Anatomically preserved *Woodwardia virginica* (Blechnaceae) and a new Filicalean fern from the middle Miocene Yakima Canyon flora of central Washington, USA

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Anatomically preserved *Woodwardia virginica* (Blechnaceae) and a newly recognized onocleoid fern are described from the middle Miocene Yakima Canyon flora of central Washington State, USA. Identification of the *W. virginica* fossils is based on a combination of vegetative pinnules, rhizome and stipe anatomy, and fertile pinnules with indusiate sori and sporangia like those of extant *W. virginica*. Fronds are isomorphic. Vegetative pinnules are elongated and pinnatified, with a secondary vein paralleling the midvein. Secondary veins of the pinnule lobe anastomose to form primary areoles and are either simple or dichotomize toward the margin. Rhizomes have a simple dictyoistele with 3–5 cauline vascular bundles and often a sclerotic hypodermis. Leaf traces contain two large adaxial vascular bundles that occur laterally and adaxially, flanking an arc of 4–6 smaller bundles. Fertile pinnules have linear sori that are somewhat embedded in the laminae and are enclosed by a thin indusium. Leptosporangia display a vertical annulus and an elongated stalk. A second fern, *Wessiea yakinmaensis* gen. et sp. nov., is represented by anatomically preserved branching rhizomes and attached frond bases that conform to the *Onoclea*-type pattern of rhizome and frond-base vasculature. Rhizomes have a simple dictyoistele of 4–5 cauline meristoles. Leaf divergence is helical, with paired hippocampiform radial traces. These two ferns occur in the same matrix with specimens of *Osmunda wehrii*. They demonstrate that filicalean fern assemblages similar to those of extant temperate floras were well established in western North America by the middle Miocene and further emphasize the exceptional species longevity of some homosporous pteridophytes.

Key words: Blechnaceae; fossil Filicales; Miocene; silicified; *Wessiea; Woodwardia virginica*.

Filicalean ferns are well known as components of Cretaceous and Tertiary vegetation, where they usually have been included in floristic treatments of compressed angiosperm-dominated assemblages (Tidwell and Ash, 1994; Collinson, 1996, in press; Skog, in press). Much less commonly, species have been described from particularly pteridophyte-rich deposits (e.g., Smith, 1938; Andrews and Pearsall, 1941; Pabst, 1968; Crabtree, 1988). Although numerous occurrences have been documented, relatively few Cretaceous and Tertiary ferns have been studied in detail necessary to understand their precise taxonomic relationships to living species. Some of the most completely understood filicalean ferns come from compressed specimens collected in western North America and include *Lygodium kauflussii* (Manchester and Zavada, 1987) and *Onoclea sensibilis* (Rothwell and Stockey, 1991).

Other fossil ferns are represented by anatomically preserved remains (Ogura, 1972). In the Cretaceous, for example, there are cyatheaceous, schizaeaceous, thyrsoperid, and osmundaceous ferns from Hokkaido, Japan (Nishida and Nishida, 1979; Nishida, 1981, 1982; Yoshida, Nishida, and Nishida, 1996a, b) and California (Lantz, Rothwell, and Stockey, 1999), gleicheniaceous ferns from eastern North America (Gandolfo et al., 1997), a variety of filicalean ferns from south–central Alberta, Canada (Serbet, 1996; Serbet and Rothwell, 1999), and the famous *Tempskya* ferns of Idaho and many other localities (e.g., Tidwell and Hebbert, 1992). In the Paleogene, permineralized forms include osmundaceous ferns from the Paleocene and Eocene of Wyoming and New Mexico (e.g., Tidwell and Parker, 1987; Tidwell and Medlyn, 1991), middle Eocene ferns from the Clarno Formation of Oregon (Arnold and Daugherty, 1963, 1964), and coeval Princeton chert of British Columbia (Basinger, 1976; Basinger and Rothwell, 1977; Cevallos-Ferriz, Stockey, and Pigg, 1991; Rothwell, Stockey, and Nishida, 1994; Pigg and Stockey, 1996; Stockey, Nishida, and Rothwell, 1999). In the middle Miocene of central Washington State, silicified *Osmunda wehrii* occurs at several localities (Miller, 1982; including the same locality as material described in the current study), and *O. cinnamomea* has been described from an unspeciated locality (Miller, 1967, 1971; Serbet and Rothwell, 1999).

