TODEA FROM THE LOWER CRETACEOUS OF WESTERN NORTH AMERICA: IMPLICATIONS FOR THE PHYLOGENY, SYSTEMATICS, AND EVOLUTION OF MODERN OSMUNDACEAE[1]

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The first fossil evidence for the fern genus *Todea* has been recovered from the Lower Cretaceous of British Columbia, Canada, providing paleontological data to strengthen hypotheses regarding patterns of evolution and phylogeny within Osmundaceae. The fossil consists of a branching rhizome, adventitious roots, and leaf bases. The dictyoxylic stem has up to eight xylem bundles around a sclerenchymatous pith. Leaf traces diverge from cauline bundles in a typical osmundaceous pattern and leaf bases display a sheath of sclerenchyma around a C-shaped xylem trace with 2–8 protoxylem strands. Within the adaxial concavity of each leaf trace, a single sclerenchyma bundle becomes C-shaped as it enters the cortex. The sclerotic cortex is heterogeneous with an indistinct outer margin. The discovery of *Todea tidwellii* sp. nov. reveals that the genus *Todea* evolved by the Lower Cretaceous. A phylogenetic analysis combining morphological characters of living and extinct species with a previously published nucleotide sequence matrix confirms the taxonomic placement of *T. tidwellii*. Results also support the hypothesis that *Osmunda* s.l. represents a paraphyletic assemblage and that living species be segregated into two genera, *Osmunda* and *Osmundastrum*. Fossil evidence confirms that Osmundaceae originated in the Southern Hemisphere during the Permian, underwent rapid diversification, and species extended around the world during the Triassic. Crown group Osmundaceae originated by the Late Triassic, with living species appearing by the Late Cretaceous.

Key words: Cretaceous; fern phylogeny; Osmundaceae; *Osmundastrum*; rhizome; *Todea*.

Abundant fern fossils representing the family Osmundaceae L. occur in deposits that range from the Upper Permian to the Recent (Miller, 1971; Tidwell and Ash, 1994), providing a wealth of data for inferring patterns of leptosporangiate fern evolution and phylogeny. The Osmundaceae traditionally has been regarded as the most basal family of living Filicales (Bower, 1926; Wagner, 1969; Bierhorst, 1971; Holttum, 1973), probably diverging from an extinct filicalean sister group in the Upper Pennsylvanian or Lower Permian (Miller, 1971; Tidwell and Ash, 1994). That systematc hypothesis is supported by recent phylogenetic analyses of both morphological and nucleotide sequence characters (Rothwell, 1999; Smith et al., 2006). The genus *Osmunda* L. s.l. is also extremely ancient, extending from the mid-Triassic (Phipps et al., 1998), with at least one living species (*O. cinnamomea* L.) having evolved by the Upper Cretaceous (Serbet and Rothwell, 1999). While there are more than 200 species of fossil osmundaceous ferns worldwide (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Tidwell and Ash, 1994), living representatives of the family are restricted to a small number of genera with a total of only 14–21 species (Kramer, 1990). These traditionally have been understood as conforming to three genera: *Osmunda*, *Leptopteris* Presl., and *Todea* Willdenow ex Bernhardi, with *Osmunda* being widely recognized as forming three natural groups, *Osmunda*, *Osmundastrum*, and *Plenasium* (Diels, 1898; Clausen, 1938; Hewitson, 1962; Miller, 1967).

Although the paleontological record of Osmundaceae is exceedingly rich, most osmundaceous fossils are assigned to morphotaxa because they consist of either compressed frond fragments or anatomically preserved rhizomes/rachides that cannot be assigned with confidence to genera with living species (Miller, 1971; Tidwell and Ash, 1994). Whole-plant concepts have yet to be developed for extinct genera and species. Nevertheless, there is a growing fossil record for the genus *Osmunda*, which has provided a wealth of data for inferring evolution and phylogeny of the family (Phipps et al., 1998; Serbet and Rothwell, 1999; Vavrek et al., 2006). Fossil remains for *Todea* and *Leptopteris* have not been described previously.

Over the past several years Lower Cretaceous deposits at Apple Bay on Vancouver Island along the west coast of southern British Columbia, Canada have yielded large numbers of plant fossils with superb anatomical preservation (Stockey and Rothwell, 2006). These include fertile frond segments described as *Osmunda vancouverensis* Vavrek, Stockey et Rothwell and the first fossil evidence for the genus *Todea*, which is the focus of the current study. The material consists of a permineralized rhizome with attached leaf bases and adventitious roots, and is described as *Todea tidwellii* sp. nov. Several distinctive characters reveal that *T. tidwellii* is assignable to the genus *Todea*, but other features distinguish it from the two living species *T. barbara* (L.) Moore and *T. papuana* Hennipman.

A phylogenetic analysis was conducted that combined morphological characters of living and extinct species with data from a previously published nucleotide sequence matrix (Yatabe et al., 1999). Results of that analysis confirm the assignment of *T. tidwellii* to the genus *Todea* and resolve *Osmunda* s.l. as a paraphyletic assemblage. That analysis supports the segregation of living *Osmunda* species to at least two genera, including

Osmundastrum for *O. cinnamomea* and *Osmunda* for the remaining species. The results strengthen hypotheses that crown group Osmundaceae evolved before the breakup of Pangaea, explaining the worldwide distribution of living species, and inferring that broad laminar fertile pinnules may be derived within the crown group.

MATERIALS AND METHODS

The current study is based on a fossil rhizome found in the Lower Cretaceous (Hauterivian–Valanginian) sediments on the shore of Apple Bay, Vancouver Island, British Columbia, Canada (49°54′42″N, 125°10′40″; UTM 10U CA 5531083N 343646E; Smith et al., 2003). The rhizome is preserved in a greywacke matrix as an isolated calcareous cellular permineralization. The specimen was exposed in an oblique longitudinal plane on the surfaces of two adjacent blocks. The two surfaces were photographed (e.g., Fig. 1), glued back together with epoxy, cut into wafers ~1 cm thick, and then serially sectioned in both transverse and longitudinal views (Figs. 2–9) by the cellulose acetate peel technique (Joy et al., 1956). Peels for microscopic examination and image capture were mounted on microscope slides with Eukitt mounting medium (O. Kindler GmbH, Freiburg, Germany). Images were captured with Microlumina (Leaf Systems, Bedford, Massachusetts, USA) and Photophase (Phase One A/S, Frederiksberg, Denmark) digital scanning cameras and processed with Adobe Photoshop (San Jose, California, USA). Specimens, peels, and microscope slides are housed at University of Alberta Paleobotanical Collections, Edmonton, Alberta, Canada.

