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SENFTENBERGIA OREGONENSIS (ARNOLD) COMB. NOV. (FILICALES): DELIMITING RELATIONSHIPS AMONG PALEOZOIC TEDELEACEAE

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Reexamination of fossilized plant material from the westernmost Pennsylvanian-age wetland flora in North America reveals that material of *Pecopteris oregonensis* Arnold represents a filicalean fern frond with annulate sporangia and anatomically preserved vascular tissues of the rachis. The frond, which is redescribed as *Senftenbergia oregonensis* (Arnold) Hillier et Rothwell comb. nov., is pinnately compound, with five orders of catadromous dissection, and it appears to have reached a length of 80 cm or more. The rachis displays an anchor-shaped xylem bundle, and dichotomizing aphlebiae are produced at the base of primary pinnae. The rachis, primary pinnae, and secondary pinnae have a dense covering of coarse trichomes. Secondary and tertiary pinnae display a length : width ratio of 2.5 : 1. The pecopterid pinnules measure 1.5–6 mm in length and 1.0–2.0 mm in width, with dichotomous venation, smooth-to-undulating margins, and a rounded tip. Sporangia are marginal and recurved under the abaxial pinnule surface to form two rows that are parallel to the midvein. Each sporangium has a narrow stalk, longitudinal dehiscence, and a terminal multiseriate annulus. The fern is assigned to the Tedeleaceae, and a combination of characters for distinguishing genera within the family is proposed.

Keywords: filicalean fern, fossil, Paleozoic, Tedeleaceae, *Senftenbergia*.

Introduction

Wetland vegetation is far less common in Pennsylvanian deposits of western North America than in the paleotropical belt that extends from what is now midcontinent North America, through eastern North America and Europe, to the Ural Mountains of western Russia (Read and Mamay 1964; Phillips 1980). The westernmost flora of this type was originally discovered by Read and Merriam (1940) within the Spotted Ridge Formation of central Oregon (Merriam and Berthiaume 1943; Orr and Orr 2011), with more detailed descriptions of the plants subsequently provided by Arnold (1953) and Mamay and Read (1956). That occurrence is part of an exotic terrane that was accreted to the west coast of North America during the Mesozoic (Cannings et al. 2011). The locality yields specimens that have been interpreted as coalified compressions that presumably display little or no evidence of internal anatomy, cuticular remains, or palynomorphs (Arnold 1953).

By far the most abundant plant fossils in the assemblage are fern fronds assigned to *Pecopteris oregonensis* Arnold, with calamitean remains also commonly present (Arnold 1953; Mamay and Read 1956). Other plant fossils (i.e., *Stigmaria ficoides* [Sternberg] Brongniart) and/or taxa of equivocal affinities (i.e., lepidodendrid branchlet; *Dicranophyllum rigidum* Mamay and Read; Mamay and Read 1956) are rare. Among the specimens collected and described by Mamay and Read (1956) is a large number of frond segments of *P. oregonensis* that W. DiMichele recognized several years ago as having preserved rachis anatomy (Perrine 1992). Reexamination of those specimens confirms the earlier suspicion (Arnold 1953) that the frond fragments represent a filicalean fern with annulate sporangia and with rachis anatomy similar to that of *Ankyropteris* Stenzel (W. DiMichele in Perrine 1992).

The purposes of this article are to more thoroughly characterize the morphology of *P. oregonensis*, to describe for the first time the rachis anatomy of the species, and to interpret the taxonomic affinities and systematic relationships of the plant. Specimens consist of pinnately dissected frond segments with five orders of dissection, an anchor-shaped xylem bundle in the rachis, and marginal sporangia with longitudinal dehiscence and a terminal annulus. Such specimens can be assigned to the genus *Senftenbergia* Corda of the extinct family Tedeleaceae Eggert and Taylor. The distinguishing combination of characters displayed by the fossils allows for the circumscription of *Senftenbergia oregonensis* comb. nov. Moreover, the discovery of unique character combinations among species of Tedeleaceae allows for the recognition of *Senftenbergia* and *Ankyropteris* as clearly distinct genera that coexisted throughout the Pennsylvanian and Early Permian of Euramerica.

Material and Methods

Material for this study was collected by Mamay and Read (1956) at the same locality where the type material of *Pecopteris oregonensis* was collected (Arnold 1953), it is housed at

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the National Museum of Natural History (NMNH; Washington, DC), and it clearly represents the same species as the type specimen of *P. oregonensis*. Frond segments are preserved on the surfaces of olive-green siltstone blocks, with little coal and no cuticle remaining on the surface. Some of the largest axes are oval in cross sections, and cells of the xylem are partially preserved by iron oxides of limonite or marcasite. Segments of permineralized axes were removed from the rock matrix and embedded in Wards Bioplastic (Wards Natural Science, Rochester, NY). Embedded axes were wafered using a Hillquist low-speed sectioning saw (Hillquist, Denver, CO), etched in concentrated HNO_3, neutralized in dilute $NaCO_2$, rinsed with water, and dried in a warm oven at 60°C. Wafers were mounted on microscope slides with the xylene-soluble mounting medium Eukitt (O. Kindler, Freiburg, Germany).

Specimens were photographed under 70% EtOH to increase resolution and contrast. Low-magnification images were captured with a Leaf Microlumina System, version 1.2 (Leaf Systems, Westborough, MA). Higher-magnification images were captured with a Photophase (Phase One, Copenhagen, Denmark) digital scanning camera mounted on a Leitz Aristophot bellows camera or a Zeiss WL compound microscope. Images were processed with Adobe Photoshop CS2. All specimens, embedded blocks, wafers, and slides are housed at NMNH.

