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MESOZOIC DIVERSITY OF OSMUNDACEAE: *OSMUNDACAULIS WHITTLESII* SP. NOV. IN THE EARLY CRETACEOUS OF WESTERN CANADA

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Premise of research. A distinctive new species of osmundaceous fern, based on a permineralized trunk from Lower Cretaceous deposits of Haida Gwaii (formerly the Queen Charlotte Islands) off the west coast of mainland Canada, provides additional data for addressing the Mesozoic diversity and the overall pattern of phylogeny for osmundaceous filicalean ferns.

Methodology. The specimen was cut into segments and studied from both external morphology and anatomical sections prepared by the cellulose acetate peel technique. Microscope slides of sections were examined, and images were captured under transmitted light.

Pivotal results. The fossil represents a new species of *Osmundacaulis*, which is only the third Northern Hemisphere representative of this predominantly Southern Hemisphere genus.

Conclusions. *Osmundacaulis whittlesii* sp. nov. increases the Northern Hemisphere diversity of Cretaceous Osmundaceae, thus providing new data about Mesozoic diversity of the clade, potential sister-group relationships of crown-group Osmundaceae, and the overall pattern of phylogeny for Osmundaceae.

Keywords: Albian, Early Cretaceous, Haida Gwaii, Mesozoic, *Osmundacaulis*, Osmundaceae.

Introduction

Among the numerous families of extant leptosporangiate ferns that traditionally have been included in the order Filicales (Rothwell 1999; Smith et al. 2006), the Osmundaceae Brecht. & J.C. Presl. has the most extensive fossil record (Tidwell and Ash 1994; Tian et al. 2014). Up to the present, more than 150 extinct species have been described from all of the major land masses of the Earth and from deposits that range from at least the Permian onward (Taylor et al. 2009). Fossils typically are preserved either as compression/impression specimens of vegetative and fertile fronds or as permineralized trunks or trunk segments that show anatomical features of the stem, frond bases, and adventitious roots (Stewart and Rothwell 1993).

There are 21 living osmundaceous species, assigned to four genera: *Osmundastrum* C. Presl., *Osmunda* L., *Todea* Willdenow ex Bernhardi, and *Leptopteris* C. Presl. (Hewitson 1962; Yatabe et al. 1999; Jud et al. 2008), but fossil Osmundaceae have considerably wider ranges of structural variation and systematic diversity and greater species richness than do the living species (Tidwell and Ash 1994). This diversity through

time is most abundantly represented by anatomically preserved trunks from Mesozoic strata, where several genera have been recognized (Tian et al. 2008). These include the crown-group genera *Osmundastrum* and *Todea* (Serbet and Rothwell 1999; Jud et al. 2008) as well as the extinct, putative stem-group genera *Osmundacaulis* Miller ex Tidwell emend., *Ashicaulis* Tidwell, *Millerocaulis* Erasmus ex Tidwell, and *Aurealcaulis* Tidwell (Tidwell and Ash 1994). Whereas many of the stem-group species probably represent extinct clades, other fossils may be the sister group or sister groups to some or all of the living species. Still others may actually be species of crown-group genera that are not recognized as such because whole-plant concepts have yet to be developed for any of the extinct osmundaceous species represented by trunk fossils (e.g., *Ashicaulis woolfei*; Rothwell et al. 2002).

A large, anatomically preserved fossil osmundaceous trunk that conforms to the predominantly Southern Hemisphere genus *Osmundacaulis* has been recovered from Cretaceous deposits of Haida Gwaii (formerly the Queen Charlotte Islands) in far western Canada. This fern is described here as *Osmundacaulis whittlesii* M.A. Smith, Rothwell et Stockey, sp. nov., and is only the third species of the genus to be discovered in the Northern Hemisphere. The new species adds to our knowledge of the paleobiogeography of the genus and provides an opportunity to develop additional data for addressing important questions about evolution and pattern of phylogeny for the family Osmundaceae.

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Material and Methods

The holotype of *Osmundacaulis whittlesii* was found within a large marine carbonate concretion collected from an exposure on the north shore of Cumshewa Inlet, Moresby Island, Haida Gwaii, British Columbia, Canada (fig. 1). Also preserved in the concretion is the ammonite *Desmoceras* Zittel sp. (J. Haggart, personal communication, 2014; fig. 2A). The concretion was recovered from the Haida Formation of the Queen Charlotte Group (Haggart 1986). The Haida Formation is a transgressive sequence that was deposited from the Albian of the Early Cretaceous through the Turonian of the Late Cretaceous (Dalby et al. 2009). Haida Formation sediments grade upward into siltstone, mudstone, and shale, the upper part of which recently has been reassigned to the Bearskin Bay Formation (Dalby et al. 2009). The Bearskin Bay Formation ranges from Albian to Cenomanian, but molluscan and foraminiferal taxa indicate a middle to late Albian age for the deposits from which the fern-bearing concretion was recovered (Stritch and Schröder-Adams 1999; Dalby et al. 2009; Haggart et al. 2009).

The fern trunk was exposed in cross section on the surface at one end of the concretion (fig. 2B), and the concretion was split open in the field to reveal a longitudinal view of the specimen (fig. 2A). The half of the concretion containing the largest segment of the trunk (i.e., the part) was cut into 10 slabs ca. 2.5 cm thick, revealing morphology and anatomy of the specimen in cross section (fig. 2C) over a distance of ~20 cm. Serial anatomical sections were prepared from the top and the bottom of each of the slabs. One slab was subsequently ground to expose the specimen in longitudinal view, and serial sections were prepared from the ground surface. The other half of the concretion (i.e., the counterpart) also shows the ammonite *Desmoceras* sp. (J. Haggart, personal communication,

2014) on the split surface (fig. 2A) and has not been prepared further.

Specimens were sectioned by the well-known cellulose acetate peel technique (Joy et al. 1956). Slides were mounted in Eukitt (O. Kindler, Freiburg, Germany) xylene-soluble mounting medium. Images were captured with a Better Light large-format digital scanning camera (Better Light, San Carlos, CA) and processed with Adobe Photoshop CS5 extended (Adobe, San Jose, CA). The concretion containing the holotype of *O. whittlesii* was originally designated specimen CUM 300 in the Vancouver Island Paleontological Museum, Qualicum Beach, Vancouver Island, British Columbia, Canada. It is now housed at the Royal BC Museum, Victoria, British Columbia, Canada, where it bears acquisition numbers RBCM.EH2014.034.0001.001.A (part) and RBCM.EH2014.034.0001.001.B (counterpart). The accompanying ammonite is designated RBCM.EH2014.034.0001.001.C.

Results

Systematics

Order—*Osmundales sensu Smith et al. 2006*

Family—*Osmundaceae Brecht. & J.C. Presl*

Genus—*Osmundacaulis Miller emend. Tidwell*

Species—*Osmundacaulis whittlesii M.A. Smith, Rothwell et Stockey, sp. nov.*

Specific diagnosis. Stem 16–18 mm in diameter; pith parenchymatous with included sclerotic nests and peripheral