Relationships among osmundaceous ferns were evaluated using a combination of nucleotide sequences of the chloroplast gene *rbcL* and morphological characters. This follows established practice, wherein fossil taxa and morphological characters can be added to gene sequence matrices to test hypotheses of tree topology and place the extinct species on the tree (e.g., Sun et al., 2002). Aligned sequence data from an earlier analysis (i.e., 1227 characters; Yatabe et al., 1999) were supplemented by a newly developed matrix of 41 morphological characters (Appendix 1) for six living Osmundaceous species representing each of the subgenera of *Osmunda* [i.e., *O. cinnamomea*, *O. regalis* L, *O. vachellii* (C. Presl.) Hook], one living species each of *Leptopteris* and *Todea* [i.e., *L. hymenophyllides* (A. Rich.) C. Presl., *T. barbara* (L.) Moore], and *T. tidwellii*. As in the earlier analysis by Yatabe et al. (1999) two geographically distant representatives of *O. cinnamomea* and *O. claytonia* were included in our analyses, and each species pair resolved as sisters in the results. For clarity of the overall pattern of cladistic relationships, only one terminal of each species pair is included in the figured phylogeny (Fig. 12). The matrix also included *Ophioglossum reticulatum* L., *Angiopteris lygodifolia* Ros., *Cephalomanes thysanostomum* (Makino) K. Iwats., *Gleichenia japonica* Spr., *Lygodium japonicum* (Thumb) Sw., *Dryopteris cristata* (L.) Gray, and *Stegnogramma pozoi* (Lagasca) K. Iwats. as outgroups. The outgroups have been condensed to a single taxon in the results (Fig. 12). Character concepts and state definitions for morphological characters are presented in Appendix 2.

Phylogenies were reconstructed using tree-search maximum parsimony analyses (i.e., parsimony rachet analysis; Nixon, 1999) performed in a Dell (Round Rock, Texas, USA) Inspiron 8600 personal computer using the program NONA (Goloboff, 1999), spawned through the program Winclada (Asado, version 1.1 beta, by K. Nixon, Cornell University). To minimize a priori assumptions about the relative value of characters, all characters were unweighted and unpolarized, and multistate characters were unordered. Branch support was estimated by the bootstrap option in Winclada.

SYSTEMATICS

Order—Filicales
Family—Osmundaceae L.
Genus—*Todea* Willdenow ex Bernhardi
Species—*Todea tidwellii* Jud, Rothwell et Stockey sp. nov.

Specific diagnosis—Small osmundaceous trunks with closely spaced frond bases and adventitious roots. Rhizomes ~4.5 cm long, up to 3 cm wide; branching distally; phyllotaxis helical; with heterogeneous sclerotic cortex. Cortex with indistinct outer boundary and prominent sclerotic ring surrounding frond and root traces from inner margin of sclerotic cortex. Rhizome dictyoxylic and ectophloic, with up to five cauline bundles and thin C-shaped leaf traces; one foliar protoxylem at divergence of trace, dividing in two in inner cortex, and increasing to six to eight in stipe base. Pith sclerenchymatous, up to 2 mm in maximum diameter; sclerenchyma lobes of pith diverge as a rod adaxial to each leaf trace becoming C-shaped at stipe base. Sclerotic ring of stipe heterogeneous; thinner adaxially. Diarch adventitious roots diverging from cauline bundles, one per frond.

Holotype hic designatus–Permineralized slabs, peels, and slides of specimen P14,466 housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA), Edmonton, Alberta.

Collecting locality—Apple Bay, northern Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″W; UTM 9U WG 951068).

Stratigraphic position and age—Longarm Formation equivalent. Valanginian–Hautervian boundary, Early Cretaceous.

Etymology—The specific epithet *tidwellii* is proposed in honor of William D. (Don) Tidwell, Brigham Young University, for his numerous contributions to our understanding of fossil Osmundaceae.

RESULTS

Todea tidwellii is represented by a small trunk that consists of a branching stem with closely spaced, diverging frond bases and root traces (Fig. 1). The specimen is roughly conical, at least 4.5 cm long, 3.0 cm in maximum width at the distal end, and tapering to less than 2 mm at the most basal level preserved. Transverse sections reveal sclerotic pith surrounded by a dictyoxylic stele with well-preserved xylem (Figs. 2, 3, 6). Phloem, endodermis, and parenchymatous inner cortex, like those that characterize living osmundaceous ferns, are incompletely preserved. However, such tissues are present in some frond bases (Figs. 5, 7). A sclerotic cortex surrounds the stele and is heterogeneous (Figs. 1–4, 6). All sclereids of the cortex are thick walled, but several layers of cells at the inner margin of the stem have thicker walls and smaller lumens than more peripheral cells (Fig. 6). Similar rings of thick-walled sclereids also are preserved around frond and root traces. Closely spaced frond bases and diverging roots enclose the rhizome (Figs. 1–3), producing an indistinct outer margin of the cortex (Figs. 2, 3). Longitudinal sections reveal that fronds diverge at angles of 40–45° (Fig. 4) and that adventitious root traces remain within the sclerotic frond base cortex for some distance beyond the margin of the stem.

Stem—The stem increases in diameter from less than 2 mm at the most proximal level preserved to more than 2 cm distally. The stem divides ~2 cm from the base of the specimen, forming two steles distally (Fig. 8, at arrows). Although each branch is surrounded by diverging frond bases, both remain within a common sclerotic cortex for the length of the specimen preserved.