Systematic Descriptions

Order—Filicales

Family—Tedeleaceae Eggert and Taylor

*Genus—*Senftenbergia *Corda*

*Species—*Senftenbergia oregonensis *(Arnold) Hillier & Rothwell comb. nov.*

*Basionym—*Pecopteris oregonensis *Arnold. Palaeontographica Abt. B. 93, P. 63, Text Figs. 1–5, Plate 25, Figs. 9–20. 1953.*

Holotype. University of Michigan, Museum of Paleontology (UMMP) specimen number 31608; fig. 12 of Arnold (1953).

Diagnosis, emended here. Pinnately dissected fronds ~78 cm long and 26 cm wide, with five orders of alternate catadromous branching. Rachis, primary pinnae, and secondary pinnae clothed with dense coarse trichomes; pair of dichotomously branched aphlebia attached at positions of primary pinna divergence. Rachis 5–10 mm wide, with anchor-shaped xylem bundle up to 4.5 mm wide and 3.0 mm high; abaxial antennae shorter than adaxial antennae; cross bar stout, up to 5 cell layers thick. Axes of secondary pinnae 2–4 mm wide; axes of tertiary pinnae 0.6–1.0 mm wide. Vegetative and fertile pinnules 1.5–6 mm long, 1.0–2.0 mm wide, with rounded tip; small pinnules broadly attached with smooth margins, intergrading with larger, narrowly attached pinnules with sinuous margins; sinuous midvein dividing to produce lateral veins that dichotomize up to two times. Sporangia marginal and solitary, reflexed under abaxial surface with apex oriented toward midvein; 0.38–0.88 mm long, 0.13–0.40 mm wide; with short stalk and apical multiseriate annulus; dehiscence longitudinal. Spores unknown.

Locality. Spotted Ridge locality of Arnold (1953; equal to locality 115 of Merriam and Berthiaume 1943), located on the western slope of Spotted Ridge, which is 2 mi east and 200 ft from Wade Butte, in section 20, T18S, R25E, Crook County, Oregon (Arnold 1953).

Stratigraphic position and age. Spotted Ridge Formation, Pennsylvanian Period (Merriam and Berthiaume 1943; Orr and Orr 2011).

Description

Morphology of the frond. *Senftenbergia oregonensis* is represented by pinnate fronds (figs. 1*A*–1*D*, 3*A*, 3*B*, 3*F*) with five orders of alternate catadromous branching (fig. 1*D*), including lobed pinnules (figs. 1*A*–1*D*, 3*B*, 3*F*). Some fronds appear to be entirely fertile (figs. 1*A*, 1*B*, 3*B*). Others appear to be entirely vegetative (figs. 1*C*, 1*D*, 3*F*), while some show both vegetative and fertile pinnules. Measurements of individual frond axes (fig. 2) reveal that the widths of rachides/pinna fall into four distinct categories: (1) 5–10 mm ($n = 27$), (2) 2–4 mm ($n = 50$), (3) 0.6–1.0 mm ($n = 50$), and (4) 0.3–0.5 mm ($n = 50$). These measurements suggest that the frond of *S. oregonensis* displays five orders of dissection, including laminar pinnules. This hypothesis is confirmed by a specimen that shows all five orders in organic connection (fig. 1*D*). For the purposes of this description, these axes are termed rachis, primary pinnae, secondary pinnae, tertiary pinnae, and pinnules (fig. 1*D*).

Large frond segments reveal that branching of the rachis is alternate in a single plane (fig. 3*A*) and the branching pattern is repeated at successively more distal levels of the frond (figs. 1*A*–1*D*, 3*B*, 3*F*). The longest distance between the divergences of successive primary pinnae is 6 cm (fig. 3*A*), with successively narrower rachides branching at progressively shorter intervals. The surface of the rachis is clothed by numerous pointed trichomes (fig. 3*C*) that are up to 0.2 mm long. In surface views of the rachis, the trichomes appear as punctae consisting of coalified material (fig. 3*C*). Other rachides have a striated appearance (fig. 1*D*) that apparently results from the decortication and exposure of cortical sclerenchyma fibers.

Dichotomously branched aphlebiae occur at the levels of primary pinna divergence (figs. 1*D*, 3*A*, 3*E*). A single aphlebia is typically represented in surface views of fronds (figs. 1*D*, 3*A*). Aphlebia have a consistent position immediately distal to the point of primary pinna divergence (figs. 1*D*, 3*A*) and are oriented with the base of the aphlebia toward the point of divergence, but none of the available specimens show actual attachment (fig. 3*E*). This suggests that the aphlebia were attached lateral to the plane of primary pinna divergence (one to each side), as they are attached in several other species of *Senftenbergia* (Kidston 1924), such that only one of a pair is seen on each split surface.

Primary pinnae are up to 4 mm wide at the base and are clothed by pointed trichomes (fig. 3*C*) unless decorticated. Decorticated specimens show a striated surface similar to that of decorticated rachides (figs. 1*D*, 2, 3*A*). Divergence of secondary pinnae is somewhat irregular, but it occurs at an average distance of about 2.5 cm near the base of the frond and at shorter distances toward the apex of the frond (e.g., 1.4 mm in fig. 1*B*).