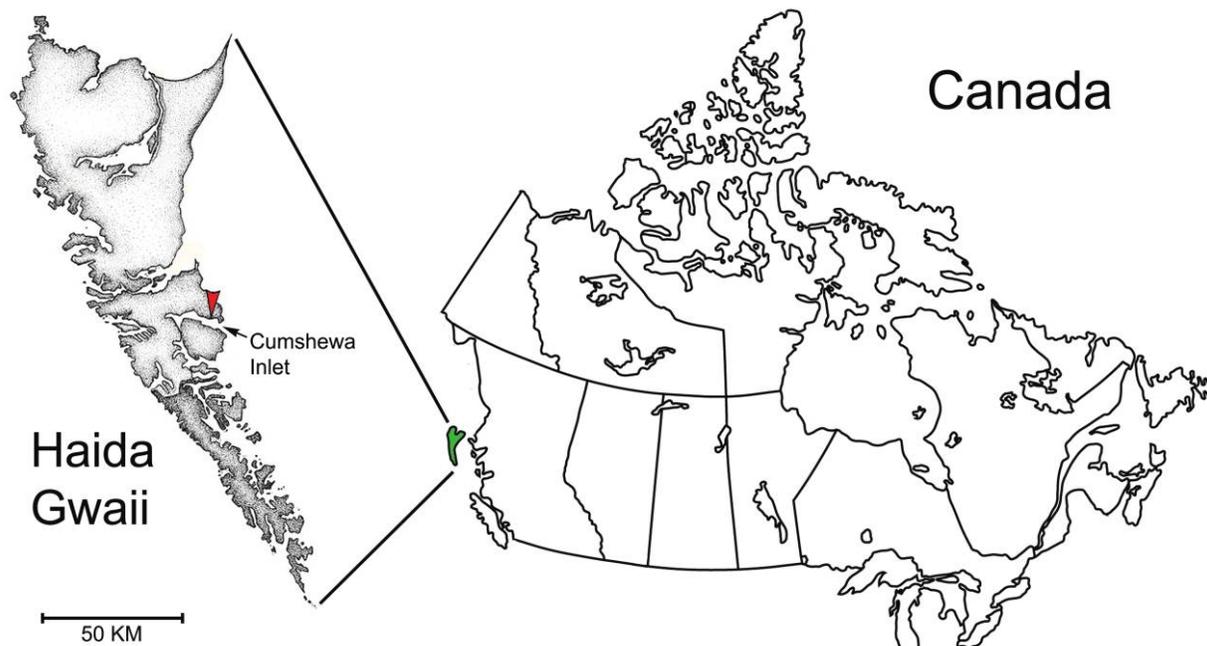


Fig. 1 Map of Canada with Haida Gwaii (in green) enlarged at left to show collecting locality (at arrowhead) on north shore of Cumshewa Inlet.

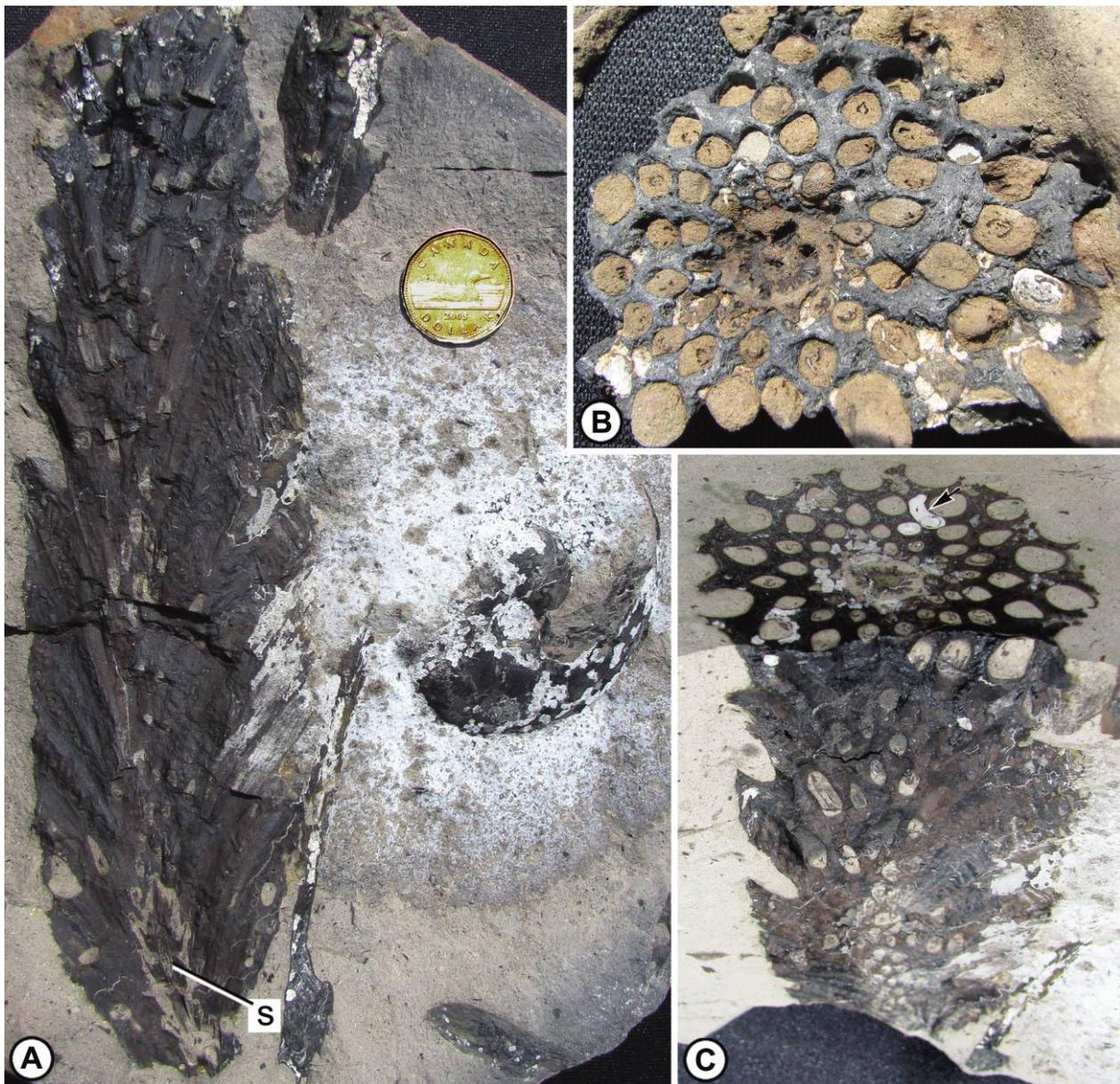


Fig. 2 *Osmundacaulis whittlesii* M.A. Smith, Rothwell et Stockey sp. nov., holotype. **A**, Trunk specimen on split surface of concretion, showing stem (s) near base and closely spaced, helically arranged stipe bases. Note ammonite *Desmoceras* sp. on split surface of concretion. Counterpart of concretion; specimen RBCM.EH2014.034.0001.001.B; $\times 0.6$. **B**, Weathered apical end of trunk specimen on surface of concretion, showing stem surrounded by closely spaced, helically arranged stipe bases. Pith, stele, broad inner cortex, and narrow outer cortex (darker rim) of stem show well in this view. Specimen RBCM.EH2014.034.0001.001.A; $\times 1.5$. **C**, Basal segment of part, with trunk exposed in cross section at top of slab C and split surface of basal region. Photo taken before slabs D–J were cut. Note features of stem and closely arranged, helically arranged stipe bases. Arrow identifies *Teredo* boring. Specimen RBCM.EH2014.034.0001.001.A; $\times 0.9$.

sheath of sclerenchyma fibers, medullary bundles absent. Stele with 15–17 cauline bundles 2.0–2.5 mm thick and 20–40 metaxylem tracheids thick. Inner cortex ca. 2 mm thick, outer cortex sclerotic, 1–2 mm thick. C-shaped stipe traces diverging, with 2–3 protoxylem strands, 3–4-lobed adaxial band of sclerenchyma, one large and several small secreto/sclerotic nests in parenchymatous ground tissue. Stipes closely spaced, diverging at $\sim 20^\circ$, diamond shaped, width/thickness ratio 1.3:1;

central ground tissue with several small secreto/sclerotic nests, C-shaped trace amphiphloic, with up to 25 endarch protoxylem strands and distally incurved margins. Stipular wing homogeneous, sclerenchyma strands absent.