Anatomically preserved material often provides an opportunity to study internal structural detail as well as external form and therefore to characterize a broad spectrum of systematically informative characters, particularly if fertile remains are present. When enough material is available to reconstruct fossil taxa as whole plants, recent studies have documented that Cretaceous and Tertiary filicalean ferns may be remarkably similar to their extant counterparts, often being assignable to modern genera, sections, or sometimes even species (e.g.,
In the present study we describe two filicalean ferns from the middle Miocene Yakima Canyon flora of central Washington State, USA. Among ferns represented at this locality are specimens of the previously described *Osmunda wehrii* Miller (1982) and two additional smaller rhizomatous species. The first of these is identified as *Woodwardia virginica* (L.) J. E. Smith (Smith, 1793). This fern is represented by specimens that are structurally identical with the modern *W. virginica* of eastern North America in all features of pinnule morphology, venation, rhizome and stipe anatomy, soral configuration, and sporangial characters, thus adding additional data to our growing realization that some homosporous pteridophytes display exceptional species longevity. A second, smaller species, *Wessiea yakimaensis* Pigg et Rothwell gen. et sp. nov. is represented by branching rhizomes with diverging stipes and adventitious roots. *Woodwardia virginica* and the smaller fern *Wessiea yakimaensis* are found within the same matrix as *Osmunda wehrii* and taxodiaceous conifers, pine, and dicot remains. Floristic comparisons of this fossil assemblage to modern plant communities reveal habitat similarities of the fossil ferns to their modern fern counterparts, suggesting that plant community associations of this type were well established by the middle Miocene in western North America.

**MATERIALS AND METHODS**

Fossils occur in silicified deposits in outcrops of the Yakima Canyon area in central Washington State, USA, between the cities of Ellensburg and Yakima (Pigg, Sophy, and Wehr, 1996; Rothwell, Arnone, and Pigg, 1996; Borgardt and Pigg, 1999; Pigg and Tcherepova, 2000). Additional remains from this same locality include *Osmunda wehrii* (Miller, 1982), *Pinus foisyi* (Miller, 1992), *Quercus hiholensis* (Borgardt and Pigg, 1999), *Liquidambar infrutescences* (Pigg, 1997), several interesting fruits of uncertain affinities (Pigg and Manchester, 1998), and additional typical Miocene elements including members of Taxodiaceae, Vitaceae, Rosaceae, and Cornaceae (Pigg and Tcherepova, 2000).

Fern fossils were obtained from the area locally known as the “County Line Holes” and from the area within the locality designated the “Ho Ho” by the original collectors. Fractured surfaces show laminar vegetative pinnules and small fragments of fertile pinnules, while numerous rhizomes with attached stipes are matted together throughout the matrix. These specimens occur with abundant taxodiaceous and piceaceous conifer remains, dicot foliage, and woody axes and occasional seed and fruit remains. These fossils are preserved below pillows of basalt at the base of the Museum Flow Package within the interbeds of the Sentinel Bluffs Unit of the central Columbia Plateau N2 Grande Ronde Basalt of the Columbia River Basalt Group (Upper Tertiary, middle Miocene) and are dated 15.6 ± 0.2 million years old by Ar/Ar dating technique (Borgardt and Pigg, 1999).

Weathered surfaces showing laminar foliage were dagged and photographed. Small fragments of indusiate sori from surfaces were photographed with reflected light and mounted on stubs for study with the scanning electron microscope (SEM). Rhizomes and frond bases were studied serially from wafered sections cut on a Buehler Isomet slow speed saw (Lake Bluff, Illinois, USA) or an intermediate-size trim saw, with some specimens ground thin enough for study with transmitted light. Sections were mounted on microscope slides with UV-adhesive mounting medium from T.H.E. Company (Lakewood, Colorado, USA) and studied with both reflected and transmitted light. Specimens were photographed with reflected light, which proved most successful in revealing anatomical detail. Living material of *Woodwardia virginica* was collected in August 1998 during a field trip to the New Jersey Pine Barrens associated with the Botanical Society of America meeting in Baltimore (Figs. 1, 11, 14). Material was collected along a roadside on the edge of a red maple swamp on County Road 613, Waterford Township, Burlington County, New Jersey, USA. Additional fertile material of extant *W. virginica* was supplied by Kathleen M. Pryer from the Field Museum (Specimen F 2090338; collected in Hillsborough Co., Florida, USA; Fig. 5) and Donald J. Pinkava, ASU (Sheet 39569; collected in Jasper Co., South Carolina, USA; Fig. 16). Extant material was prepared by standard techniques for light microscopy and SEM.