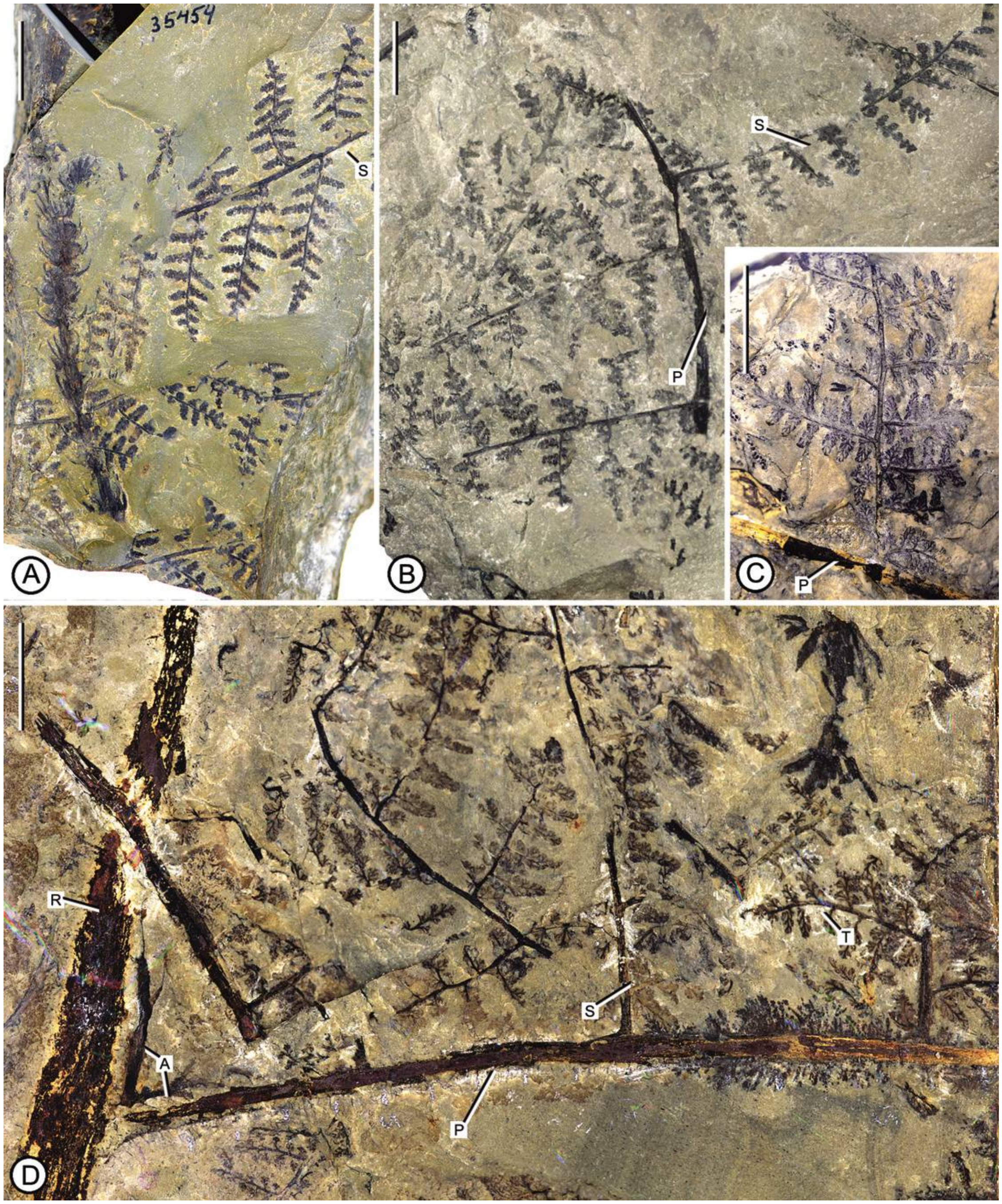

Fig. 1 *Senftenbergia oregonensis* comb. nov. *A*, Frond specimens on rock surface, with fertile calamitean shoot at left. From specimen NMNH 35454-2 X 1.2. Scale bar = 1 cm. *B*, Fertile frond showing four orders of alternate catadromous branching. From specimen NMNH 539050 X 1.1. Scale bar = 1 cm. *C*, Segment of vegetative frond showing four orders of alternate catadromous branching and lobed pinules. From specimen NMNH 35454-3 X 1.6. Scale bar = 1 cm. *D*, Vegetative frond showing all five orders of dissection, including pinnules, as well as an aphlebia (A) that is attached at the level of primary pinna (P) divergence from the rachis (R; S = secondary pinna, T = tertiary pinna). From specimen NMNH 539053 X 2.0. Scale bar = 1 cm.

Secondary pinnae are 0.6–1.0 mm wide and bear tertiary pinnae with pinnules (figs. 1*A*, 1*B*, 3*B*). Two secondary pinnae are complete enough to measure, and these range 6.3–6.5 (mean, 6.4) cm in length and 2.5–2.7 (mean, 2.6) cm in width. The mean length : width ratio for secondary pinnae with attached tertiary pinnae and pinnules is 2.5 : 1.