Holotype hic designatus. Segment of anatomically preserved arborescent trunk, preserved in large concretion, consisting of unprepared fragment, slabs, cellulose acetate peels, and slides of specimens RBCM.EH2014.034.0001.001.A

(part) and RBCM.EH2014.034.0001.001.B (counterpart) in the Royal BC Museum, 675 Belleville Street, Victoria, British Columbia V8W 9W2, Canada (figs. 2–4).

Type locality. Beachfront exposure on north shore of Cumshewa Inlet, Moresby Island, Haida Gwaii (formerly Queen Charlotte Islands), British Columbia, Canada (53°02' 69"N, 131°45'14"W; fig. 1).

Stratigraphic position and age. Haida Formation, probably Albian Stage, Early Cretaceous.

Etymology. The specific epithet *whittlesii* is proposed in honor of Jack Whittles of Nanaimo, British Columbia, who collected the type specimen and graciously provided it for study.

Description

The holotype of *O. whittlesii* is a 27-cm-long trunk segment (fig. 2A) that is up to 8 cm in diameter and consists of a stem surrounded by tightly packed, highly abraded stipe bases and adventitious roots (figs. 2, 3). Because of prepreservational deterioration and *Teredo* borings, much of the parenchymatous ground tissue is not preserved and has been replaced by sediment (figs. 2B, 2C, 3A, 4A). The stem measures 16–18 mm in diameter. It has a large pith and a dictyoxylous or dictyostelic siphonostele consisting of 15–17 xylem bundles, as counted with the Hewitson method (Hewitson 1962; fig. 3A). Stipes diverge from the stem at an angle of ca. 20° (fig. 2A, 2C). The pith consists of thin-walled parenchyma cells that are largely incompletely preserved and a large number of nests of cells with dark contents that probably represent a combination of sclereids and secretory cells. Within these secreto/sclerotic nests, the cells with dark internal contents may be thin walled, but those without internal contents appear to be sclereids (figs. 3A, 4A). There is a prominent sheath of thick-walled fibers with dark internal contents at the periphery of the pith (figs. 3A, 4A). The sheath extends radially, in association with leaf-trace divergence, and is of variable thickness, up to 6–7 cells wide in some places (figs. 3A, 4A). The stem stele is represented by tracheids of the xylem, which form a ring of radially elongated meristemes (figs. 3A, 4A). Because phloem is not preserved, it is not possible to determine whether the stele is dictyostelic (i.e., with gaps in both the xylem and phloem) or dictyoxylous (i.e., with no gaps in the phloem).

The cortex of the stem consists of an inner zone ca. 2 mm thick, in which putative thin-walled cells are not preserved (figs. 3A, 4A), and an outer sclerenchymatous zone that is 1–2 mm thick (figs. 2B, 3A). In anatomical sections the outer margin of the cortex is difficult to identify among the tightly packed stipe bases and numerous adventitious roots, but on the eroded surface of the concretion the sclerenchymatous outer cortex is clearly visible (fig. 2B). The outer cortex is distinctly thinner than the inner cortex (fig. 3, arrow at “oc”).

Cauline meristemes are radially elongated (figs. 3A, 4A), each measuring 1.1–1.6 mm in radial extent (mean = 1.4 mm; $n = 10$). Each is 2–8 tracheids wide and up to ca. 40 cells long. Mesarch protoxylem accompanies many of the meristemes but does not form a continuous sympodial system. Metaxylem tracheids measure 39–114 μm in diameter and show multiseriate scalariform pitting on all walls (fig. 4F). Leaf-trace divergence can be recognized for some distance below each node by changes in the cauline meristemes. A cauline meristeme

from which a leaf trace will diverge is first recognized by the appearance of a cavity near the peripheral end of the band of tracheids (fig. 4A, at “a”) and the origin of a protoxylem strand (fig. 4E, at left). Progressing distally, the cavity expands centripetally (fig. 4A, at “b”), and a bundle of sclerenchyma fibers originates to the inside (fig. 4A, at “c”). The cavity and the sclerenchyma bundle both expand centripetally (fig. 4A, at “d”) until the xylem bundle opens to the pith and becomes U-shaped and the sclerenchyma becomes continuous with the sheath at the periphery of the pith (fig. 4A, at “e”). Continuing distally, the width of the sclerenchyma increases, particularly at the peripheral margin (fig. 4A, at “f”). The peripheral end of the sclerenchyma then becomes lobed (fig. 4A, at “g”), and the sclerenchyma strand opens centripetally to become U-shaped (fig. 4A, at “h”). The number of peripheral lobes of the sclerenchyma increases to three or four, and the number of protoxylem strands increases to two (fig. 4A, at “h”) or three (fig. 4A, at “i”), with one protoxylem strand adjacent to the sinus between two sclerenchyma lobes (fig. 4A).

The stipe trace diverges as a C-shaped bundle of tracheids, one side of the trace separating from the cauline meristeme at a slightly lower level than the other (figs. 3A, 4A, at “i”). Just proximal to the level of the stipe-trace separation, the lateral margins of the trace expand and the tracheids become distorted, marking the positions of divergence for adventitious root traces (figs. 3A, 4A, at “r”). As the C-shaped xylem bundle of the stipe diverges, the peripheral segment of the sclerenchyma bundle separates to accompany the stipe trace as a lobed adaxial sclerotic strand (fig. 3A, arrowheads at right and upper left). At progressively more distal levels, the stipe trace traverses the inner cortex and enters the outer cortex (fig. 3A), where the cortical sclerenchyma surrounds the trace to produce a homogeneous sclerotic sheath of thick-walled fibers in each stipe (figs. 3, 4B, 4C, 5A).

Progressing from the center outward, each stipe has a C-shaped vascular bundle and a lobed, adaxial sclerenchyma bundle that are surrounded by thin-walled cells and secreto/sclerotic nests (figs. 3, 4B, 4C, 5A), the sclerotic sheath (figs. 3B, 3C, 4B, 4C), and an outer zone of homogeneous, thinner-walled cells that make up the stipular wings (fig. 3B, 3C). As is characteristic of *Osmundacaulis* species, stipe traces are distinctly C-shaped at the level of divergence. At this level, metaxylem is typically 1–2 cell layers thick (fig. 3A). Extending into the bases of the stipes, the trace remains deeply C-shaped (figs. 3A, 4B). Toward the periphery of the trunk, the margins of the trace turn inward (figs. 3D, 4C, 5A) and the metaxylem thins to only one metaxylem tracheid (figs. 3C, 3D, 4C, 5A) between positions of the endarch protoxylem strands (fig. 4D, white arrowhead). A combination of the stipular wings and tight packing produces a diamond-shaped outer periphery on each stipe (fig. 3C, at white arrowheads). Stipes are slightly wider than thick, having a width/thickness ratio of ca. 1.3:1.0. Margins of the tightly packed stipe bases are inconspicuous, but the periphery of each can be identified by a row of somewhat larger cells that lack dark internal contents (fig. 3C, between arrowheads).