The stele is characterized by a prominent sclerotic pith (Figs. 2, 3, 6). At some levels cells of the pith are thick walled throughout (Figs. 3, 6), but at other levels there are thin-walled cells at the center (Fig. 2). Distal to the level of branching, cells are not preserved at the center of the pith (Fig. 8), suggesting that they were thin walled in life or immature at the time of fossilization. In cross sections the pith region is stellate (Figs. 2, 3, 6), a shape that results from large sclerotic bundles separating from the pith and diverging to the adaxial side of each leaf trace (Figs. 4, 6). In a series of sections through which a frond trace diverges, the
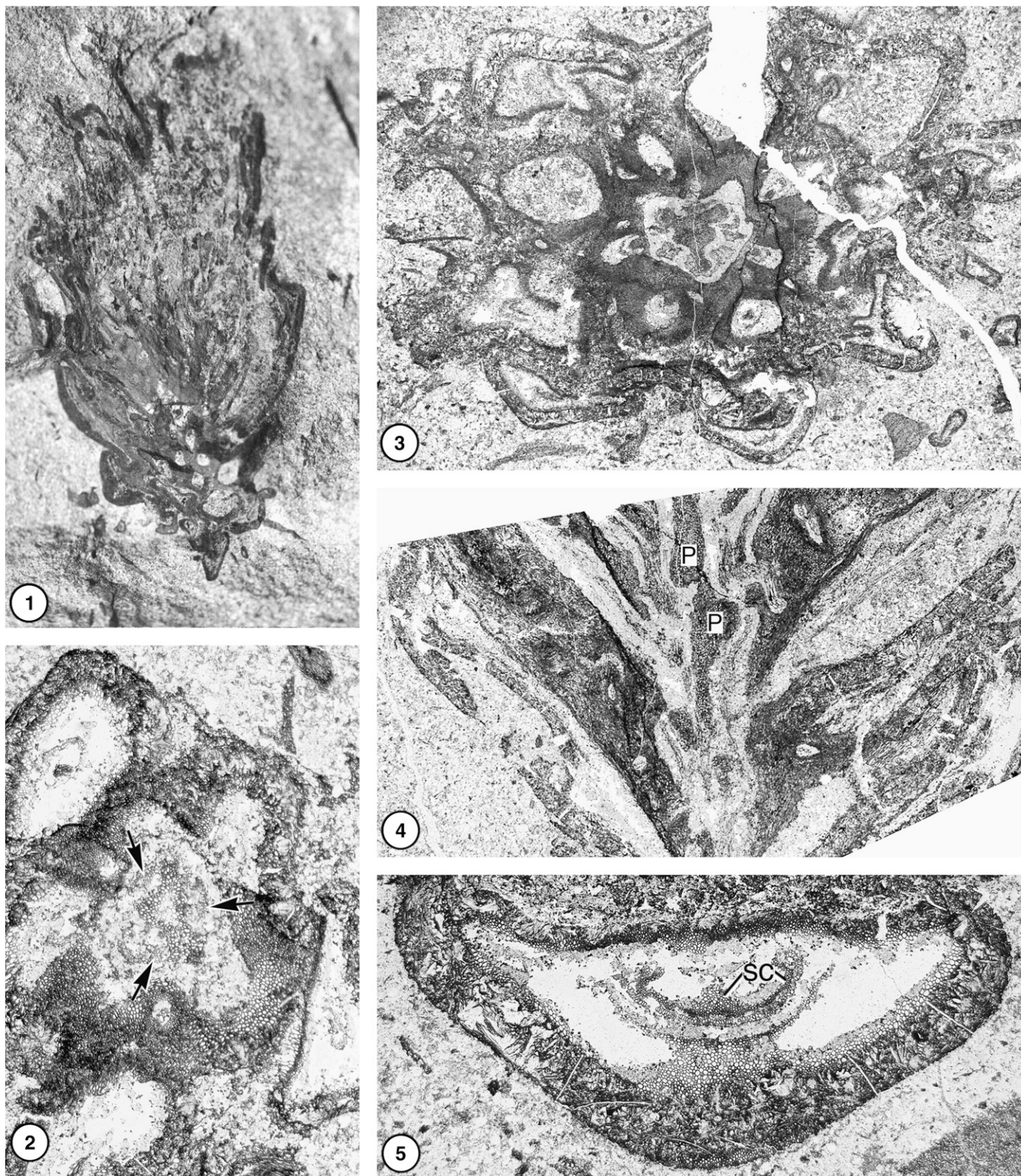
Figs. 1–5.   *Todea tidwellii* sp. nov. (holotype). **1.** Oblique view of trunk exposed on split rock surface. P14,466. 2.2×. **2.** Cross section of trunk (near base) with fronds and root traces. Note thin-walled cells at center of sclerenchymatous pith. Arrows indicate positions of cauline xylem bundles. P14,466 B Top 22, 12×. **3.** Cross section of trunk in midregion, below level of branching. Note heterogenous sclerotic cortex and indistinct outer boundary of stem cortex. P14,466 B_{2a} Bot 17, 7×. **4.** Near-radial longitudinal section. Note sclerenchymatous pith (P) and sclerenchyma bundles that bulge outward to diverge with leaf traces. Also note diverging root traces within sclerenchymatous cortex and stipe bases. P14,466 B_{2b} Side A 19, 14×. **5.** Cross section of rachis immediately distal to divergence from stem showing C-shaped trace, sclerenchyma (SC) in adaxial concavity of trace, and differentially thickened sclerotic hypodermis. Note that sclerenchyma is thinner on adaxial side and that cells are preserved toward inside of zone. P14,466 B_{2c} Top 2, 22×.
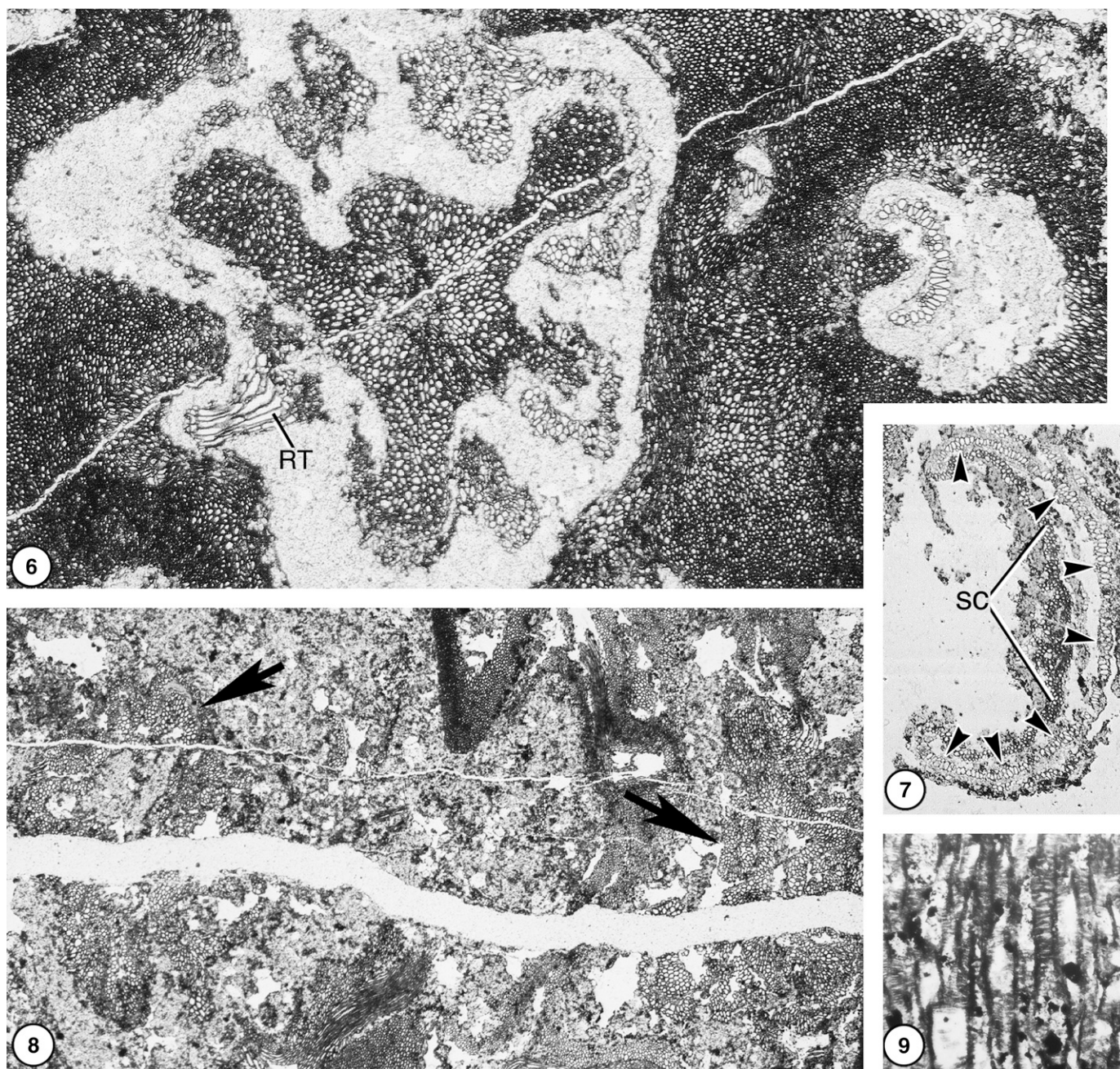
Figs. 6–9. *Todea tidwellii* sp. nov. (holotype). **6**. Cross section of stem in midregion (below level of branching) showing sclerotic pith, vascular architecture, diverging frond traces, diverging root traces (RT), and histology of heterogeneous cortex. Note fibers of inner cortex and those surrounding frond trace have smaller lumens than sclerotic cells in rest of zone, and two protoxylem strands in concavity of diverging stipe trace. P14,466 B_{2a} Bot 3 19×. **7**. Cross section of frond trace immediately distal to divergence from trunk showing narrow xylem of trace surrounded by incompletely preserved phloem. Note adaxial sclerenchyma (SC) forms thin C-shaped bundle at this level. Positions of protoxylem strands indicated by arrow points. P14,466 B_{2b} Bot 26, 44×. **8**. Cross section of stem at level of branching showing two steles (at arrows). P14,466 B_{2b} Bot 29, 20×. **9**. Longitudinal section showing scalariform wall thickenings of metaxylem tracheids of cauline bundle. P14,466 B_{2b} Side A 19, 200×.