Tertiary pinnae (pinna rachis) diverge alternately at intervals of up to 4.5 mm near the base of secondary pinnae, with the catadromous basal tertiary pinna being attached immediately distal to the divergence of the secondary pinna to which it is attached (fig. 3*B*, near top). Tertiary pinnae with attached pinnules are widest near the base and range from 6 to

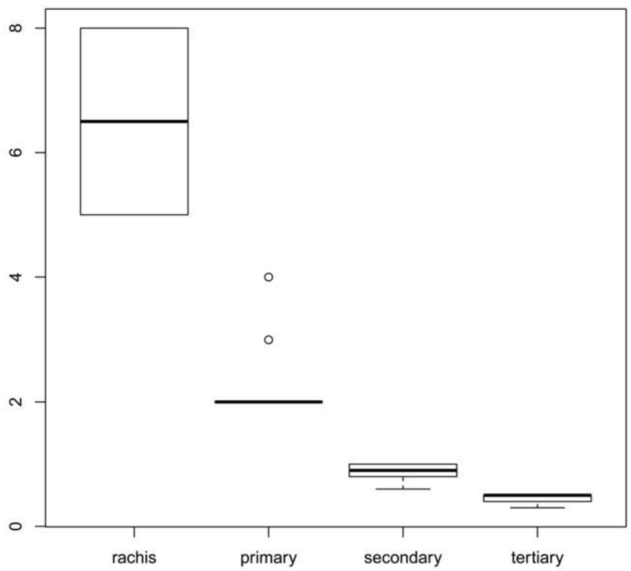

Fig. 2 Box plot showing size distribution for the widths of rachis and three orders of pinnae. Medians are indicated by the bold black lines. The tops and bottoms of the boxes are the seventy-fifth and twenty-fifth quartiles, respectively. Whiskers are defined as 1.5 times the interquartile range. Circles indicate outliers.

25 mm in length (mean, 16 mm; $N = 25$) and 2 to 11 mm in width (mean, 6.3; $N = 25$). The mean length : width ratio for tertiary pinnae with attached pinnules is 2.5 : 1.

Vegetative pinnules. Pinnules are attached alternately to the tertiary pinna, with the catadromous basal pinnule diverging immediately distal to the divergence of the tertiary pinna from the secondary pinna (fig. 3*F*, at arrow). Individual pinnules are 1.5–6 mm long (mean, 3.8 mm; $N = 39$) and 1.0–2.0 mm wide (mean, 1.7 mm; $N = 39$). The mean length : width ratio for pinnules is 2.2 : 1. The largest pinnules display a sinuous margin, with successively smaller and more distal pinnules having progressively smoother margins (fig. 3*F*). The basalmost pinnules are narrowly attached, but more distal pinnules become broadly attached and are somewhat decurrent, with the distalmost pinnules becoming pinnatified. Each pinnule has a weakly developed midvein from which laterals diverge (fig. 3*F*). Laterals dichotomize up to two times, but many are unbranched (fig. 3*F*).

Anatomy. Several frond segments are permineralized with iron oxides (fig. 3*D*), and these reveal the xylem configuration of the rachis on the surface of etched wafers (fig. 3*G*, 3*H*). In cross sections, rachides are roughly oval and the rachis trace is anchor shaped, measuring ~4.5 mm wide and 3.0 mm high as viewed with the abaxial surface oriented downward (fig. 3*G*). The xylem forms a robust cross bar (termed "apolar" in Bertrand 1909) that is up to 1.2 mm thick and 2.5 mm long between pairs of adaxial and abaxial antennae (fig. 3*G*). Adaxial antennae are up to 1.5 mm long. When undistorted they are oriented slightly outward. Abaxial antennae are oriented slightly inward and are up to 1.0 mm long. As is characteristic of Tedeleacean rachides, distinct bands of smaller tracheids occur at the outer margins of the antennae (fig. 3*G*, 3*H*). These latter tracheids traditionally have been interpreted as representing positions of the protoxylem. Metaxylem tracheids are angular in cross section, measuring 72–165 μm in diameter. The putative protoxylem tracheids are noticeably smaller, ranging from 24 to 48 μm in diameter.

Fertile pinnules and sporangia. A large percentage of the dispersed frond segments display fertile pinnules, and on most of these specimens all of the attached pinnules are fertile (figs. 1*A*, 1*B*, 3*B*). The lamina of fertile pinnules is somewhat obscured by the numerous sporangia borne on each (figs. 3*B*, 4*A*, 4*B*), but careful examination of many fertile pinnules reveals that they conform closely in size, shape, features of the margin, and venation to the vegetative pinnules (fig. 4*B*). Elongated sporangia are solitary and closely spaced in two rows, with the sporangia oriented roughly at right angles to the pinnule margin and midvein (fig. 4*B*, 4*C*). Some sporangia appear to be clustered (fig. 4*C*), but closer examination reveals that this appearance probably results from oblique orientation of compressed sporangia and apparently taphonomic redirection of a few sporangia. Sporangial position is uniform among the specimens, with the stalk located adjacent to the pinnule margin and the apex directed toward the midvein (fig. 4*C*, 4*E*).

Numerous specimens reveal that the sporangia are attached to the margin of the pinnule (fig. 4*A*–4*C*, 4*E*). The strictly marginal attachment is not always immediately apparent (fig. 4*D*), because of the manner in which the sporangia are folded under the abaxial surface of the pinnule (fig. 4*A*–4*C*). In a few specimens the rock surface is split at the fertile pinnule margin (at arrowheads in fig. 4*D*; at bottom in fig. 4*E*). Such specimens reveal that both the pinnule lamina and the sporangial stalks are bent to recurve the body of each sporangium parallel to the pinnule lamina and that there is more bending of the thin pinnule lamina than of the sporangial stalks. Such bending over of the margin of the pinnule lamina often makes attachment of the sporangia appear to be submarginal on the abaxial surface. However, the fortuitously split (fig. 4*E*), somewhat weathered (fig. 4*D*, arrowheads) specimens clearly show the folded-under margin to which the sporangia are attached.