Typically, near the base of the stipe there is one large secreto/sclerotic strand adaxial to the lobed sclerenchyma strand and several smaller secreto/sclerotic nests that accompany the xylem bundle (fig. 3A, at upper right; fig. 4B). Distally, the nests are

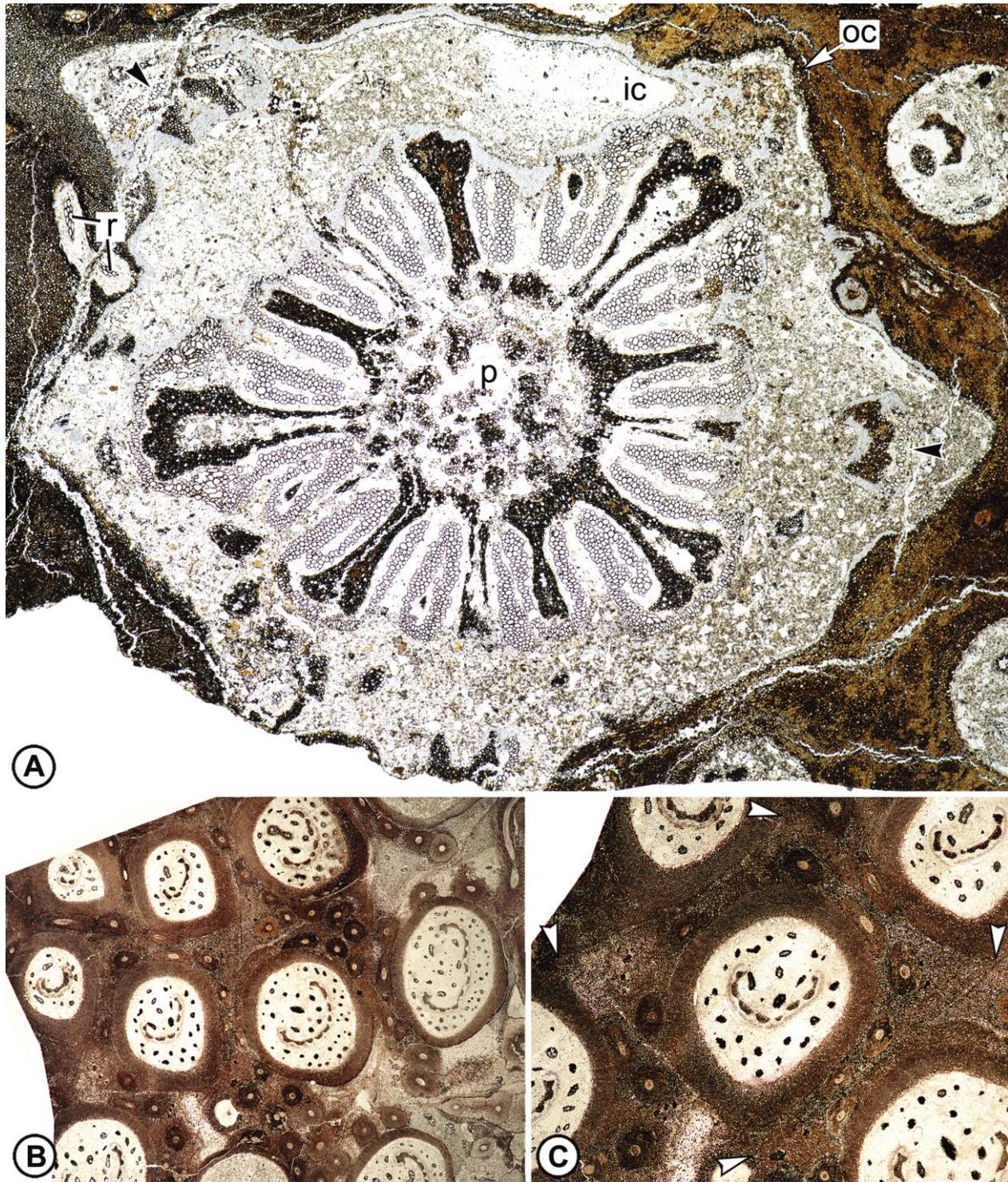


Fig. 3 *Osmundacaulis whittlesii* M.A. Smith, Rothwell et Stockey sp. nov., holotype; specimen RBCM.EH2014.034.0001.001.A. **A**, Cross section of stem, showing characters of pith (p), stele, diverging frond traces (arrowheads), diverging root trace (r), and stipe bases outside thin, sclerotic outer cortex (oc). Note tissue of inner cortex (ic) replaced with sediment infill. H Bot #5; $\times 14$. **B**, Helical rows of stipe bases, showing changes in cross section at successively more distal levels progressing from left (closest to stem) to right (farthest from stem). Note numerous adventitious roots among stipes. G Top #15; $\times 3.2$. **C**, Stipe in cross section at periphery of stem cortex, showing C-shaped trace with lobed adaxial sclerenchyma, sclerotic nests, sclerenchymatous sheath, and stipular wings. Corners of diamond-shaped stipe base are identified by white arrowheads. Note somewhat larger cells with no internal contents that mark position where adjacent stipe bases abut. G Top #15; $\times 5.4$.