Specimens are housed as part of the Tuggle/Foisy Collection at the Burke Museum of Natural History and Culture, University of Washington, Seattle, (UWBM), USA, and in the Plant Fossil Collections, Arizona State University Herbarium, Tempe (ASU), Arizona, USA, as indicated in figure captions and systematics section.

**RESULTS**

*Yakima fern remains*—Two types of silicified fern remains can be recognized as distinct from one another (Fig. 2–4, 6–10, 12, 13, 15, 17–24) and from the previously described *Osmunda wehrii* (Miller, 1982). Of the three ferns known from this locality, surface morphological views of vegetative and fertile pinnules are presently known only for *Woodwardia virginica*, with *Osmunda wehrii* and the small fern *Wessiea* represented by only rhizomes and frond bases. Vegetative and fertile pinnules of *W. virginica* are found on the highly weathered surfaces of chert blocks that tend to fracture along the plane of deposition of the fronds (Figs. 2–4, 6, 15, 17, 18). Because most of the organic material has been leached out of the matrix, it was not possible to recover spores or cuticle from macerations. However, surface fragments of indusiate sori casts have yielded taxonomically informative details of the fertile organs (Figs. 15, 17, 18). Blocks in which fern fossils are preserved typically contain masses of ramifying rhizome and frond base remains, with all three ferns intertwined with taxodiaceous conifer needles and other plant organs, primarily roots (Fig. 7). Anatomical structure of the rhizome and frond base is distinctive for both newly discovered ferns and both are considerably smaller than the *Osmunda* plants, with which they are intermixed.

*Woodwardia virginica* (L.) J. E. Smith—*Woodwardia virginica* is represented by vegetative, pinnatifid pinnules (Figs. 2–4, 6) and fragments of fertile pinnules with indusiate sori of annulate sporangia (Figs. 15, 17, 18) that are preserved on fractured surfaces and by branching rhizomes with diverging frond bases and adventitious roots that reveal internal cellular anatomy (Figs. 7–10, 12, 13).

Foliage—The most extensively preserved pinnae are incomplete, but consist of opposite-subopposite pinnatifid segments up to 7.9 cm long and 2.4 cm wide (Fig. 2) that are remarkably similar to those of modern *W. virginica* (Fig. 1). Individual lobes are 3–14 mm long (mean = 9.92 mm) and 3–6 mm wide (mean = 4.63 mm) with the shortest lobes occurring toward the apex. The venation pattern includes a pinnule midvein 0.3–1.1 mm wide, a pinnule lobe midvein, and higher order veins (Figs. 2–4, 6). There is a secondary vein that extends between successive pinnule lobe midveins and that parallels the pinnule midvein in both the living and fossil specimens (Figs. 4, 5). Secondary veins in each pinnule lobe anastomose to form primary areoles that parallel the pinnule lobe midvein, and then extend to the margin (Figs. 4–6). Some veins are unbranched distal to the areoles, whereas others fork one or two times. Although most pinnule lobes are relatively smooth, teeth can occasionally be found along the margin of...
some frond lobes (Fig. 6). Teeth are up to 0.2 mm long and 0.3 mm wide and occur at vein endings (Fig. 6 at arrows).

**Rhizomes and attached frond bases**—Elongated branching rhizomes of *W. virginica* extend through the matrix at several levels (Fig. 7) and are often intertwined with those of other ferns. Rhizomes range 2–5 mm in diameter, and most sections are of internodal regions (Fig. 8). Rhizome branching is dichotomous (Fig. 9), and frond bases are inflated to about two-thirds the diameter of the rhizome (Fig. 10). In agreement with living specimens of *W. virginica* (Fig. 11), rhizomes display a simple dicyostele with 3–5 cauline vascular bundles (meristele) and leaf traces surrounding the pith (Figs. 8–10). The pith is up to 1.5 mm in diameter and composed of thin-walled
Figs. 7–14. *Woodwardia virginica* rhizomes and frond bases. 7. Chert block showing distribution of fern rhizomes and frond bases (ASU, ASUYC 24 Side). ×0.64. 8. Transverse section of fossil rhizomes (ASU, ASUYC 24). ×7.5. 9. Transverse section of two fossil rhizomes showing vascular strands (arrows) (ASU, ASUYC 24). ×8. 10. Transverse section of fossil rhizome and frond base. Note three meristoles and hypodermis in rhizome (at left), frond base (right) adventitious root (upper right) (UWBM 96958 A Bot. #1). ×11.4. 11. Transverse section of rhizome from extant plant showing four meristoles, smaller traces, narrow hypodermis, adventitious root (bottom), and scales (ASU, Rhizome series A #2D). ×9.4. 12. Fossil frond base in transverse section showing two major
parenchyma cells (Fig. 10). Individual meristeles of both the living and fossil rhizomes are round to oval in cross sections (Figs. 8–11) and ~0.6 mm thick. Individual meristeles of the fossils have a central region that consists of angular tracheids, surrounded by a narrow light-colored zone and a dark line (Fig. 13) that conform to the positions of phloem and an unsierate bundle sheath in living W. virginica (Fig. 14). Smaller, apparently protoxylem tracheids like those at both the inside and outside of living W. virginica meristeles (Fig. 14) are usually not apparent in the fossil rhizomes (Fig. 13), but can sometimes be identified in exceptionally well-preserved specimens. The cortex is typically ~0.4 mm wide and composed of two zones of cells. As in the living specimens (Figs. 11, 14), most of the cortex in the fossils consists of thin-walled parenchyma like that of the pith (Figs. 10, 13), but there is a thin zone consisting of several layers of thicker walled cells at the periphery (Figs. 10, 13) that conforms to the hypodermis of living rhizomes (Figs. 11, 14; Payne and Peterson, 1973). Also as in the living rhizomes (R. Cranfill, Jepson Herbarium, Berkeley, California, personal communication), epidermis is usually not present in the fossils.