pith first extends radially forming ribs and then each rib separates as a rod-shaped bundle near the adaxial surface of the frond trace. As each trace diverges through the cortex of the rhizome, the rod of sclerenchyma first becomes continuous with the sclerotic ring of the stipe (Fig. 6, at right), and then detaches from the ring to occupy the space within the C-shaped xylem bundle (Figs. 5, 7). Through the same distance the rod of scler-

enchyma diminishes in radial thickness until it becomes a thin zone that lies adjacent to the C-shaped frond trace (Fig. 5, 7).

The stem stele consists of a small number of cauline bundles and diverging leaf traces throughout the length of the specimen. At the base, there are only three cauline bundles (Fig. 2, at arrows) and diverging leaf traces, but the number increases distally. At the level of Fig. 2, there are three frond traces diverging

from the stele in a single section and about five orthostichies of leaves. More distally at the level of Figs. 3 and 6, the number of diverging traces has increased to four, and there are about 10 orthostichies. Above the level of branching, distortion and incomplete preservation make the number of cauline bundles and phyllotaxis difficult to determine (Fig. 8).

***Cauline vascular architecture and leaf trace divergence***—In a typical cross section of the rhizome, the stele includes both elliptical cauline bundles and C-shaped leaf traces, which are interconnected in various combinations (Fig. 6). Some leaf traces are not connected to a cauline bundle (Fig. 6, at right), while others have a cauline bundle attached either to the right or left side. A few traces appear to have a cauline bundle attached to each side (Fig. 6, at upper right). In addition, most sections show a root trace diverging from the periphery of a cauline bundle (Fig. 6, at left). These configurations are typical of osmundaceous ferns with dictyoxylic steles (Hewitson, 1962; Serbet and Rothwell, 1999).

Production of a leaf trace can be described from an acropetal series that begins at a level where a cauline bundle has no protoxylem strand (i.e., Fig. 6, at left). Progressing distally, a protoxylem strand appears in the bundle, and then the bundle becomes bilobed (Fig. 6, at upper left). The lobe with no protoxylem represents the cauline bundle, while the other lobe is the developing leaf trace. Continuing distally, the trace broadens tangentially, and metaxylem adaxial to the protoxylem strand diminishes in thickness. The leaf trace then becomes endarch and is clearly C-shaped (Fig. 6, at right). Distal to the level where the leaf trace separates from the cauline bundle, the cauline bundle fuses to an adjacent bundle/trace complex, thereby closing a leaf gap.

The single protoxylem strand located at the inner margin of the diverging leaf trace divides in two within the inner zone of the sclerotic cortex (Fig. 6, at right). The number of protoxylem strands continues to increase distally up to approximately six to eight at the level of frond divergence (Fig. 7, at arrowheads). Leaf trace metaxylem is typically one to two cell layers thick. It consists of tracheids that are 40–50 μm in diameter and that display scalariform secondary wall thickenings (Fig. 9).

Stipe bases—As is characteristic of living *Todea barbara*, cross sections of *T. tidwellii* reveal several stipes at various levels of divergence from the periphery of the rhizome (Figs. 2, 3), producing an irregular surface and obscuring the outer boundary of the cortex (Figs. 2, 3). Stipe bases are oval to elliptical in cross section and often distorted. The stipe bases are relatively isodiametric toward the outer margin of the rhizome cortex, broadening tangentially at the level of divergence (Figs. 2, 3). Individual stipe bases have a thin C-shaped xylem bundle (1–2 cells thick) with slightly recurved margins (Figs. 5, 7). There is a narrow space surrounding the xylem, that represents the position of phloem which otherwise is not preserved. The thin C-shaped
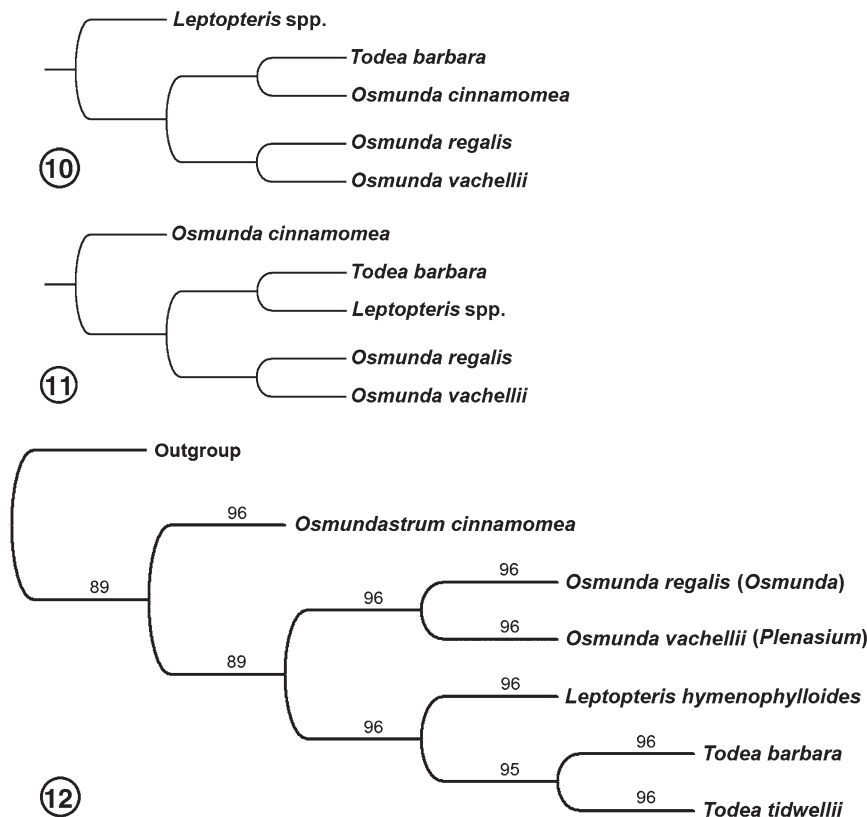
Figs. 10–12. **10.** Condensed phylogenetic tree of Miller (1971) showing relationships among representatives of major osmundaceous clades as illustrated by species included in this study. **11.** Condensed phylogenetic tree of Yatabe et al. (1999) showing relationships among representatives of major osmundaceous clades as illustrated by species included in this study. **12.** Cladogram of results from combined parsimony analysis of *rbcL* gene sequence and morphological character matrix showing relationships among *Todea tidwelli* and living representatives of major osmundaceous clades. See Discussion, *Systematics and phylogeny* for details.

sclerenchyma bundle occupies a position adjacent to the space on the concave adaxial side of the xylem (Figs. 5, 7). In some sections a layer of cells with prominent walls is preserved on the convex abaxial side of the vascular bundle (Fig. 7). Such cells are continuous with sclerenchyma of the cortex (Fig. 5), which is largely replaced by destructive calcite recrystallization. However, the preservation of a few patches of cells in this zone (Fig. 5) reveals that the cortical ring was originally composed of sclerenchyma throughout. Cortical sclerenchyma cells are 20–45 μm in diameter and have prominent lumens. There is a space between the leaf trace and the sclerenchyma ring like that which is occupied by parenchymatous ground tissue in living osmundaceous ferns (Hewitson, 1962; Bierhorst, 1971).