Individual sporangia are elongated, with a rounded apex and short stalk (fig. 4*E*–4*G*). Sporangia range from 0.38 to 0.88 mm in length (mean, 0.59 mm; $n = 39$) and from 0.13 to 0.40 mm in width (mean, 0.28 mm; $n = 39$). As is characteristic of other species of *Senftenbergia*, sporangia of *S. oregonensis* also show some variation in overall shape. All have a short stalk that is ~0.1 mm wide and increases in diameter distally (fig. 4*C*, 4*E*, 4*G*). Some are widest in the midregion (fig. 4*E*, second sporangium from right), whereas others continue to increase in diameter until they form the rounded apex (fig. 4*F*). All dehisce via a distinct longitudinal stomium (at arrowheads in fig. 4*C*; fig. 4*D*, 4*E*). In many sporangia the stomium is oriented away from the abaxial surface of the pinnule (fig. 4*C*–4*E*), but in some it is not.

The apical region of each sporangium is notably darker (fig. 4*G*), with a thicker layer of coalified sporangial wall than exists in other areas of the sporangium (fig. 4*F*, arrowhead). This marks the position of the apical annulus. In some sporangia the annulus conforms to the overall shape of the sporangium (fig. 4*D*, 4*F*, 4*G*) but in others it forms a somewhat bulbous apical region (fig. 4*E*, second sporangium from right), as it