A distinctive character of W. virginica (Lucansky, 1981; R. Cranfill, personal communication) is frond traces consisting of two large adaxial vascular bundles that are located laterally and adaxially, flanking an arc of 4–6 (rarely 7) smaller bundles (Fig. 12). Developing frond traces can be identified in cross sections of the rhizome by several small bundles located between larger meristeles in both living and fossil specimens (Figs. 8, 9, 11). Adventitious roots are rarely preserved in the fossils, but a small number of incompletely preserved examples have been identified, diverging at approximately right angles to the rhizome periphery (Fig. 10; Schneider, 1996).

**Fertile pinnules**—Most frond segments appear to be vegetative, but a small number of fertile pinnule lobe fragments have been recognized with elongated sori on the abaxial surface. These are all preserved on bedding planes of the rock matrix and are usually found with the indusium partly or completely broken away (Figs. 15, 18). As in living specimens, sori of the fossils are located over and elongated parallel to the pinnule lobe midvein. The indusium is attached along the side of the sorus that lies adjacent to the midvein in both living

bundles adaxially (at left) and five smaller strands abaxially, at right (ASU, ASUYC 24). ×24. 13. Detail of fossil rhizome showing anatomy of meristele. Note narrow hypodermis, at right (ASU, ASUYC 14 #9). ×28. 14. Detail of rhizome in extant plant showing anatomy of meristele to compare with Fig. 13. Note protoxylem around periphery and hypodermis, at right (ASU, Rhizome series C #2C). ×36.
Figs. 19–24. *Wessiea yakimaensis* rhizomes and frond bases. Figs. 19–22. Serial sections showing rhizome vasculature and frond trace divergence from proximal (Fig. 22) to distal levels (Fig. 19). Individual numbers indicate positions of leaf trace origin in stele and leaf trace divergence. Holotype specimen on 56441 A1 and E2 series. 19. UWBM 56441 A1 Bot #3. ×12. 20. UWBM 56441 A1 Top #1. ×14. 21. UWBM 56441 E2 Top #1. ×20. 22. UWBM 56444 E2 Top #3. ×12. 23. Transverse section of rhizome showing root gap (rg), root trace (rt), and frond trace (ft). UWBM 56444 F1 Top #2. ×32. 24. Transverse section of rhizome showing meristele with prominent protoxylem strands (px and at arrow), and omega to hippocampiform frond traces (ft). UWBM 56445 A1 Bot #1. ×38.
and fossil specimens (Figs. 15 and 16 at right, and 18 at top), and the sorus is somewhat sunken into the pinnule surface.

Although nearly all of the organic material has been leached away from most Yakima Canyon fossils and specimens often have little contrasting mineral stain, features of the sporangia are preserved as molds and casts on the rock surface (Figs. 15, 17, 18). Under SEM, these features are represented by the rock surface (Fig. 17), and in light microscopy, the annulus is revealed by differential patterns of light refraction (Fig. 18). Sometimes both light and SEM preparations of the same specimen are required to see overall features of the sorus as well as details of the sporangia (cf. Figs. 17 and 18). Sori are usually impenetrable to see overall features of the sorus as well as details of the sporangia (cf. Figs. 17 and 18). Sori are ~1 mm wide and 1.5–5 mm long. The smaller sizes are comparable to sori of living W. virginica before sporangial dehiscence (e.g., Figs. 16–18; Small, 1964; R. Cranfill, personal communication), while the largest fossil representatives (Fig. 15) are comparable to the much larger sizes of sorus that we measured in living specimens that were pressed after the sporangia had dehisced.