The sclerenchyma ring is heterogeneous, being distinctly thinner on the adaxial surface than in other areas (Figs. 2, 3, 5). It forms the outer margin of the stipe in all sections. There is no evidence of thin-walled paranchyma or lateral parenchymatous wings like those of other fossil and living osmundaceous species. Because of the calcite recrystallization of the sclerenchyma ring, we cannot be certain that lateral wings were absent in life.

Adventitious roots—As far as can be determined, one adventitious root trace diverges from the periphery of a cauline bundle in association with each frond trace (Figs. 4, 6). Root traces diverge from a cauline bundle (Fig. 6, at left), traverse the space between the stele and sclerotic cortex of the rhizome, and become surrounded by a ring of sclerenchymatous cells with small cell lumens (Fig. 6, at right). Roots extend obliquely toward the periphery of the trunk within the rhizome cortex and stipe bases (Fig. 4), eventually extending into the substrate from the abaxial surface of a stipe. There is complete histological continuity between the cortex of the rhizome and that of the root. Therefore, adventitious roots of *T. tidwellii* differentiated simultaneously with the other vegetative organs of the plant. Xylem of the roots is diarch, consisting of a plate of 6–8 tracheids in cross section (Figs. 3, 4).

Phylogenetic analyses—To test our hypothesis of generic affinities for *T. tidwellii* and of the broader phylogenetic relationships within Osmundaceae, we conducted a numerical cladistic analysis (maximum parsimony) using a combination of 1227 nucleotide sequences of the chloroplast gene *rbcL* (Yatabe et al., 1999) and 41 morphological characters (i.e., characters 1228–1268; Appendices 1, 2). The resulting tree was compared to results of previous phylogenetic analyses of the family (Figs. 10, 11). Results of this analysis yielded one most parsimonious tree of 1819 steps (CI = 54; RI = 51), that is identical to the results of Yatabe et al. (1999) except that *T. tidwellii* appears as the sister to *T. barbara* (Fig. 12). In this tree (Fig. 12) *O. cinnamomea* (i.e., *Osmundastrum*) is sister to the remaining Osmundaceae, and representatives of subgenera *Osmunda* and *Plenasium* (i.e., *O. regalis* + *O. vachellii*) form the sister group to a clade that includes the species of *Todea* and *Leptopteris* (i.e., *L. hymenophylloides* + [*T. barbara* + *T. tidwellii*]). Bootstrap support values for nodes on the tree range from 89 to 96% (Fig. 12).

DISCUSSION

Todea tidwellii consists of an anatomically preserved fern trunk with a dictoxylic rhizome and sclerenchymatous cortex. It has closely spaced frond bases with C-shaped traces that diverge in a helical phyllotaxis. This combination of characters is diagnostic for the filicalean family Osmundaceae (Hewitson, 1962; Miller, 1971; Tidwell and Ash, 1994). Within the Osmundaceae histological features of the trunks are characteristic of specific genera, and in some cases, even species (Hewitson, 1962; Miller, 1967, 1971; Serbet and Rothwell, 1999; Stockey and Smith, 2000). Whereas species of *Osmunda* have relatively uniform cortical sclerenchyma fibers that form a distinct outer surface of the rhizome, species of *Leptopteris* and *Todea*, including *T. tidwellii* (Fig. 3), have heterogeneous cortical sclerenchyma and an obscured outer margin of the rhizome (Hewitson, 1962). Species of *Leptopteris* have a parenchymatous pith, but *Todea barbara* and *T. tidwellii* have a sclerenchymatous pith. The rachis in species of *Leptopteris* displays a sclerenchymatous ring that is distinctly thicker than that of *T. barbara*. The sclerenchymatous ring of both *T. papuana* (Hennipman, 1968) and *T. tidwellii* is intermediate in thickness on the abaxial and lateral sides, but distinctly thinner on the adaxial side of the rachis (Fig. 5). This type of sclerenchymatous ring heterogeneity is not known to occur in other osmundaceous species.

Whereas *T. tidwellii* and species of both *Osmunda* s.l. and *Leptopteris* all display sclerenchyma in the adaxial concavity of the rachis trace, no sclerenchyma is present in that position in *T. barbara* (Hewitson, 1962) or *T. papauana* (Hennipman, 1968). In all other osmundaceous species where sclerenchyma is present abaxial to the leaf trace, it forms one or more bundles much thicker than the thin C-shaped band located at that position in *T. tidwellii* (Hewitson, 1962). Most osmundaceous rachides have scattered sclerenchyma within the parenchymatous tissue of the inner cortex, but this feature is absent from species of *Leptopteris* (Hewitson, 1962). Thin-walled ground tissue is not well enough preserved in *T. tidwellii* to determine the disposition of that feature. Another taxonomically useful character that varies among osmundaceous species is the distribution of sclerenchyma within the parenchymatous wings that occur at the base of the stipe (i.e., stipular wings). In *T. tidwellii* there is no evidence of stipular wings or of other parenchyma tissue outside the sclerenchymatous ring of the rachides. Although such wings may have been absent from *T. tidwellii* in life, their presence in virtually all other species of Osmundaceae suggests that absence may be due to incomplete preservation.

Systematics and phylogeny—The genus *Todea* is represented by the well-known species *T. barbara* and a second living species, *T. papuana*, which has been briefly described only once (Hennipman, 1968). Most features of *T. papuana* have not been characterized or critically compared to those of *T. barbara* and other osmundaceous ferns. The most distinctive known characters separating the two living species of *Todea* are differences in the sclerenchyma sheath surrounding the frond trace and sclerenchyma distribution within the stipular wings, but Hennipman (1968) also stresses that the latter character is highly variable at different levels with a single frond of *T. papuana*. Therefore, we are unsure whether more detailed studies of *T. papuana* will support segregation of such ferns at the species level, or if they will ultimately be regarded as falling within the range of variation that encompasses *T. barbara*. Because of a paucity of data, *T. papuana* was not included in the phylogenetic analyses.