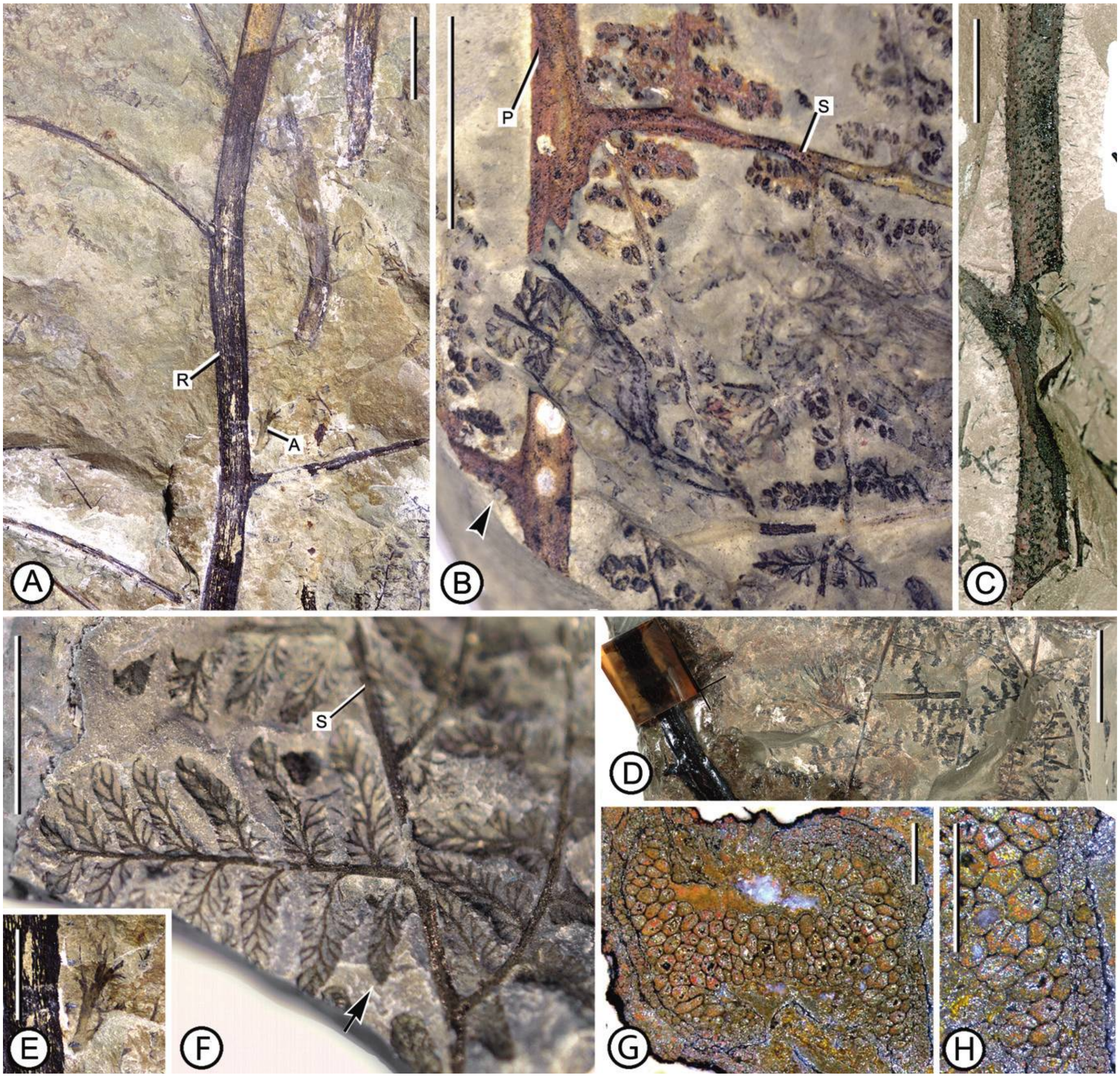

Fig. 3 *Senftenbergia oregonensis* comb. nov. *A*, Rachis (R) showing opposite divergence of primary pinnae and longitudinal striations. Note aphlebia (A). From specimen NMNH 539053 X 0.67. Scale bar = 2 cm. *B*, Specimen showing all four orders of alternate branching in distal part of frond, terminating with lobed fertile pinnules. Note catadromous divergence of secondary pinna from primary pinna (P), near top. Also note spines at divergence of second-order pinna (S and arrowhead) and fragments of vegetative frond showing dichotomous venation of pinnules. From specimen NMNH 35454-3 X 3.5. Scale bar = 1 cm. *C*, Rachis with diverging primary pinna showing coarse trichomes at margin and punctations of coalified material that mark positions of trichomes on surfaces. From specimen NMNH 40719 X 1.7. Scale bar = 1 cm. *D*, Various frond parts including permineralized rachis, part of which is embedded in bioplastic, from which wafers have been made. From specimen NMNH 8702-2 X 3. Scale bar = 0.5 cm. *E*, Aphlebia enlarged from fig. 1*A*. From specimen NMNH 539053 X 1.5. Scale bar = 1 mm. *F*, Primary pinna with alternately arranged secondary pinnae and vegetative pinnules. Pinnules show range of variation in size and shape, with smaller pinnules having entire margins and larger pinnules having lobed margins. Note the open dichotomous venation and the catadromous divergence of both the pinnule (arrow) and the veins. From specimen NMNH 539051 X 2.8. Scale bar = 1 cm. *G*, Cross section of rachis showing anchor-shaped xylem. Note the slightly longer antennae toward the adaxial side (bottom) and smaller tracheids of protoxylem (sides). From specimen NMNH 8702-2 X 10. Scale bar = 1 mm. *H*, Enlargement of tracheids from fig. 1*A* showing features of protoxylem (right) and metaxylem tracheids. From specimen NMNH 8702-2 X 20. Scale bar = 0.25 mm.