As in the living specimens (Fig. 16) each sorus consists of numerous sporangia with narrow stalks (Fig. 17 at arrow) and a capsule with a uniseriate vertical annulus (Figs. 16–18). Also as in living specimens, the capsule is round-oval when viewed margin in cross sections (Figs. 19–22). Each consists of two diverging frond traces that extend into a stipe from the gap formed by the diverging root (e.g., Figs. 19–22 at 3 and at 4). This conforms to the pattern of trace divergence recently recognized as characteristic of many dryopterid ferns (White and Weidlich, 1995; Stockey, Nishida, and Rothwell, 1999). Periodically, two calyce meristeles fuse distally to close a gap from which frond traces have diverged at a lower level, and this returns the number of calyce meristeles to four (e.g., Figs. 20–22, 24).

Stipes of Wessiea are roughly D-shaped with an irregular margin in cross sections (Figs. 19–22). Each consists of two oval frond traces embedded in ground tissue like that of the rhizome. The frond traces are typically incompletely preserved (Fig. 22), but well-preserved examples in the rhizome cortex and stipe display hippocampiform xylem strands (Figs. 19, 20, 24). Small diaphragm roots occur in the rock matrix. They have a parenchymatous cortex with the same brown coloration as the ground tissues of Wessiea, but have not been found in organic attachment to the rhizomes.

**Wessiea yakimaensis Pigg et Rothwell gen. et sp. nov.—**

*Wessiea* is represented by elongated, narrow rhizomes and helically arranged frond bases (Figs. 19–22). Rhizomes measure 1.5–3.0 mm in diameter and typically are surrounded by several stipes (Fig. 19). In cross section the rhizome displays a simple dictyostele with 4–5 calyce meristeles and paired, diverging frond traces (Figs. 19–24). Calyce meristeles are represented primarily by xylem, the other vascular tissues not being evident in most specimens. However, in a few sections there is a narrow zone of small cells surrounding each meristele, and this suggests the position of phloem and possibly a thin bundle sheath of that of *W. virginica*. Calyce meristeles are ovoid to tangentially elongated in cross section, measuring 0.4–1.2 mm long and 0.2–0.4 mm thick. Metaxylem tracheids are angular in cross sections and 28–69 × 42–97 μm in diameter. Small tracheids reveal the positions of protoxylem strands in some bundles (Fig. 24 at px and at arrow). In other bundles protoxylem could not be identified.

In most specimens the ground tissue consists of uniformly thin-walled parenchyma cells in both the pith region and cortex (Fig. 23). Thicker walled hypodermal cells like those of *W. virginica* are typically absent, but a lighter colored zone near the periphery of the cortex in some *Wessiea* specimens suggests that hypodermis may be weakly developed (Fig. 19). The outer margin of the rhizome is relatively smooth in most specimens, suggesting that the tissues are complete. However, an outer layer of differentiated epidermal cells usually can be identified. Leaf trace divergence is helical, as indicated by the series of cross sections in Figs. 19–22.

There are typically 4–6 vascular bundles plus two diverging frond trace bundles in each cross section (Figs. 19–24). Four or five of these are calyce meristeles and the sixth (when present) represents the xylem of a diverging adventitious root. When followed through an acropetal series of transverse sections (from Fig. 22 to Fig. 19), the vascular architecture of *Wessiea* can be identified as conforming to the general pattern exhibited by asplenioid ferns (sensu Ogura, 1972; White and Weidlich, 1995; Stockey, Nishida, and Rothwell, 1999). Progressing distally from a level where there are four calyce meristeles (Fig. 22), a large meristele with a more-or-less centrally located protoxylem strand (as in Fig. 24, at arrow) divides into three (Fig. 23, at bottom). The central strand diverges as a root trace (as in Fig. 23, at bottom), and this produces a root gap between the other two resulting bundles (Fig. 23, at rg). At this level there are five calyce meristeles. Distally, the two resulting calyce meristeles each divide tangentially to produce a pair of frond traces that extend into a stipe from the gap formed by the diverging root (e.g., Figs. 19–22 at 3 and at 4). This conforms to the pattern of trace divergence recently recognized as characteristic of many dryopterid ferns (White and Weidlich, 1995; Stockey, Nishida, and Rothwell, 1999). Periodically, two calyce meristeles fuse distally to close a gap from which frond traces have diverged at a lower level, and this returns the number of calyce meristeles to four (e.g., Figs. 20–22, 24).