Classical studies of osmundaceous ferns have established that living species conform to three genera *Osmunda*, *Todea*, and *Leptopteris* and that *Osmunda* s.l. may be further segregated to *Osmunda* L., *Osmundastrum* Presl., and *Plenasium* Presl. (Diels, 1898; Miller, 1967; Kramer, 1990). Most authors recognize *Todea* and *Leptopteris* as separate genera, but others favor including

species of both within *Todea* (e.g., Hewitson, 1962). Whereas some authors recognize segregates of *Osmunda* as distinct genera, most consider them to be subgenera (Hewitson, 1962; Miller, 1967; Kramer, 1990). Except for *O. claytoniana*, which Miller regards as a member of subgenus *Osmunda* and Kramer (1990) recognizes as a species of *Osmundastrum*, species composition of the osmundaceous genera and subgenera are relatively uniformly agreed upon. Phylogenetic relationships among the living osmundaceous genera and subgenera have been less clearly understood (Miller, 1967, 1971; Kramer, 1990).

Miller (1971) was the first to employ phylogenetic systematics methods to resolve relationships among species of Osmundaceae. Using Wagner's Ground Plan/Divergence methodology (Wagner, 1969) Miller developed a set of 18 systematically informative morphological characters with at least two states each (Miller, 1971). Results of that analysis more or less supported the accepted segregation of living species into three genera (*Osmunda*, *Leptopteris*, and *Todea*), and resolved the three recognized subgenera of *Osmunda* s.l. However, *T. barbara* nested within a clade of *Osmunda* species, rendering the genus *Osmunda* a nonmonophyletic assemblage (Fig. 10). In that tree (Fig. 10), species of *Leptopteris* were least specialized and formed a clade that was the sister group to the remaining Osmundaceous species (Fig. 8 of Miller, 1971). *Osmunda cinnamomea* (subgenus *Osmundastrum*) plus *T. barbara* formed a small clade attached to the stem at the next more distal node, with remaining species of *Osmunda* resolving as two clades at the apex of the tree (Fig. 10). The latter included species of subgenus *Osmunda* (i.e., *O. claytoniana*, *O. regalis*, *O. japonica*, and *O. lancea* Thunb.) as the sister group to species of the subgenus *Plenasium* [i.e., *O. vachellii*, *O. javanica* l., *O. bromeliaefolia* (C. Prest.) Kuhn, and *O. banksiaefolia* (C. Presl) Kuhn].

More recently, Yatabe et al. (1999) assessed relationships among living osmundaceous species using nucleotide sequences of the chloroplast gene *rbcL*. Included in the analyses were representatives of each of the widely recognized osmundaceous genera and subgenera (i.e., *Leptopteris hymenophylloides* (A. Rich.) C. Presl., *L. wilkesiana* (Brack.) H. Christ, *T. barbara*, *Osmunda japonica*, *O. lancea*, *O. regalis*, *O. claytoniana*, *O. cinnamomea*, *O. banksiaefolia*, *O. javancia*, *O. vachellii*). One species of Ophioglossales, one species of Marattiales, and six species of other filicaleans were included as outgroups (Yatabe et al., 1999). Analyses were conducted using both maximum parsimony and neighbor-joining methodologies.

Results of the two analyses conducted by Yatabe et al. (1999) were concordant (Fig. 11) except for relationships among species of the subgenus *Plenasium*. As with the results of the Miller analysis (1971), *Osmunda* s.l. forms a nonmonophyletic assemblage (i.e., Fig. 1 of Yatabe et al., 1999), but the composition of the clade attached at the basal nodes of the tree differs from the results of Miller (1971) (Fig. 11). Whereas a *Leptopteris* spp. clade is attached at the basal node of the Miller (1971) tree and *Osmunda cinnamomea* + *Todea barbara* form a small clade attached to the stem at the next node, the Yatabe et al. (1999) results resolve *Osmunda cinnamomea* as sister to all other species of the family (Fig. 11). At the next more distal node of the Yatabe et al. tree, species of *Leptopteris* and *Todea* form a small clade that is the sister group to all of the remaining species of *Osmunda* s.l. Those results support Miller's recognition of *O. cinnamomea* as the only species of *Osmundastrum*, but contradict a basal position for *Leptopteris* within the osmundaceous clade (Fig. 11).

Our analysis used both the nucleotide sequence characters of Yatabe et al. (1999) and 41 morphological characters, most of which could be scored for all of the taxa (Appendix 1). The results of this analysis (Fig. 12) are fully concordant with those of Yatabe et al. (1999) (Fig. 11) except that *T. tidwellii* is added to the tree as the sister to *T. barbara* (Fig. 12). These results strongly support both the appropriateness of assigning *T. tidwellii* to the genus *Todea* and the accuracy of the Yatabe et al. tree. They also support segregating *Osmundastrum* (i.e., *O. cinnamomea*) to a separate genus (Table 1), as indicated by its location at the base of the tree that includes genera with living species (Fig. 12).

To test whether the much larger number of nucleotide sequence characters in the matrix were swamping a possible alternative topology generated by the morphological characters alone, the nucleotide sequence characters and the nonosmundaceous leptosporangiate taxa were all removed, and the morphological characters were analyzed separately. The results of that analysis yielded four most parsimonious trees of 30 steps. In the strict consensus tree of those results, the two species of *Todea* resolved as sisters, but the remaining osmundaceous taxa formed a polytomy with the *Todea* clade. Therefore, while results of the morphological analysis support a sistergroup relationship between *T. barbara* and *T. tidwellii*, they do not resolve relationships among the other osmundaceous ferns.

The occurrence of sporangia on laminar pinnules that are similar to those of vegetative fronds in *Todea* and *Leptopteris* contrasts with fertile fronds (or frond segments) of *Osmunda*, which have narrow laminae that are highly reduced as compared to vegetative pinnules (Bower, 1926; Hewitson, 1962). This character has added to the perception that *Todea* and *Leptopteris* may be basal among living genera of Osmundaceae (e.g., Miller, 1971) because of their wide fertile pinnules. However, attachment of the *Todea* + *Leptopteris* clade at a node above *Osmundastrum* on the Yatabe et al. (1999) tree (Fig. 12) indicates that the common ancestor of living Osmundaceae could have borne sporangia on pinnules with highly reduced laminae. If the topology of the Yatabe et al. (1999) tree is accurate, then the laminar fertile pinnules of *Todea* and *Leptopteris* either represent a derived character among osmundaceous genera with living species or else narrow fertile pinnules evolved independently in *O. cinnamomea* and in the remaining species of *Osmunda* (Fig. 11).

Paleobiogeography of Osmundaceae—As early as the Late Permian, unequivocal osmundaceous species (sensu Phipps et al., 1998) were present in Australian Gondwana (Gould, 1970), with many species occurring in Australia, South America, Antarctica, Russia, and China by the Early Triassic (Cleal, 1993; Skog, 2001). This distribution suggests that the family originated on the Gondwana continent of the Southern Hemisphere during the Permian (Gould, 1970), spreading to the Northern Hemisphere through Asia and South America, and arriving in

TABLE 1. Proposed classification of living Osmundaceae.

Family:	Osmundaceae
Genus:	*Osmunda*
Subgenus:	*Osmunda*
Subgenus:	*Plenasium*
Genus:	*Osmundastrum*
Genus:	*Todea*
Genus:	*Leptopteris*

Europe and North America by the late Triassic (Skog, 2001). The origin of crown-group Osmundaceae by Late Triassic time (Phipps et al., 1998) suggests that some extant genera and species could be extremely ancient. If true, that would help explain the widely disjunct distributions of many living species (e.g., Hewitson, 1962; Yatabe et al., 1999). It also would account for the occurrence of *Todea tidwellii* in western North America, whereas restricted ranges of the two living species are half way around the world in New Zealand and New Guinea.

