the sporangial base and adjacent to the stalk (i.e., separated by only one or two layers of cells) to lateral and located midway between the stalk and sporangial tip (table 1; Hewitson 1962). The former is characteristic of *Leptopteris superba* (Col.) Presl, *Leptopteris hymenophylloides*

Table 1

Characters of Fertile Structures in the Osmundaceae

Taxon characters	*Osmunda vancouverensis*	Subgenus *Osmunda*[a]	Subgenus *Osmundastrum* (*O. cinnamomea*)	Subgenus *Plenasium*	*Todea barbara*	*Leptopteris* spp.
Fertile pinnules	Terete	Terete	Terete	Terete	Laminar	Laminar
Sporangial position	Terminal/marginal	Terminal/marginal	Terminal/marginal	Terminal/marginal	Abaxial	Abaxial
Position of annulus	Near stalk	Intermediate between stalk and equator	Intermediate between stalk and equator	Intermediate between stalk and equator	Equatorial	Near stalk
Diameter of sporangium (μm)	550–650	420–700	420–480	420–590	460–630	330–550
Width of annulus[b]	1/3	1/3	<1/2	<1/2	1/4	<1/2
No. annulus cells (breadth)	9–13	7–14	8–10	7–15	4–12	10–16
No. annulus cells (depth)	2–3	2–5	2–3	2–5	2–3	2–4
Total no. annulus cells	24–38	16–40	16–25	21–40	9–24	25–40
Annulus and stomium overlap	Yes	No	No	Yes/no	No	No

Sources. Characters are condensed from Eames (1936), Hewitson (1962), and Tryon and Lugardon (1991).

[a] Subgenera *sensu* Miller (1967).

[b] Fraction of the diameter of the capsule.

(A. Rich.) Presl, and *O. vancouverensis*, while in *T. barbara* the annulus is located midway between the stalk and sporangial apex (Hewitson 1962). Living species of *Osmunda* tend to have the annulus positioned in a location intermediate between the stalk and the midregion of the sporangial capsule.

Osmunda vancouverensis and living species of *Osmunda* subgenus *Osmunda* (*sensu* Miller 1967) have a relatively small number of cells of the annulus (i.e., 24–38 and 16–40, respectively), and an annulus that extends one-third of the way around the capsule or less. *Osmunda* subgenus *Osmundastrum* (i.e., *O. cinnamomea*) also has a relatively small number of cells in the annulus (i.e., 16–25), with an annulus that extends less than halfway around the sporangium. However, the sporangia in this subgenus are smaller (<420–480 μm) than those of *O. vancouverensis*, which range from 550 to 650 μm. In this feature, the sporangia of *O. vancouverensis* are more similar to those of all other living osmundaceous species except those of *Leptopteris*, which range from 330 to 550 μm (table 1).

Spores of *O. vancouverensis* are generally similar to those of living Osmundaceae (Tryon and Lugardon 1991). All osmundaceous taxa have spores that are subspheroidal and trilete and have a dense wall with tuberculate sculpturing. Likewise, among living species, size ranges of the spores overlap considerably (Tryon and Lugardon 1991). The surface sculpturing of spores of *O. vancouverensis* are most similar to *Osmunda regalis* in that some of the tubercles are interconnected and fused into microrugulae (Tryon and Lugardon 1991). Moreover, the tubercles of the fossils sometimes show pointed projections that are similar to eroded echinae (perispore) of living *O. regalis* (fig. 10.11 of Tryon and Lugardon 1991). Spores of *O. vancouverensis* also compare favorably to the *sporae dispersae* genus *Osmundacidites* Cooper, which previously was found *in situ* in the Jurassic fern *Osmundopsis sturii* (Raciborski) Harris (Van Konijnenburg-van Cittert 1978) and in a Triassic species of *Todites* (Litwin 1985).