**SYSTEMATICS**

**Order**—Filicales.

**Family**—Dryopteridaceae sensu Kramer (1990).

**Genus**—Wessiea Pigg et Rothwell gen. nov. (Figs. 19–24).

**Species**—*Wessiea yakimaensis* Pigg et Rothwell gen. et sp. nov. (Figs. 19–24).

**Combined generic and specific diagnosis**—*W. yakimaensis* gen. et sp. nov.

Dictyostelic filicalean fern rhizomes with diverging stipes displaying two hippocampiform-shaped leaf traces. Gaps in stele formed by diverging root; more distal leaf traces diverging tangentially from amphiicular meristeles, and extending through common leaf gap before entering stipe base.

**Holotype**—Specimen on 3A #1–3 and 3 E, #1–3, UWBM 56441, Figs. 19–22.

**Paratypes**—Specimen on 3F #2 top, UWBM 56441, (Fig. 23), 2A, #1 bot, UWBM (Fig. 24).

**Type locality**—The “Ho Ho” known locally as one of the “County Line Holes” is ~7.3 km north of the Interstate 82 Firing Center Exit, Yakima County, on Yakima Canyon Road (T14N, R19E, NE 1/4 of NW 1/4 of Sec. 3).

**Age and stratigraphy**—Upper Tertiary, middle Miocene, 15.6 ± 0.2 Ma. In the Museum Flow Package within the in-
terbeds of the Sentinel Bluffs Unit of the central Columbia Plateau, Grande Ronde Basalt of the Columbia River Basalt Group (Borgardt and Pigg, 1999).

Etymology—The generic name, Wessiea, honors Wesley C. Wehr for his numerous contributions to Tertiary paleobotany of western North America. The specific epithet, yakimaeensis, refers to the locality in Yakima Canyon.

DISCUSSION

Systematics of Woodwardia—Woodwardia (Blechnaceae) is a genus of 11 temperate to subtropical species and two possible hybrids of terrestrial habitat that occur today in disjunct areas of the northern hemisphere with centers of diversity in eastern Asia and North America (Chiu, 1974; Lucansky, 1981; Tryon and Tryon, 1982; Cranfill, 1998; R. Cranfill, personal communication). The main center of diversity is in eastern Asia, especially within mountainous regions of central China and Taiwan. Asian species include W. kempi, W. japonica, and W. harlandii, while Eurasian species are W. prolifera, W. unigemmata, W. orientalis, and W. radicans. In North America, five species occur naturally and one is introduced. Woodwardia virginica, the Virginia chain fern, and the dimorphic W. aerolata are native to eastern coastal North America (McVagh and Pyron, 1951; Shaver, 1954; Small, 1964; Lucansky, 1981; Cranfill, 1993). Woodwardia fimbriata occurs along the west coast of North America, from British Columbia to Baja California and Sonora, Mexico, while W. spinulosa appears from Sonora, Mexico to Costa Rica. Woodwardia martinezii is narrowly endemic in the highlands of central Mexico (Tryon and Tryon, 1982). Possible hybrids include W. apogama and a new form of probable hybrid origin between W. martinezii and W. spinulosa also occurs in Mexico and Central America (R. Cranfill, personal communication). The southern European native W. radicans is rarely also an escaped cultivar in eastern North America.

Features of fossil and living W. virginica—The silicified Woodwardia fossils from Yakima Canyon are identical to extant W. virginica in all features of pinnule morphology, veination, rhizome and stipe anatomy, sorus configuration and sporangial details and can thus be assigned to the extant species with confidence. This determination is possible in part because of these numerous differences between W. virginica and other extant Woodwardia species and because many of these distinguishing characters are clearly seen in the fossils.

Foliage of W. virginica is pinnate pinnatifid, with pinnules that are broadest at or near the middle, tapered slightly at the base and with broad, blunt segments with little or no sinus. Pinnule size and shape of fossil and extant W. virginica are strikingly similar (Figs. 1, 2), with elongate pinnatifid pinnules with opposite to subopposite segments to each pinna. Whereas foliage of fossil W. virginica from Yakima is represented by isolated and incomplete pinnules, the general form is quite comparable to ultimate segments of extant fronds (Figs. 1, 2). Moreover, extant W. virginica pinnules abscise from the rachis in the fall (R. Cranfill, personal communication, 2000). Given the many similarities of the Yakima material and extant W. virginica, this phenomenon most likely also occurred in the Miocene forms, explaining in part why we find exclusively dispersed pinnules rather than larger segments of complete fronds. Venation in the Yakima pinnules is also identical to that of extant W. virginica (Figs. 4, 5). Pinnules have a mid-vein, as well as a conspicuous secondary vein that parallels the long axis of the pinna. Other secondaries fork once or twice with occasional, but relatively few primary anastomoses, when compared to some other extant species such as W. arrosetata. Of modern species of Woodwardia, W. virginica is distinguished by its relatively small number of anastomoses, partly as a result of its relatively narrow lamina. Scales, which are usually present in modern species (Fig. 11), but not particularly diagnostic (Lucansky, 1981; Cranfill, 1998), are not preserved in the fossils.