Calibration of clade ages for Osmundaceae—Osmundaceae and closely related ferns are represented by an unusually large number of morphospecies that range from the Late Permian, through the Mesozoic and Tertiary, and up to the present (Gould, 1970; Miller, 1971; Tidwell and Ash, 1994; Serbet and Rothwell, 1999; Stockey and Smith, 2000; Skog, 2001). More ancient dates for the clade (e.g., Schneider et al., 2004) remain unverified, either because they are calculated from inaccurate tree topologies (Rothwell and Nixon, 2006) and/or because the fossils have equivocal systematic relationships to modern Osmundaceae (i.e., Thamnopteridaceae sensu Miller, 1971).

Fossils of the Osmundaceae and the closely related family Guaireaceae Herbst form one of the most extensive paleontological records (Tidwell and Ash, 1994) for inferring evolution and phylogeny to be found anywhere among fern clades of the euphyllophytes (Rothwell, 1999). However, inferring the antiquity of crown group Osmundaceae from the paleontological record is complicated by almost all of the fossils being described as morphotaxa, rather than being understood as extinct species of plants. Up through the Jurassic, most morphospecies of compressed fertile osmundaceous fronds do not show synapomorphies for living genera (e.g., *Todites* Seward; Harris, 1961). Therefore, without knowledge about the rest of the sporophyte, those species cannot be assigned to a living genus with confidence. Likewise, most anatomically preserved osmundaceous trunks (Tidwell and Ash, 1994; Cantrill, 1997; Stockey and Smith, 2000) lack diagnostic features of living species, and little is known of their frond architecture, pinnule morphology, sporangia, or spores. Therefore, such fossils could represent either species of extinct genera or extinct species of genera with living representatives.

Compressed fertile frond segments described from the Late Triassic of Antarctica as *Osmunda claytoniites* Phipps, T N. Taylor, E. L. Taylor, Cuneo, Boucher & Yao (Phipps et al., 1998) provide the oldest unequivocal evidence for the genus *Osmunda* s.l., and establish a minimum age for crown group Osmundaceae of around 220 million years. Likewise, *Todea tidwellii* provides a minimum age of ca. 136 million years for the *Todea* clade. The earliest evidence for a living species of Osmundaceae consists of anatomically preserved trunks of *Osmundastrum cinnamomea* from the Campanian stage of the Upper Cretaceous (ca. 75 Ma [million years ago]; Lerbekmo and Braman, 2002) in western Canada (Serbet and Rothwell, 1999). That age establishes *O. cinnamomea* as having the greatest known species longevity of all vascular plants (Serbet and Rothwell, 1999).

Together, the minimum clade ages established by fossil Osmundaceae confirm hypotheses that the crown group evolved by the early Mesozoic, that the *Todea+Leptopteris* clade was present by the Early Cretaceous, and that living species began to appear no later than the Late Cretaceous. However, if the tree topology presented in Fig. 12 is accurate, then at least some of the Triassic morphospecies of Osmundaceae may actually represent the *Osmundastrum* clade. In this regard, we eagerly

await the testing of these hypotheses by the future reconstruction of osmundaceous fossils as species of extinct plants and by the accurate placement of more fossil species on the phylogenetic tree.

LITERATURE CITED

BIERHORST, D. W. 1971. Morphology of vascular plants. Macmillan, New York, New York, USA.

BOWER, F. O. 1926. The ferns (Filicales), vol. II. Cambridge University Press, Cambridge, UK.

CANTRILL, D. J. 1997. The pteridophyte *Ashicaulis livingstonensis* (Osmundaceae) from the Upper Cretaceous of Williams Point, Livingston Island, Antarctica. *New Zealand Journal of Geology and Geophysics* 40: 315–323.

CLAUSEN, R. T. 1938. A monograph of the Ophioglossaceae. *Memoirs of the Torrey Botanical Club* 19: 1–177.

CLEAL, C. J. 1993. Pteridophyta,. *In* M. J. Benton [ed.], The fossil record 2, 779–794. Chapman and Hall, London, UK.

DIELS, L. 1898. Osmundaceae. *In* A. Engler [ed.], Die natürlichen Pflanzenfamilien, 372–380, Verlag von Wilhelm Engelmann, Leipzig, Germany.

GOLOBOFF, P. A. 1999. Analyzing large data sets in reasonable times: Solution for composite optima. *Cladistics* 15: 415–428.

GOULD, R. 1970. *Palaeosmunda*, a new genus of siphonostelic osmundaceous trunks from the Upper Permian of Queensland. *Palaeontology* 13: 10–28.

HARRIS, T. M. 1961. The Yorkshire Jurassic flora. I. Thallophyta—Pteridophyta. British Museum, London, UK.

HENNIPMAN, E. 1968. A new *Todea* from New Guinea, with remarks on the generic delimitation of recent Osmundaceae. *Blumea* 16: 105–108.

HEWITSON, W. 1962. Comparative morphology of the Osmundaceae. *Annals of the Missouri Botanical Garden* 49: 57–93.

HOLTTUM, R. E. 1973. Posing the problems. *In* A. C. Jermy, J. A. Crabbe, B. A. Thomas [eds.], The phylogeny and classification of ferns. *Botanical Journal of the Linnean Society* 67 (Supplement 1): 1–10.

JOY, K. W., A. J. WILLIS, AND W. S. LACEY. 1956. A rapid cellulose acetate peel technique in palaeobotany. *Annals of Botany, new series* 20: 635–637.

KRAMER, K. U. 1990. Osmundaceae. *In* K. Kubitzki [ed.], The families and genera of vascular plants, vol. 1, Pteridophytes and gymnosperms, 197–200. Springer, Berlin, Germany.

LERBEKMO, J. F., AND D. R. BRAMAN. 2002. Magnetostratigraphic and biostratigraphic correlation of late Campanian and Maastrichtian marine and continental strata from the Red Deer Valley to the Cypress Hills, Alberta, Canada. *Canadian Journal of Earth Sciences* 39: 539–557.

MILLER, C. N. 1967. Evolution of the fern genus *Osmunda*. *Contributions from the Museum of Paleontology, University of Michigan* 21: 139–203.

MILLER, C. N. 1971. Evolution of the fern family Osmundaceae based on anatomical studies. *Contributions from the Museum of Paleontology, University of Michigan* 23: 105–169.

NIXON, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.

PHIPPS, C. J., T. N. TAYLOR, E. L. TAYLOR, N. R. CUNEO, L. D. BOUCHER, AND X. YAO. 1998. *Osmunda* (Osmundaceae) from the Triassic of Antarctica: An example of evolutionary stasis. *American Journal of Botany* 85: 888–895.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* 65: 188–218.

ROTHWELL, G. W., AND K. C. NIXON. 2006. How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences* 167: 737–749.

SCHNEIDER, H., E. SCHUETTPELZ, K. M. PRYER, R. CRANFILL, S. MAGALLÓN, AND R. LUPIA. 2004. Ferns diversified in the shadow of angiosperms. *Nature* 428: 553–557.