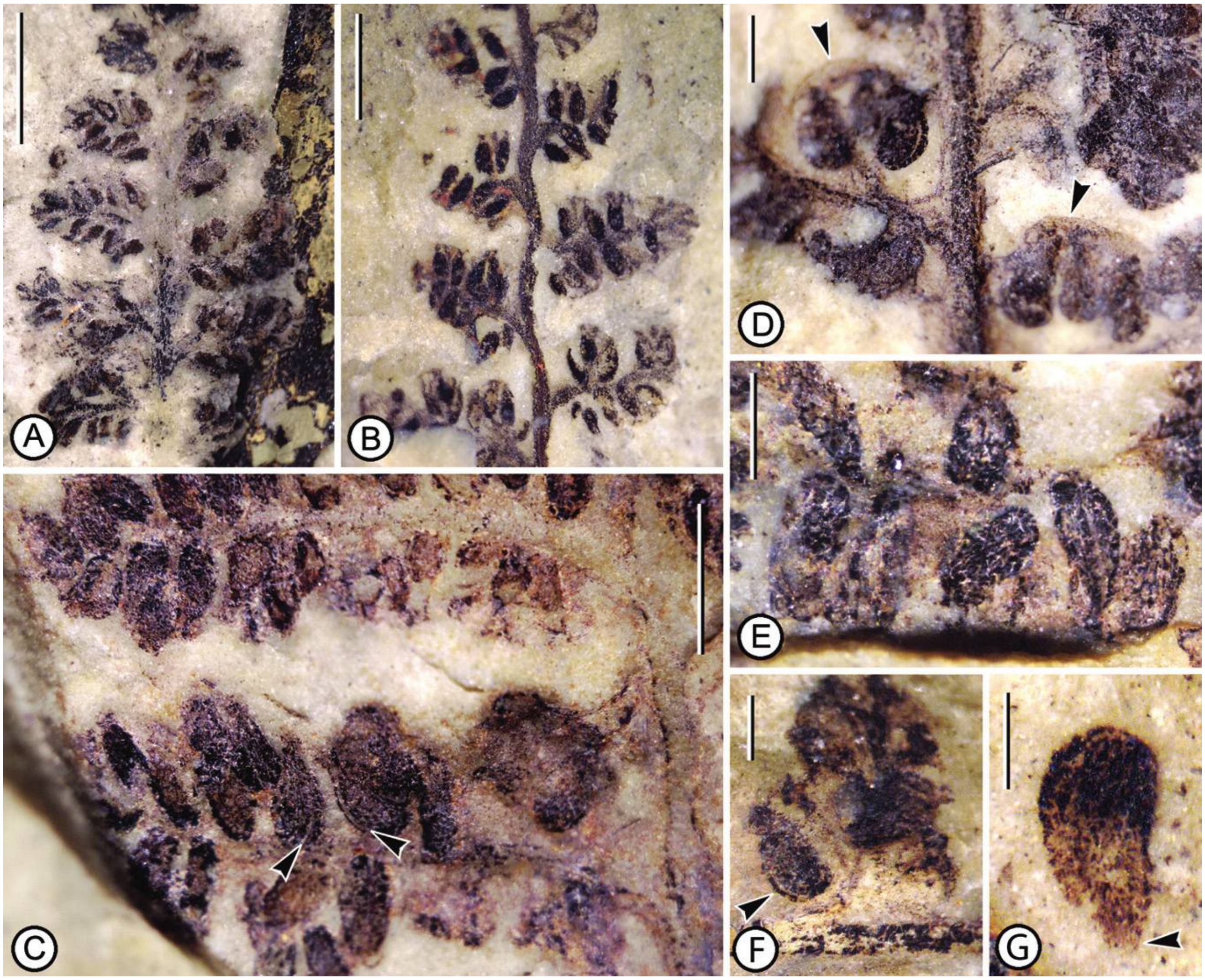

Fig. 4 *Senftenbergia oregonensis* comb. nov. *A*, Abaxial surface of tertiary pinna with attached fertile pinnules. Note two rows of attached sporangia that are folded under toward center of pinnule. From specimen NMNH 539046 X 10. Scale bar = 2 cm. *B*, Adaxial surface of tertiary pinna and fertile pinnules showing marginal attachment of stalked sporangia. From specimen NMNH 539048 X 8. Scale bar = 2 cm. *C*, Closer view of adaxial surface of fertile pinnules showing longitudinal dehiscence (arrowheads) of attached sporangia. NMNH 8702-2 X 23. Scale bar = 1 mm. *D*, Fertile pinnule showing attachment of sporangia to margins that are folded under (arrowheads) to give the superficial appearance that the stalked sporangia are submarginal. From specimen NMNH 539043 X 20. Scale bar = 0.5 mm. *E*, Abaxial view of fertile pinnule showing attached stalked sporangia folded under to parallel surface of pinnule. Note bulbous apical annulus of some sporangia. From specimen NMNH 8702-2 X 32. Scale bar = 0.5 mm. *F*, Attached sporangium showing thicker coal-filled annulus cells (arrowhead) in apical region. From specimen NMNH 8702-2 X 20. Scale bar = 0.5 mm. *G*, Dispersed sporangium showing basal stalk (arrowhead) and darker, more heavily coalified apical region that shows position of annulus. From specimen NMNH 539046 X 60. Scale bar = 0.25 mm.

does in some sporangia of other *Senftenbergia* species (figs. 5–7 of Bek and Pšenička 2001). The cellular structure of the annulus is not fully preserved, with cells of the annulus represented by a darker apical zone of the sporangial wall and indistinct striations (fig. 4*E*, 4*G*). However, from the large area of sporangial wall covered by the annulus, the indistinct cellular patterns of the annulus, and comparisons to the sporangia of other *Senftenbergia* species, we infer that the annulus is multiseriate. As was also the case in previous studies of material from the Spotted Ridge locality, no spores have been recovered from macerations of *S. oregonensis* sporangia.

Discussion

Although *Senftenbergia oregonensis* was originally assigned to the morphogenus *Pecopteris*, which is a genus of fronds that is most often associated with marattialean ferns, affinities of the species have remained ambiguous because pecopterid pinnules are known to be produced by other fern clades as well (Taylor et al. 2009). Moreover, filicalean affinities have been suspected for *Pecopteris oregonensis* since the original description of the species was made (Arnold 1953). The annulate sporangia of *S. oregonensis* reveal that the species can indeed be assigned to the Filicales (Eames 1936; Bierhorst

1971). Among Paleozoic filicaleans, elongated sporangia with a short stalk, a multiseriate terminal annulus, and longitudinal dehiscence conform to the family Tedeleaceae (Eggert and Taylor 1966). An anchor-shaped xylem bundle in the rachis and the dichotomizing aphlebia that occur at the divergence of the primary pinnae are additional diagnostic characters of species that can be assigned to the Tedeleaceae (Jennings and Eggert 1977; Mickle 1980; Bek and Pšenička 2001), thus confirming the familial affinities of *S. oregonensis*.

Frond Complexity and Size

The frond of *S. oregonensis* shows five orders of dissection (figs. 1*D*, 2), and therefore it is more complex than all other Tedeleacean fronds that have been described to date (table 1). This suggests that *S. oregonensis* fronds were relatively large, but the fragmentary nature of available specimens precludes direct measurements. Nevertheless, we have been able to estimate frond shape and a minimum overall frond size for *S. oregonensis* by applying characteristics common to other Tedeleacean species to our measurements of the frond fragments. Although there is some variation among and within species, for segments of Tedeleacean fronds, (1) they tend to maintain a common overall shape and length : width ratio from order to order of pinnae (except pinnules) and (2) the maximum width of each order of dissection tends to approach the distance between successive attachment levels on the same side of the next-larger frond order (Kidston 1924; Radforth 1938, 1939; Barthel 1976; Pšenička and Bek 2003; fig. 1*A*–1*D*). The secondary and tertiary pinnae of *S. oregonensis* each have a length : width ratio of 2.5 : 1. The widest-available primary pinna of *S. oregonensis* measures 13 cm (fig. 1*B*), which approaches the longest distance between the divergence of successive primary pinnae on the same side of available rachides of *S. oregonensis* (i.e., 12 cm in the specimen in fig. 1*A*). Therefore, that pinna specimen can be estimated to ~32 cm in length (i.e., 2.5×13 cm = 32 cm). Doubling that length provides an estimate of frond width at the base of the stipe (i.e., combined length of the primary pinnae on each side of the rachis; 26 cm), and multiplying that width by 2.5 (i.e., length : width ratio of secondary and tertiary pinnae) gives a minimum estimate of overall frond length as 78 cm without a stipe. As a result, fronds of *S. oregonensis* easily could have approached 1 m in length. This is larger than the fronds of most other Tedeleacean species and is consistent with the greater complexity of *S. oregonensis* fronds (i.e., five orders of rachis/pinnae/pinnules, as compared with only three or four orders in other species; table 1).