Rhizome morphology is a taxonomically valuable character in extant Woodwardia. Rhizomes of modern W. virginica are described as being long-creeping, with the external appearance of a stretched rope with very few twists, and having relatively few adventitious roots in a current year’s growth (Cranfill, 1993). Extant W. virginica rhizomes range in size from 0.6 to 1.5 cm in diameter. Those of the Yakima Canyon plants are smaller, at 2–5 mm in diameter and bear relatively few adventitious roots. Rhizomes of the Yakima fossils are elongate, branch infrequently and dichotomously, and are characterized by inflated stipe bases like those of extant W. virginica, that may be up to two-thirds the diameter of the axis (Figs. 9, 10).

Stelar architecture and anatomy are also like that of extant W. virginica, with rhizomes having a simple dictyosteole containing 3–5 round to oval meristeles and numerous leaf traces (compare Figs. 9–11). Although details of rhizome histology are somewhat limited by preservation, characteristic bundle sheaths of the meristeles and a narrow hypodermis at the margin of the rhizome are noted (compare Figs. 10, 11, 13, 14). While Lucansky (1981) demonstrated that histological features of rhizomes were fairly similar in various species of Woodwardia, he observed that W. virginica tends to have more aerenchymatous ground tissue and suggested this was because of its frequently submersed plant habit in swampy environments. As is common in extant Woodwardia virginica, the epidermis appears to be sloughed off in the fossil forms.

Another characteristic definitive for W. virginica is the number and configuration of traces to stipes. While most woodwardias typically have two large adaxial bundles surrounding a variable number of smaller strands, in W. virginica the pattern is two large, adaxial bundles occurring on either end of a semicircle of 4–7 smaller abaxial strands (Lucansky, 1981). We see this organization in the Yakima fossil material as well (Fig. 12).

In addition to vegetative features, the Yakima fossils show details of indusiate sori and sporangia that are characteristic of W. virginica. While indusia in some species of Woodwardia are thick and persistent, those of W. virginica tend to be thinner and more ephemeral. As sporangia mature and dehisce, they expand to displace the delicate, flap-like indusia and individual sorus so can no longer be clearly delimited. Specimens of Yakima plants show a size range comparable from younger undehisced sporangia to older fronds in which mature sporangia have dehisced, and both show remnants of indusia (Figs. 15–18). Sporangia are typical leptosporangia with a small diameter and a long stalk (Fig. 17). Sporangia show a conspicuous vertical annulus that characterizes the genus (Figs. 15–18). Because little to no organic material remains and we were unable to macerate for spores, we cannot report on spore shape or organization, which is typically monolete with diffuse, pappilate surface in extant W. virginica (Tryon and Lugardon, 1990).
Plant community ecology—From what is known of the floristics and depositional setting of the Yakima Canyon flora, fern and other floral associations of the Yakima plants are remarkably similar to those of extant Woodwardia virginica. Living W. virginica is a plant of the Atlantic Coastal Plain that occurs from Canada through Florida and into Texas. Its most common habitats are in open swampy pine woods, wet swampy woods, acid bogs, and along streams and roadside ditches (McVaugh and Pyron, 1951; Shaver, 1954; Lucansky, 1981). In some cases it occurs directly as a submerged plant and even produces floating mats of rhizomes (Power, 1914; Gams, 1938).