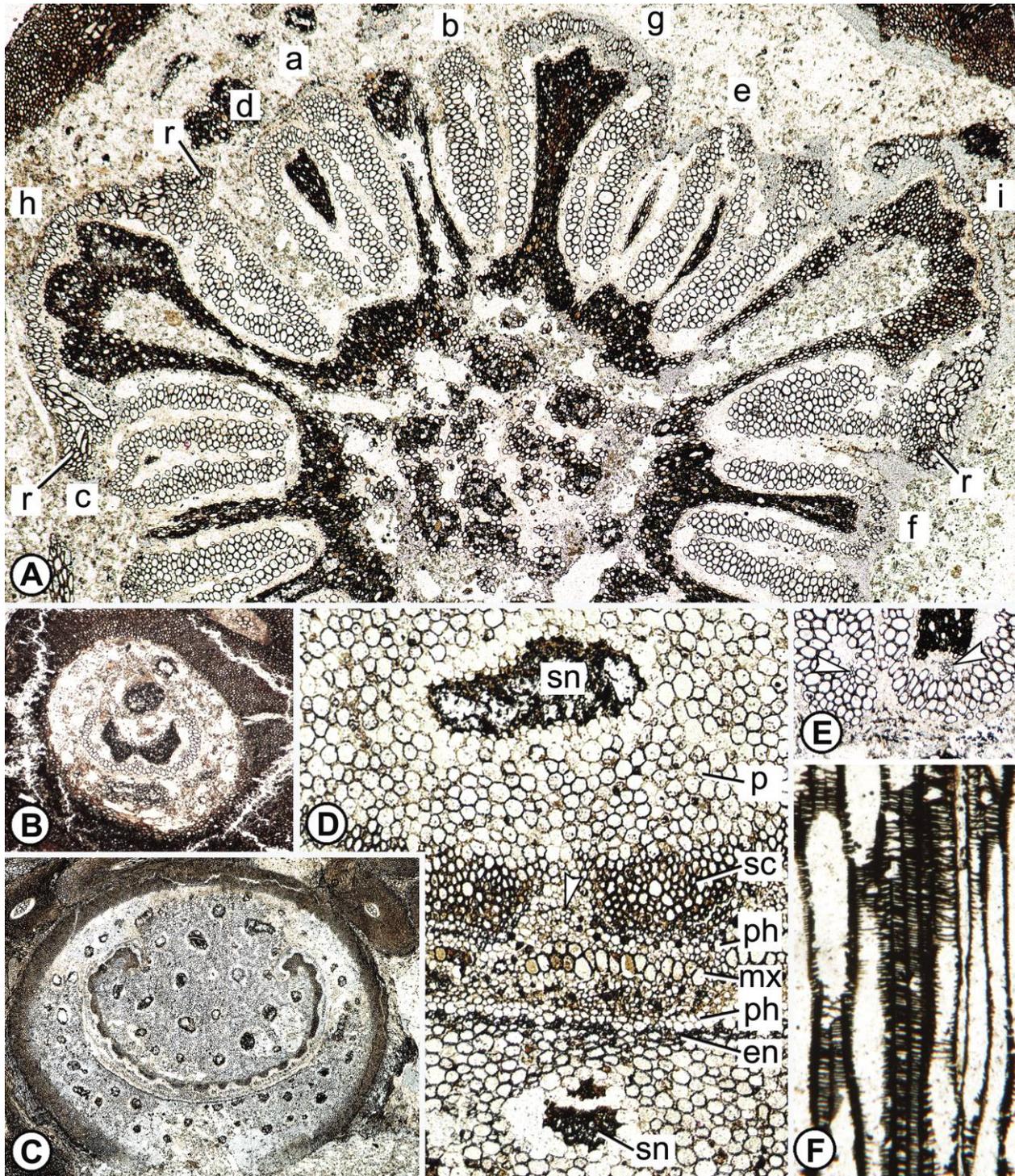


Fig. 4 *Osmundacaulis whittlesii* M.A. Smith, Rothwell et Stockey sp. nov., holotype; specimen RBCM.EH2014.034.0001.001.A. **A**, Cross section of stem, showing histological features of pith and meristemes at several successively more distal levels of leaf-trace divergence (a–i). See text for details. Note sclerotic nests and sclerotic sheath of pith, and root-trace (r) divergence from margins of diverging leaf traces. I Top #5; $\times 17$. **B**, Cross section of stipe base immediately outside the sclerotic cortex, showing three protoxylem strands, four-lobed adaxial sclerenchyma, and large accessory sclerenchyma bundle. I Top #5; $\times 9$. **C**, Cross section of stipe base near periphery of specimen, showing delicate, C-shaped xylem bundle with large number of protoxylem strands and many-lobed adaxial sclerenchyma. Note numerous sclerotic nests within parenchymatous ground tissue, sclerenchyma sheath of stipe, and diarch adventitious roots. F Bot #11; $\times 7.5$. **D**, Histology of stipe in cross section near periphery of specimen; adaxial surface toward top. Sclerotic nests (sn) in parenchymatous ground tissue (p); within the endodermis (en; near bottom) are outer phloem (ph), xylem tracheids (mx), inner phloem (ph), and fibers of lobed sclerotic bundle (sc) on adaxial side of leaf trace. Note protoxylem at arrowhead. F Bot #9; $\times 68$. **E**, Cross section near outer margin of two cauline meristemes, showing one mesarch protoxylem strand (at arrowheads). I Top #5; $\times 40$. **F**, Longitudinal section of metaxylem tracheids, showing multiseriate scalariform pitting. E Side #33; $\times 135$.

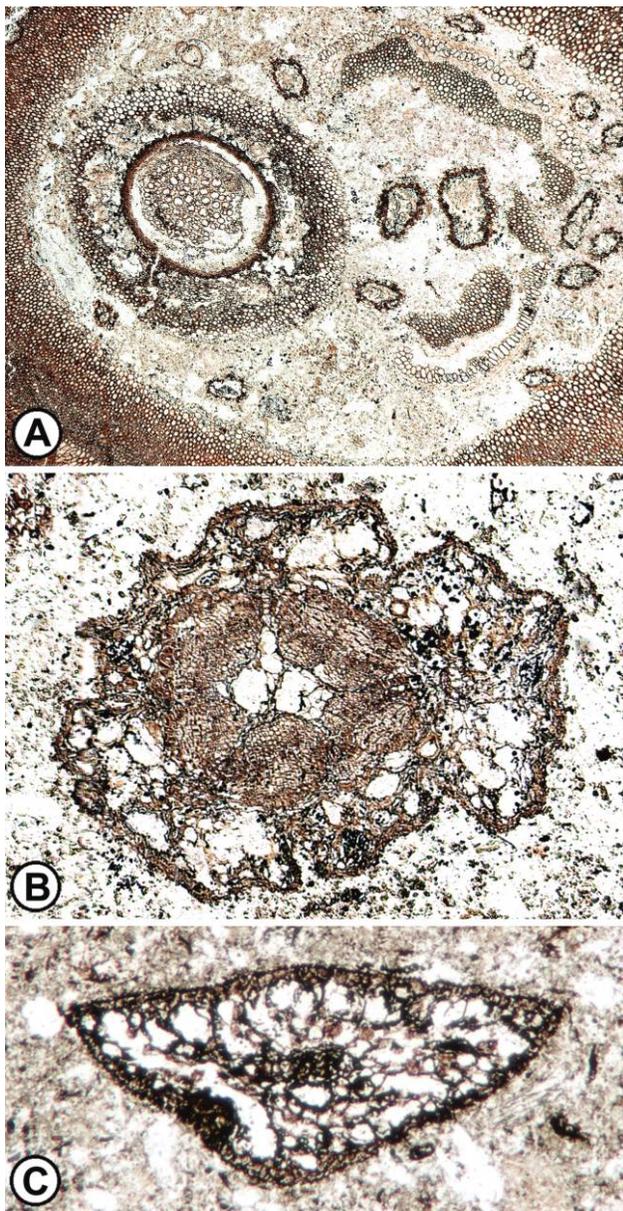


Fig. 5 Dispersed plant fragments within stipe bases of holotype; specimen RBCM.EH2014.034.0001.001.A. **A**, Cross section of stipe showing features within sclerotic sheath and protostelic gleicheniaceus fern rhizome at internodal level. Note thin-walled parenchyma of *Osmundacaulis whittlesii* ground tissue replaced by sediment. E Bot #13; $\times 18$. **B**, Cross section of cupressaceous conifer stem, showing eustele with secondary xylem and diverging leaf bases. B Top #16; $\times 37$. **C**, Cunninghamioid needle leaf of cupressaceous conifer, in cross section showing characteristic shape, one central resin canal, and terete bundle within transfusion tissue. E Top #5; $\times 61$.

more numerous and uniformly small (figs. 3B, 3C, 4C). As a stipe base extends distally, it increases in size (fig. 3B), the C-shaped xylem bundle becomes larger, and the number of protoxylem strands increases to ca. 25. Over the same distance, the number of lobes of the adaxial sclerenchyma strand also increases, with the number of lobes roughly equaling the number

of protoxylem strands at a given level. In some stipes the lobed sclerotic bundle remains intact, while in others some of the lobes separate from each other (figs. 3B, 3C, 4B, 4C).

In the most completely preserved stipes, most of the thin-walled cells are preserved (fig. 4D). Such stipes reveal that the leaf trace is a bicollateral bundle, with both exterior and interior phloem (fig. 4D, at “ph”) accompanying the tracheids of the xylem (fig. 4D, at “mx”). Such stipes also preserve an exterior endodermis (fig. 4D, at “en”) and protoxylem strands (fig. 4D, arrowhead) in the concavity between adjacent lobes of the adaxial sclerenchyma (fig. 4D, at “sc”). Secreto/sclerotic nests have dark internal contents, and cell walls are difficult to identify (fig. 4D, at “sn”).

Numerous diarch adventitious roots (fig. 4C) are preserved within the outer tissue zone of each stipe base (fig. 3B, 3C). Adventitious root traces have a distinctive thick, sclerotic cortex that is histologically similar to the sclerotic sheath of the stipes (fig. 3C). Pairs of root traces diverge from the margins of each incipient stipe trace (figs. 3A, 4A), just below the level (fig. 4A, at left and lower right) where the ends of the trace separate from the cauline meristemes (fig. 4A, at upper right). The traces traverse the inner cortex and enter the outer cortex, where they become surrounded by sclerenchyma (fig. 3A, at “r”). Upon leaving the outer cortex, the sclerenchyma continues as the root cortex (figs. 3B, 3C, 4B).