The occurrence of *O. vancouverensis* in Lower Cretaceous sediments of western North America reveals that essentially modern anatomical features of osmundaceous fertile pinnules and sporangia had evolved by at least as early as the Lower Cretaceous. Given the antiquity of the family as a whole (i.e., Pennsylvanian/Permian; Tidwell and Ash 1994), of the genus *Osmunda* (i.e., Triassic; Phipps et al. 1998), and of the living species *O. cinnamomea* (i.e., Upper Cretaceous; Serbet and Rothwell 1999), reconstruction of the whole plant that produced *O. vancouverensis* fertile structures has great potential to help resolve the pattern of systematic relationships among the genera *Osmunda*, *Todea*, and *Leptopteris*. With the ongoing discovery of abundant new specimens within the remarkable pteridophyte flora at the Apple Bay locality, we are optimistic that such a discovery will be forthcoming in the near future.

Acknowledgments

We thank Joe Morin, Mike Trask, Gerald Cranham, Sharon Hubbard, Thor Heinrich, Graham Beard, Dan Bowen, and Pat Trask of the Vancouver Island Paleontological Society for help in the field and for calling the site to our attention and George Braybrook, University of Alberta, for SEM assistance. This research was supported in part by Natural Sciences and Engineering Research Council of Canada grant A-6908 to R. A. Stockey.

Literature Cited

Arnold CA 1964 Mesozoic and Tertiary fern evolution and distribution. Mem Torrey Bot Club 21:58–66.

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.

Eames A 1936 Morphology of vascular plants, lower groups. McGraw-Hill, New York. 433 pp.

Good C 1979 *Botryopteris* pinnules with abaxial sporangia. Am J Bot 66:19–25.

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 *rbc*L nucleotide sequences. Am Fern J 85:134–181.

Hewitson W 1962 Comparative morphology of the Osmundaceae. Ann Mo Bot Gard 49:57–93.

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.

Kramer KU 1990 Osmundaceae. Pages 197–200 *in* K Kubitzki, ed. The families and genera of vascular plants. Vol 1. Pteridophytes and gymnosperms. Springer, Berlin.

Litwin RJ 1985 Fertile organs and in situ spores of ferns from the Late Triassic Chinle Formation of Arizona and New Mexico, with discussion of the associated dispersed spores. Rev Palaeobot Palynol 44:101–146.

Matsumoto M, H Nishida 2003 *Osmunda shimokawaensis* sp. nov. and *Osmunda cinnamomea* L. based on permineralized rhizomes from the Middle Miocene of Shimokawa, Hokkaido, Japan. Paleontol Res 7:153–165.

Miller CN 1967 Evolution of the fern genus *Osmunda*. Contrib Mus Paleontol Univ Mich 21:139–203.

——— 1971 Evolution of the fern family Osmundaceae based on anatomical studies. Contrib Mus Paleontol Univ Mich 23:105–169.

Phipps CJ, TN Taylor, EL Taylor, NR Cúneo, LD Boucher, X Yao 1998 *Osmunda* (Osmundaceae) from the Triassic of Antarctica: an example of evolutionary stasis. Am J Bot 85:888–895.

Pryer KM, E Schuettpelz, PG Wolf, H Schneider, AR Smith, R Cranfill 2004 Phylogeny and evolution of ferns (Monilophytes) with a focus on the early leptosporangiate divergences. Am J Bot 91:1582–1598.

Serbet R, GW Rothwell 1999 *Osmunda cinnamomea* (Osmundaceae) in the Upper Cretaceous of western North America: additional evidence for exceptional species longevity among filicalean ferns. Int J Plant Sci 160:425–433.

Smith SY, RS Currah, RA Stockey 2004 Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. Mycologia 96:180–186.

Smith SY, GW Rothwell, RA Stockey 2003 *Cyathea cranhamii* sp. nov. (Cyatheaceae), anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. Am J Bot 90:755–760.

Sweet AR 2000 Applied research report on two samples of Cretaceous age from Vancouver Island, British Columbia as requested by J. Haggart (GSC Pacific, Vancouver). Geol Surv Can Paleontol Rep ARS-2000-02.

Tidwell WD, SR Ash 1994 A review of selected Triassic to Early Cretaceous ferns. J Plant Res 107:417–442.

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.

Van Konijnenburg-van Cittert JHA 1978 Osmundaceous spores in situ from the Jurassic of Yorkshire, England. Rev Palaeobot Palynol 26:125–141.

Yatabe Y, H Nishida, N Murakami 1999 Phylogeny of Osmundaceae inferred from *rbcL* nucleotide sequences and comparison to the fossil evidences. J Plant Res 112:397–404.