SERBET, R., AND G. W. ROTHWELL. 1999. *Osmunda cinnamomea* (Osmundaceae) in the Upper Cretaceous of western North America:

Additional evidence for exceptional species longevity among filicalean ferns. *International Journal of Plant Sciences* 160: 425–433.

SKOG, J. E. 2001. Biogeography of Mesozoic leptosporangiate ferns related to extant ferns. *Brittonia* 53: 236–269.

SMITH, A. R., K. M. PRYER, E. SCHUETTPELZ, P. KORALL, H. SCHNEIDER, AND P. G. WOLF. 2006. A classification for extant ferns. *Taxon* 55: 705–731.

SMITH, S. Y., G. W. ROTHWELL, AND R. A. STOCKEY. 2003. *Cyathea cranhamii* sp. nov. (Cyatheaceae), anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. *American Journal of Botany* 90: 755–760.

STEWART, W. N., AND G. W. ROTHWELL. 1993. Paleobotany and the evolution of plants. Cambridge University Press, Cambridge, UK.

STOCKEY, R. A., AND G. W. ROTHWELL. 2006. The last of the pre-angiospermous vegetation: A Lower Cretaceous flora from Apple Bay, Vancouver Island. In proceedings of Advances in paleobotany—Recognizing the contributions of David L. Dilcher and Jack A. Wolfe on the occasion of their 70th birthday, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA Website http://www.flmnh.ufl.edu/paleobotany/meeting/abstract.htm#Stockey (Abstract).

STOCKEY, R. A., AND S. Y. SMITH. 2000. A new species of *Millerocaulis* (Osmundaceae) from the Lower Cretaceous of California. *International Journal of Plant Sciences* 161: 159–166.

SUN, G., J. QIANG, D. L. DILCHER, S. ZHENG, K. C. NIXON, AND X. WANG. 2002. Archaefructaceae, a new basal angiosperm family. *Science* 296: 899–904.

TAYLOR, T. N., AND E. L. TAYLOR. 1993. The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

TIDWELL, W. D., AND S. R. ASH. 1994. A review of selected Triassic to Early Cretaceous ferns. *Journal of Plant Research* 107: 417–442.

VAVREK, M. J., R. A. STOCKEY, AND G. W. ROTHWELL. 2006. *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. *International Journal of Plant Sciences* 167: 631–637.

WAGNER, W. H. 1969. The construction of a classification. *In* U.S. National Academy of Science Publication no. 1692, 230–256. National Academy Press, Washington, D.C., USA.

YATABE, Y., H. NISHIDA, AND N. MURAKAMI. 1999. Phylogeny of Osmundaceae inferred from *rbc*L nucleotide sequences and comparison to the fossil evidences. *Journal of Plant Research* 112: 397–404.

APPENDIX 1. Matrix of scorings for states of morphological characters 1228 1268 as defined in Appendix 2.

Taxon	Scores for states 1228–1268
Ophioglossum reticulatum	44545545454455544444?5444444444444444444444
Angiopteris lygodiifolia	44545555455455546455555444454454444454446554
Cephalomanes thysanostomun	44444554444444444454???54?54?244?44?44?4??544
Lygodium japonicum	55444454444444744??44?54?54??54?444444545
Gleichenia japonica	55444454444454544544545455444544544454554
Dryopteris cristata	44545455454445545548??244?44??5??44?4?6554
Stegnogramma pozoi	55545455454444447??46??24?44??5??44?4??554
Todea barbara	44554555545555445454546545444544555444444545
Osmundastrum cinnamomea	445545555455554444445554554444555444554544554
Leptopteris hymenophylloides	44554555545555445444554544445544544445445
Osmunda regalis	44554555455554444547545444455554654444554
Osmunda vachellii	44554555455555444544555544455554454445554
Todea tidwellii	4455455554??54454545455445445?5455444???

APPENDIX 2. Definitions and states for morphological characters 1228–1268.

1228. Rhizome orientation (4) diagonal, (5) erect or horizontal.

1229. Internodes (4) short, (5) long.

1230. Protostele (4) present, (5) absent.

1231. Dictyoxylic stele (4) absent, (5) present.

1232. Dictyostele (4) absent, (5) present.

1233. Gap in xylem formed by leaf trace divergence (4) absent, (5) present.

1234. Cauline protoxylem (4) endarch, (5) mesarch, (6) exarch.

1235. Pith (4) absent, (5) present.

1236. Primarily sclerenchymatous pith (4) absent, (5) present.

1237. Primarily parenchymatous pith (4) absent, (5) present.

1238. Winged stipe base (stipular wings) (4) absent, (5) present.

1239. Sclerenchyma bundles in stipular wings (4) absent, (5) present.

1240. Number of differentiated cortical regions in stem (4) one, (5) two, (6) more than two.

1241. Inner cortex composition (4) sclerenchyma, (5) parenchyma.

1242. Outer cortex composition (4) sclerenchyma, (5) parenchyma.

1243. Heterogeneous sclerotic cortex (4) absent, (5) present.

1244. Leaf trace xylem configuration at frond base (4) single, (5) C-shaped bundle, (6) two hippocampiform bundles, (7) C-shaped arc of 3 or more bundles, (8) trapezoid.

1245. Recurved leaf trace xylem margins (4) absent, (5) present.

1246. Stele of roots (4) primarily diarch, (5) polyarch.

1247. Roots diverging per leaf trace (4) zero, (5) one, (6) one to two, (7) two, (8) three to five.

1248. Roots diverging from cauline xylem (4) absent, (5) present.

1249. Roots diverging from leaf traces (4) absent, (5) present.

1250. Sclerenchyma sheath in stipe cortex (4) absent, (5) present.

1251. Stipe sclerenchyma sheath of heterogeneous cellular construction (4) absent, (5) present.

1252. Sclerenchyma sheath in stipe cortex (4) absent, (5) present.

1253. Sclerenchyma sheath thinner on adaxial side than elsewhere (4) absent, (5) present.

1253. Sclerenchyma sheath differentiating at inner margin of inner cortex (4) absent, (5) present.

1254. Sclerenchyma sheath differentiating at inner margin of outer cortex (4) absent, (5) present.

1255. Sclerenchyma sheath differentiating in outer region of outer cortex (4) absent, (5) present.

1256. Sclerenchyma sheath differentiating distal to divergence from cortex (4) absent, (5) present.

1257. Interior sclerenchyma (4) absent, (5) present.

1258. Interior sclerenchyma as scattered bundles (4) absent, (5) present.

1259. Interior sclerenchyma from pith (4) absent, (5) present.

1260. Occluded sclerenchyma bundles at adaxial margin of leaf trace (4) absent, (5) one, (6) two to many.

1261. Sclerenchyma bundles at abaxial margin of leaf trace (4) absent, (5) present.

1262. Adaxial side of sclerenchyma sheath thinner (4) absent, (5) present.

1263. Differentiated regions of sheath (4) absent, (5) present.

1264. Leaf trace protoxylem (4) adaxial, (5) mesarch, (6) abaxial.

1265. Protoxylem in diverging leaf trace (4) one, (5) two, (6) many.

1266. Root hairs (4) absent, (5) present.

1267. Sporangia abaxial on broad laminar pinnules (4) absent, (5) present.

1268. Sporangia abaxial on distinctly narrow or skeletonized pinnules (4) absent, (5) present.