Associated plant material. There are several fragments of plant material within the weathered stipe bases of *O. whittlesii* that apparently grew or washed into the plant with sediment before permineralization (fig. 5). These provide evidence for the associated flora. Included is a fern rhizome that measures 2.4 mm in diameter (fig. 5A). The specimen has a slightly lobed, vitalized protostele 1.3 mm in diameter and a sclerotic cortex 0.6 mm thick, both of which are characteristic of *Gleichenia* J.E. Smith and closely related gleicheniacous genera (Bower 1926; Chrysler 1943, 1944). The specimen has marginally mesarch protoxylem and shows no evidence of leaf-trace production. As a result, the specimen has relatively long internodes and has been exposed at an internodal region. There also are fragments of conifer wood (not figured); an ultimate leafy conifer shoot with scale leaves, resin canals in the pith and cortex, and the bases of diverging leaves (fig. 5B); and a single needle-like cunninghamioid leaf (fig. 5C). The cunninghamioid leaf is roughly triangular in cross section, with a terete trace and a single, centrally located resin canal. A band-shaped zone of cells surrounding the leaf trace appears to represent the transfusion tissue that is characteristic of both living and fossil *Cunninghamia* R. Br. ex L.C. Rich. and closely related conifers (Ghouse and Yunus 1974).

Discussion

Nearly 100 species of permineralized fern trunks with osmundalean anatomy have been described from the Permian to the Neogene (Tidwell and Ash 1994; Cantrill 1997; Stockey and Smith 2000; Collinson 2001; Vera 2007; Tian et al. 2008, 2014). Such specimens are quite diagnostic of the order, consisting of a stem with a medullated protostele, dictyoxylic siphonostele, or dictyostele (Gould 1970; Bierhorst 1971) and C-shaped leaf traces that are surrounded by a mantle of stipe bases and diarch adventitious roots (Tidwell and Ash 1994).

Within the Osmundales, the presence or absence of stipular wings and the disposition of sclerenchymatous tissue are considered to be important characters for assigning a species either to Guaiereaceae Herbst (i.e., stipular wings and outer sclerenchymatous cortex absent) or to Osmundaceae Brecht. & J.C. Presl (i.e., stipular wings and outer sclerotic cortex present). Sclerenchymatous tissues form a prominent component of stem and stipe tissues in the Osmundaceae (e.g., Tidwell and Ash 1994; Tian et al. 2014), and particular sclerenchyma configurations often are diagnostic for living genera and species (Hewitson 1962). Characters of stem cortical sclerenchyma, sclerenchyma of the sheath of the stipe, sclerenchyma accompanying the trace within the sheath of the stipe, and sclerenchyma of the stipe stipular wings are all afforded important taxonomic significance for the extinct species as well (e.g., Tidwell and Ash 1994; Jud et al. 2008; Tian et al. 2014). Within Osmundaceae, Mesozoic trunks are assignable either to a living genus (i.e., *Osmundastrum* C. Presl and *Todea Willdenow* ex Bernhardi; Serbet and Rothwell 1999; Judd et al. 2008) or to one of the three or four genera that do not have living species. Genera of extinct Mesozoic osmundaceous species are *Osmundacaulis* Miller ex Tidwell emend., *Aurealcaulis* Tidwell et Parker, *Millerocaulis* Erasmus ex Tidwell, and *Ashicaulis* Tidwell. However, there is currently disagreement as to whether *Millerocaulis* and *Ashicaulis* represent distinct genera (e.g., Tian et al. 2008, 2014) or their species intergrade such that all should be recognized as species of *Millerocaulis* (Vera 2008).

The fern described here shares with species of *Osmundacaulis* a generically diagnostic combination of characters that includes relatively large arborescent (i.e., upright; Tidwell 1987) trunks with an apparent dictyostele, cauline meristeles that are more than 25 tracheids thick, leaf traces that diverge from the stele with two or more protoxylem strands, and a sclerotic bundle adaxial to the leaf trace (table 1; Tidwell and Pigg 1993; Tidwell and Ash 1994). However, as is the case for *Osmundacaulis whittlesii*, tissues of the phloem are not preserved in several species of *Osmundacaulis*, so the possible consistency of that character among species of the genus has yet to be verified. Additional characters of *O. whittlesii* that compare favorably with previously described species of *Osmundacaulis* are a narrow outer sclerenchymatous cortex, a homogeneous sclerotic sheath on stipe bases, and a strongly adaxially curved and lobed sclerenchyma strand on the concave adaxial side of the stipe trace (Tidwell and Pigg 1993; Tidwell and Ash 1994).

Osmundacaulis whittlesii falls within the midrange for stem, stele, and pith diameters among species of the genus (table 1). However, all three measurements increase in a roughly correlated manner from the base of the sporeling to the stem apex among living osmundaceous species (Bower 1930; Hewitson 1962). This leaves open the possibility that size differences among the small number of specimens known for several species could be indicative of level of stem preserved, rather than providing reliable specifically diagnostic characters.

Among living species of Osmundaceae, patterns of sclerenchyma have proven to be diagnostic for species and sometimes for genera, particularly sclerenchyma of the outer cortex, stipe sheath, and stipular wing (e.g., Hewitson 1962); and

the same appears to be true for the extinct species as well (Tidwell and Ash 1994). All species of *Osmundacaulis* have a thin zone of outer sclerotic cortex and a homogeneous sclerotic sheath within the stipes (Tidwell and Pigg 1993; Tidwell and Ash 1994), but there are specific differences in sclerenchyma of the pith, sclerenchyma accompanying diverging leaf traces, and sclerenchyma that is either present or absent from the stipular wing (table 1). *Osmundacaulis whittlesii* shares with *O. skidegatensis*, *O. atherstonei*, *O. hoskingii* var. *hoskingii*, *O. hoskingii* var. *tabulatus*, *O. nerii*, *O. jonesii*, *O. lemonii*, *O. pruchnikii*, and *O. griggsii* the presence of secreto/sclerotic nests within the pith, but only *O. whittlesii*, *O. nerii*, and *O. lemonii* have a sheath of fibers at the periphery of the pith. Likewise, *O. whittlesii*, *O. nerii*, and *O. lemonii* are among the species of *Osmundacaulis* that lack medullary bundles (table 1), but *O. nerii* and *O. lemonii* both have extremely short leaf gaps and very few separate cauline bundles (i.e., two to five in *O. nerii* and only one in *O. lemonii*; table 1), whereas *O. whittlesii* has much longer leaf gaps and 15–17 cauline bundles in the stele. *Osmundacaulis nerii* and *O. lemonii* are further distinguished from *O. whittlesii* by the presence of sclerotic bundles or nests in the stipular wings that are absent from *O. whittlesii* and by the occurrence of two distinctive strands of large parenchyma cells abaxial to the phloem of the leaf traces that are not present in any other species of *Osmundacaulis* (table 1).

At the onset of this investigation, we suspected that *O. whittlesii* may be an additional specimen of *O. skidegatensis*, as both are from Lower Cretaceous deposits of Haida Gwaii and were collected within less than 30 km of each other. However, *O. whittlesii* has a sclerotic sheath at the pith margin that is absent from *O. skidegatensis*, and *O. skidegatensis* has a solid sclerenchyma bundle within each incipiently diverging leaf trace, whereas the sclerenchyma bundle at a comparable level of *O. whittlesii* has a parenchymatous center. *Osmundacaulis whittlesii* has a distinctively large secreto/sclerotic nest inside the sclerotic sheath at the base of the stipe that is absent from *O. skidegatensis*; and *O. whittlesii* has two or three protoxylem strands in the stipe trace at the level of divergence, whereas in *O. skidegatensis* there is only one. *Osmundacaulis skidegatensis* has larger stem, stele, and pith diameters as well as a larger number of cauline xylem meristeles than does *O. whittlesii*, but the meristeles of *O. whittlesii* have a greater radial dimension and a larger number of metaxylem tracheids in the radial plane of section than do those of *O. skidegatensis* (table 1). Therefore, the two species clearly are distinct.