In the Yakima flora Woodwardia occurs with Osmunda wethrii and the small ononcoid fern Wessiea. This type of association is similar to some of W. virginica's modern associations. Throughout its range, extant W. virginica co-occurs with Osmunda cinnamomea and O. regalis. In the northern, glaciated portion of its range, additional co-occurring ferns include Thelypteris palustris, T. simulata, Dryopteris cristata, and D. carthusiana. Onoclea sensibilis grows nearby but is seldom intermixed, as Woodwardia thrives in more acid soils. To the south, ferns found in association with W. virginica may include other species of Thelypteris, particularly T. gongyloides, W. aerolata, and various subtropical and tropical ferns in Florida (R. Cranfill, personal communication, 2000). One of us (KBP) has seen W. virginica growing along with W. aerolata, Onoclea sensibilis, Osmunda cinnamomea, and Thelypteris simulata along margins of a red maple swamp in the New Jersey Pine Barrens and in Taxodium swamps and roadside ditches in coastal North Carolina along with O. regalis, O. cinnamomea, Woodwardia aerolata, Pteridium aquilinum, and a variety of other filicalean ferns. The species is also known in a Taxodium swamp in Vinton County, Ohio, where it grows along with Osmunda, Lygodium, and Onoclea. These last two sites are interesting because they contain a number of xeromorphic species common to the Yakima swamp including taxodiaceous conifers, pines, Liquidambar, white-oak Quercus, Vitis, Nyassa, Platanaus, Cornus, and rosaceous plants (E. Bryan, Cape Fear Botanical Garden, Fayetteville, North Carolina, personal communication; K. Pigg, personal observation). In summary, although we do not imply that all the associated floral elements share an identical evolutionary or phytoecographic history, it appears that W. virginica had established modern habitat tolerances and had similar floristic associations in the Miocene as it has today.

Fossil record of Woodwardia—Woodwardia is a fairly common leaf compression form found throughout the Tertiary of Europe, North America, and Asia. Over 50 species have been listed under Woodwardia or the variant name Woodwardites in the Fossilium Catalogus (Jongmans and Dijkstra, 1965; Dijkstra and Van Amerom, 1988); one author suggests that perhaps around six are valid (Hurnick, 1976). Fossil chain ferns are typically recognized as resembling the following extant species: W. virginica, W. spinulosa, W. aerolata, W. radicans, W. martinezii, and W. japonica (Pabst, 1968; Hurnick, 1976; Collinson, in press).

Previously described fossil remains most similar to W. virginica are compressed crosiers, vegetative and fertile fronds, and sporangia from the Miocene Succor Creek flora named W. deflexipinna by Helen Smith (Smith, 1938; Graham, 1965). These ferns are found in abundance at a single locality where they dominate and otherwise are relatively rare in the flora (Graham, 1965; P. Fields, Michigan State University, personal communication). Vegetative fronds of W. deflexipinna are essentially identical to extant W. virginica and the Yakima material in details of pinnule morphology and venation (K. Pigg, personal observation). Fertile material has not been available for further study. In addition to this species, several other forms from western North America and Europe have also been compared to W. virginica. These include W. müni st eriana, W. rossneriana, and W. maxoni (Hurnick, 1976). Of these, Hurnick figures some specimens that clearly resemble W. virginica (Plate 2a, b, 4a of Hurnick, 1976) and others that may be more similar to other species. Other fossils attributed to Woodwardia from western North America, Europe, and Asia, many needing further study (Collinson, in press), have been discussed elsewhere (Knowlton, 1926; Berry, 1929; Pabst, 1968; Bourreau, 1970; Chandrasekharan, 1974; McIver and Basinger, 1993; Kvaček, 1994).

Relationships of Wessiea—In the most comprehensive survey of fern anatomy yet attempted, Ogura (1972) refers to ferns with paired hippocampiform rachetal traces like those of Wessiea as belonging to the “Onoclea stelar type” but similar traces are also produced by some other athyroid ferns such as living species of Diplazium (Ogura, 1972) and the recently described fossil genus Makotopteris (Stockey, Nishida, and Rothwell, 1999). Moreover, the production of gaps in the rhizome stelae that result from root divergence, rather than leaf trace divergence, is concordant with the stelar architecture of both athyroid and blechnoid ferns (White and Weidlich, 1995).

The combination of a simple dictyostele with amphiocribal cauleine meristoles and paired hippocampiform rachetal traces in Wessiea is characteristic of a wide range of highly derived filicalean ferns assignable to the Dryopteridaceae sensu Kramer (1990). Roots are diarch with a parenchymatous pith, another character that is consistent with this broad systematic assignment (Schneider, 1996). Although this familial concept is not fully concordant with the more widely used classification of Pichi Sermolli (1977), it encompasses a broad range of derived filicalean ferns including those with cauleine and stipe vasculature like that of Wessiea. Moreover, in the absence of frond and sporangial characters, a more precise systematic assignment for Wessiea is extremely difficult. Regardless of its more precise systematic relationships, Wessiea yakimaensis clearly represents a highly derived filicalean similar to those found in the living flora.

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