An examination of the distribution of *Osmundacaulis* species through time and space reveals that those with relatively well known ages range from Early or Middle Jurassic through the Early Cretaceous (table 1). Although that age range is relatively restricted, in comparison to those of *Aurealcaulis* and the *Millerocaulis*-*Ashicaulis* complex (i.e., Triassic–Eocene; Tian et al. 2008), species of *Osmundacaulis* do occur on both the Gondwana continent and the North American continent, and their shared characters suggest they may represent a natural group. Thirteen of the 15 *Osmundacaulis* species occur on the former Gondwana continents, suggesting a Southern Hemisphere center of origin for the genus, as has been proposed for Osmundales as a whole (Miller 1971; Tidwell and Ash 1994). It is interesting that two of the three Northern Hemisphere

Table 1
Comparative Characters of *Osmundacaulis* Species

| <i>Osmundacaulis</i> species | Age | Geography | Stem diameter (mm) | Stele diameter (mm) | Pith diameter (mm) | Pith histology | Xylem thickness (mm) |
|---|--|---|----------------------|----------------------|---------------------|-----------------------------|----------------------|
| <i>O. whitteii</i> | 90 Ma, Early Cretaceous | Cumshua Inlet, Haida Gwaii, BC, Canada | 16–18 | 8–10 | 4–5 | Par + scler strands; sheath | 2–2.5 |
| <i>O. skidegatenensis</i> | Early Cretaceous | Skidegatat Inlet, Haida Gwaii, BC, Canada | 25–30 | 17–23 | 13–15 | Par + scler strands | 2 |
| <i>O. atherstonei</i> | Early Cretaceous | Geelhoudboom, Eastern Cape, South Africa | 19 | 14–16 | 9? | Scler strands? | 2.5–4 |
| <i>O. natalensis</i> | Early Aptian, Late Barremian, Cretaceous | Hluhluwe, KwaZulu/Natal, South Africa | 17 | 11.5–13 | 3.5? | ? | 3.5–6 |
| <i>O. hoskingii</i> var. <i>hoskingii</i> | Middle–Late Jurassic | Injune Creek Beds, Surat Basin, Queensland, Australia | 8–20 | 6–12 | 4–9 | Par + scler strands | 1–3 |
| <i>O. hoskingii</i> var. <i>tabulatus</i> | Middle–Late Jurassic | Injune Creek Beds, Surat Basin, Queensland, Australia | 10–20 | 12–20 | 4–10 | Par + scler strands | 2.5–5 |
| <i>O. neri</i> | Middle Mesozoic/Tertiary | Catamaran Road, Tasmania, Australia | 20–26 | 14–18 | 3–7 | Par + scler strands; sheath | 3.5–4.7 |
| <i>O. jonesii</i> | Jurassic? | South of Ida Bay, southern Tasmania, Australia | 31 | 18–20 | 10–12 | Par + scler strands | 3–4 |
| <i>O. lemmonii</i> | Late Jurassic | Ferron, UT | 14–18 | 8–14 | 4–5 | Par + scler sheath | 1 |
| <i>O. ianii</i> | Early/Late Jurassic | South of Ida Bay, southern Tasmania, Australia | ? | ? | ? | ? | ? |
| <i>O. richmondii</i> | Early/Late Jurassic | South of Ida Bay, southern Tasmania, Australia | 22–29 | 15–20 | 8–10 | Par | 5–6 |
| <i>O. pruchnikii</i> | Early/Late Jurassic | South of Ida Bay, southern Tasmania, Australia | 22.5–31 | 13 × 22 ^a | 10 | Par + scler strands | 4 |
| <i>O. griggsii</i> | Early/Late Jurassic | South of Ida Bay, southern Tasmania, Australia | 35–45 | 20–30 | 15–20 | Par + scler strands | 3–3.5 |
| <i>O. tasmanensis</i> | Early/Late Jurassic | South of Ida Bay, southern Tasmania, Australia | 15 | 7–9 | 5 | Par? | 2–2.5 |
| <i>O. andrewii</i> | Early/Late Jurassic | North of Ida Bay, southern Tasmania, Australia | 14 × 22 ^a | 9 × 16 ^a | 2 × 10 ^a | Par | 4 |

Note. BC = British Columbia; Par = parenchyma; scler = sclerenchyma; UT = Utah.

^a Somewhat flattened, oval specimen.

Table 1 (Continued)
Comparative Characters of *Osmundacaulis* Species

| <i>Osmundacaulis</i> species | Medullary bundles | Xylem thickness (cells) | No. xylem bundles ^b | Phloem position | Gaps in phloem | Endodermis position | Inner cortex (mm) | Inner cortex cells | Outer cortex (mm) |
|---|-------------------|-------------------------|--------------------------------|-----------------|----------------|---------------------|-------------------|--------------------|-------------------|
| <i>O. whittlesii</i> | Absent | 20-40 | 15-17 | ? | ? | ? | 1-2 | ? | 1.5-3 |
| <i>O. skidegatensis</i> | Absent | 27-33 | 34-39 | Amphiphloic? | Present? | Inner, outer | 1.75-2 | Par + scler | 2-2.5 |
| <i>O. atherstonei</i> | ? | 53 | 25 | Ectophloic? | ? | Inner, outer | 1.16? | Par? | 1-1.4 |
| <i>O. natalensis</i> | ? | 50 | 24 | Ectophloic? | ? | Inner, outer | ? | ? | 3 |
| <i>O. boskingii</i> var. <i>boskingii</i> | Absent | 20-56 | 35-48 | ? | Absent | Inner, outer | 1.5-3.2 | Par + scler | .8-3 |
| <i>O. boskingii</i> var. <i>tabulatus</i> | Absent | 43-64 | 50-70 | ? | Absent | Inner, outer | 1.5-3.2 | Par + scler | .8-4 |
| <i>O. nerii</i> | Present | 50-55 | 2-5 | Ectophloic | Absent | Inner?, outer | 1-2 | Par + scler | .5-97 |
| <i>O. tonesii</i> | Present | 60 | 33 | Ectophloic | Absent | Inner?, outer | 2-5 | Par + scler | .75-1 |
| <i>O. lemonii</i> | Absent | 25-33 | 1 | ? | Absent? | Outer | 2.75-5.75 | Par + scler | 1-25 |
| <i>O. ianii</i> | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| <i>O. richmondii</i> | Present | 35-40 | 28-35 | Amphiphloic? | Absent | Inner, outer | 1.5-2 | Par | .75-1 |
| <i>O. pruchnikii</i> | Present | 68-75 | 34 | Amphiphloic? | Absent | Inner, outer | .5-1.5 | Par + scler | .5-.75 |
| <i>O. griggsii</i> | Present | 45-54 | 38-45 | Amphiphloic? | Present? | Inner, outer | 2-7 | Par + scler | .25-1.5 |
| <i>O. tasmanensis</i> | Absent | 6 x 10 | 40+ | Amphiphloic? | Present? | Inner, outer | 1.5-2 | Par | 1-1.5 |
| <i>O. andrewii</i> | Present | 45-55 | 32 | Amphiphloic? | Present? | Inner?, outer | 1-2.5 | Par | .5-1 |

Note. Par = parenchyma; scler = sclerenchyma.

^b Hewiston method (Tidwell and Pigg 1993).

Table 1 (Continued)
Comparative Characters of *Osmundacaulis* Species

| <i>Osmundacaulis</i> species | Rachis shape (width:thickness) | 2 strands of large parenchyma abaxial to phloem | Leaf-trace metaxylem thickness at trace divergence (cells) | No. of protoxylem strands immediately below trace divergence | No. of proto- xylem strands in inner cortex | No. of protoxylem strands in stipe | Sclerenchyma in trace concavity at divergence from stele | Sclerenchyma bundle in trace concavity of inner cortex |
|---|-----------------------------------|---|--|--|---|--|--|--|
| <i>O. whittlesii</i> | 1.3:1 | Absent | 1-2 | 2 | 2-3 | ~10 to ~25 | Hollow | 3-lobed ellipse |
| <i>O. skidegatenensis</i> | ? | Absent | 2-3 | 1 | 1-2 | ? | Solid | Oval or ellipse |
| <i>O. atterstonei</i> | ? | Absent | ? | 2? not preserved | ? | ? | ? | ? |
| <i>O. natalensis</i> | 3.5:1 | Absent | 2-3? | 2? | 2? | ≥4-5 | Hollow | Ellipse |
| <i>O. boskingii</i> var. <i>boskingii</i> | 6.0-8.5:1 | Absent | 2 | 2, sometimes 1 or 3 | 2-3 | 6-21 | Hollow | Continuous C-shaped |
| <i>O. boskingii</i> var. <i>tabulatus</i> | 1.6:1 | Absent | ? | 2 | 4 | 4-6 | ? | ? |
| <i>O. nerii</i> | 2.5-3.3:1 | Present | 1-2 | 4 | 7-11 | >12 | Hollow | ≥7 lobes |
| <i>O. jonesii</i> | 1.9-3.3:1 | Absent | 2-3 | 2 | 2? | ? | Hollow, segmented | 3 patches |
| <i>O. lemonii</i> | 2.6-4.1:1 | Present | 2-5 | 1 | 2 | ? | Hollow | Continuous C-shaped |
| <i>O. ianii</i> | 3.4-4.5:1 | Absent | ? | ? | ? | >20 | ? | ? |
| <i>O. richmondii</i> | 1.7-1.8:1 | Absent | 1-3 | 2 | ? | ? | Absent | Absent |
| <i>O. pruchmikii</i> | 1.8-2.0:1 | Absent | 2-3 | 2 | 4 | ? | Absent | Absent |
| <i>O. griggsii</i> | 2.1-2.3:1 | Absent | ? | 2 | ? | ? | Absent | C-shaped |
| <i>O. tasmanensis</i> | 1.9-2.7:1 | Absent | 1-3 | 2 | ? | ? | Absent | Absent |
| <i>O. andrewii</i> | 1.0-2.0:1 | Absent | 1-3 | 1 or 2 | 2 | ? | Absent | C-shaped |

Table 1 (Continued)

| <i>Osmundacaulis</i> species | Comparative Characters of <i>Osmundacaulis</i> Species | | | | | | References |
|---|--|---|--|------------------------------|--|--|--|
| | Sclerenchyma bundle at trace concavity in outer cortex | Sclerenchyma at trace concavity in stipe base | Large sclerenchyma bundle adaxial to trace concavity in cortex | Sclerenchyma sheath of stipe | Sclerenchyma in stipular wing | Additional sclerenchyma in petiolar base | |
| <i>O. tobittlesii</i> | Abaxially scalloped "C" ? | Abaxially scalloped "C" ? | Present | Homogeneous | Absent | Many, scattered | This article |
| <i>O. skidegatensis</i> | | | Absent | ? | ? | Some | Penhallow 1902; Kidston and Gwynne-Vaughan 1907; Miller 1971 |
| <i>O. atherstonei</i> | Abaxially scalloped "C" | Abaxially scalloped "C" | Absent | Homogeneous | Absent | Some | Schelpe 1956; Miller 1971 |
| <i>O. natalensis</i> | Abaxially scalloped "C," 6-lobed | Abaxially scalloped "C" | Absent | Homogeneous | Absent | . . . | Schelpe 1956; Miller 1971 |
| <i>O. hoskingii</i> var. <i>hoskingii</i> | ? | Many lobes | Present | Homogeneous | Scattered strands | Few, scattered | Gould 1973 |
| <i>O. hoskingii</i> var. <i>tabulatus</i> | ? | Many lobes | ? | Homogeneous | Numerous strands of variable size | Few, scattered | Gould 1973 |
| <i>O. neri</i> | ? | Many lobes | ? | Homogeneous | Numerous strands of variable size | Some, scattered, mainly adaxially | Tidwell and Jones 1987 |
| <i>O. jonesii</i> | 3-lobed | 3-lobed | Absent | Homogeneous | 1-6 large bundles | . . . | Tidwell 1987 |
| <i>O. lemmonii</i> | Continuous C-shaped | Continuous C-shaped | Absent | Homogeneous | 1 or 2 large bundles, numerous small strands | Many | Tidwell 1990 |
| <i>O. jani</i> | ? | None | Absent | Homogeneous | Numerous strands of variable size | Many | Tidwell and Pigg 1993 |
| <i>O. richmondii</i> | Abaxially scalloped "C" | Abaxially scalloped "C" | Absent | Homogeneous | 1 or 2-4 irregular bundles | Distal only | Tidwell and Pigg 1993 |
| <i>O. pruchnikii</i> | Abaxially scalloped "C" | Abaxially scalloped "C" | Absent | Homogeneous | 1 large bundle, 2-3 small strands | None | Tidwell and Pigg 1993 |
| <i>O. griggsii</i> | C-shaped | Abaxially scalloped "C" | Absent | Homogeneous | 1 large bundles, 3-5 small strands | Some | Tidwell and Pigg 1993 |
| <i>O. tasmanensis</i> | Absent | Absent | Absent | Homogeneous | Numerous relatively large bundles | Some | Tidwell and Pigg 1993 |
| <i>O. andrewii</i> | Abaxially scalloped "C" | Abaxially scalloped "C" | Absent | Homogeneous | 6-7 large bundles | Distal only | Tidwell and Pigg 1993 |

Osmundacaulis species (i.e., *O. skidegatensis* and *O. whittlesii*) were collected within 30 km of each other and that the third (*O. lemonii*) also is from North America. At the present time, we do not know whether that distribution represents a single extension of the genus into the Northern Hemisphere or whether the sampling density for *Osmundacaulis* is still too low for making such a determination.

In the past, *Osmundacaulis* has been considered to be a relatively derived genus among extinct osmundaceous trunks because of what is considered to be a highly derived stelar architecture (i.e., an amphiphloic dictyostele; Tidwell and Ash 1994) and a relatively late appearance in the fossil record, as compared to *Aurealcaulis* and the *Millerocaulis*-*Ashicaulis* complex (Tian et al. 2008). That impression and the presumed appearance of crown-group Osmundaceae in either the Upper Cretaceous or the Tertiary imply that modern forms were derived from species with *Osmundacaulis*, *Aurealcaulis*, *Millerocaulis*, and/or *Ashicaulis* trunks, but more recent discoveries have revealed that the crown-group genus *Osmundastrum* originated no later than the Middle Triassic (Phipps et al. 1998) and that *Todea* appeared no later than the Early Cretaceous (Jud et al. 2008). Indeed, the discovery that the living species *Osmundastrum cinnamomeum* (L.) C. Presl is at least as old as the Late Cretaceous (Serbet and Rothwell 1999) indicates that crown-group species of Osmundaceae are at least as old as some of the species assigned to the extinct Mesozoic genera (Serbet and Rothwell 1999; Tian et al. 2008). These new data leave open the possibility that some of the crown-group genera could have

been derived separately from different stem-group genera during the Mesozoic, and it is possible that stem-group Osmundaceae may not represent a monophyletic group.

Up to the present, characters that aid in taxonomic delimitation of extinct osmundaceous trunk genera and species have proven to be less useful for inferring systematic relationships among the various stem- and crown-group genera. Despite the description of an increasingly large number of extinct osmundaceous species (Tian et al. 2008), the overall pattern of phylogeny for Osmundaceae remains obscure. This is at least in part because of an extremely limited taxon sample for analysis of molecular characters (i.e., living species only) and because nearly all of the extinct osmundaceous species are essentially morphotaxa rather than species of extinct plants for which organismal concepts have been developed. In this regard, we look to occurrences of permineralized peat in which anatomically preserved Osmundaceae have been described as potential sources of fossils for the whole-plant reconstructions that have the greatest potential for resolving the overall pattern of phylogeny of Osmundaceae.

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