Generic Delimitation of Tedeleacean Species

Species of the Tedeleaceae are identified by shared characters of frond morphology and anatomy, sporangial structure, and spores (table 1), but a clear understanding of relationships among Tedeleacean taxa has been obscured by the historical development of concepts for genera that are currently assigned to the family. Whereas species of *Senftenbergia* have traditionally been recognized from compression specimens that reveal morphological characters of the vegetative and fertile fronds (Radforth 1938, 1939), *Ankyropteris* was originally characterized by the anchor-shaped xylem anatomy of permineralized frond fragments (Stenzel 1889). Over the succeeding decades, several new *Senftenbergia* species were described and knowledge of *Ankyropteris* frond and stem anatomy grew considerably (Phillips 1974; Bek and Pšenička 2001), but a close systematic relationship between the two genera was not recognized. That relationship was first established by the description of *Tedelea glabra* Eggert and Taylor, a plant with *Senftenbergia*-type sporangia and spores borne on permineralized fronds with *Senftenbergia*-type morphology and *Ankyropteris*-type anatomy (Eggert and Taylor 1966). Somewhat later, an *Ankyropteris*-like xylem bundle was discovered within the rachis of a partially permineralized species of *Senftenbergia* (Jennings and Eggert 1977), thus confirming close relationships among the three genera. The subsequent reconstruction of the *Ankyropteris brongniartii* (Renault) Stenzel plant from permineralized specimens further documented those relationships but also revealed that *A. brongniartii* and *T. glabra* are conspecific (Mickle 1980).

A survey of Tedeleacean species reveals that sporangial position (i.e., either abaxial or marginal) and sporangial grouping (i.e., either solitary or clustered) are consistently correlated characters within the family (table 1). Whereas species of *Anchoropteris* and *Tedelea* have surficial sporangia that occur in clusters on the abaxial surface of fertile pinnules (Eggert and Taylor 1966; Mickle 1980), the sporangia of most *Senftenbergia* species, including the type species *Senftenbergia elegans* (Corda 1845; Zeiller 1883), produce marginal sporangia that are solitary and are recurved under the abaxial surface of the pinnule to form two rows (table 1). However, one species and two varieties of *Senftenbergia* species display grouped abaxial sporangia (table 1). If these contrasting character combinations are valid criteria for delimiting genera and recognizing clades within the family Tedeleaceae, then *A. brongniartii* sensu Mickle (1980), *T. glabra* Eggert and Taylor, *Senftenbergia saxonica* Barthel, *Senftenbergia plumosa* var. *jonesii* Andrews, and *S. plumosa* var. *ligerensis* Grauvogel-Stamm (viz., all characterized by abaxial and grouped sporangia) represent one clade, while the remaining species of *Senftenbergia* (including *S. oregonensis*; viz., all characterized by marginal, solitary sporangia) represent a second clade.

Without a comprehensive comparative reexamination of all previously described species of *Senftenbergia*, *Ankyropteris*, and *Tedelea*, it is beyond the scope of this investigation to address nomenclatural questions or propose formal synonymies within the Tedeleaceae. However, regardless of outstanding nomenclatural issues, it is apparent that various species of the Tedeleaceae inhabited the equatorial paleotropics from the Mississippian through the basal Permian. A "*Senftenbergia* clade" appears to have evolved first, during the Mississippian of both Europe and North America (Jennings and Eggert 1977; Bek and Pšenička 2001), with the *Ankyropteris* clade appearing somewhat later. The two clades coexisted across the paleotropics throughout the Pennsylvanian and basal Permian (Rossler 2000; Phillips and Galtier 2005). In this regard, it has become apparent that the Tedeleaceae was a consistent contributor to the diversity of the late Paleozoic tropical wetland vegetation and that the family played an important role in the initial phylogenetic radiation of filicalean ferns.

Table 1

Comparative Characters among Species of Tedeleaceae

Species	Sporangial position	Sporangia solitary	Sporangia clustered	Apical annulus	Sporangial length, cm	Sporangial width, cm	Rachis trace	Spores	Reference
Senftenbergia oregonensis	Marginal	+		Multiseriate	.38–.88	.13–.40	Anchor shaped[a] (thick apolar, intermediate antennae)	?	This study
Senftenbergia elegans	Marginal	+		Multiseriate			?		Corda 1845
S. elegans	Marginal	+		Multiseriate	.85–.95	.6–.7	?		Zeiller 1883
Senftenbergia pennaeformis	Marginal	+		Multiseriate	1 mm	.6–.7	?		Bertrand 1912
S. pennaeformis	Marginal	+		Multiseriate	.9	.5	?	*Raistrickia* type	Radforth 1939
Senftenbergia ophiodermatica	Marginal	+		Multiseriate	.5	.3	?		Kidston 1924
S. ophiodermatica	Marginal	+		Multiseriate	.4	.2	?	[b]	Radforth 1938
S. ophiodermatica	Marginal	+		Multiseriate	.7–.9		?	*Raistrickia*	Remy and Remy 1955
Senftenbergia plumosa	Marginal	+		Multiseriate	.5–.75		?	*Raistrickia*	Kidston 1924; Remy and Remy 1955
S. plumosa	Marginal	+		Multiseriate	.5–.6	.2–.3	?	*Raistrickia*	Radforth 1938
S. plumosa var. *jonesii*	Surficial		+[c,d,e]	Multiseriate	.52	.26	?	*Raistrickia*	Andrews 1943
S. plumosa	Marginal	+		Multiseriate	.7–.9		?	*Raistrickia*	Remy and Remy 1955
S. plumosa	Marginal	+		Multiseriate	.3–.5		?	*Raistrickia*	Laveine 1969
S. plumosa var. *ligerensis*	Surficial		+	Multiseriate	.7–.8	.4	?	*Raistrickia*	Grauvogel-Stamm and Doubinger 1975
Senftenbergia sturii	Marginal	+		Multiseriate	.5		?		Kidston 1924
S. sturii	Marginal	+		Multiseriate	.6	.3	?	*Raistrickia*	Radforth 1939
Senftenbergia sp.	?	?	?	?	?	?	Anchor shaped (thick apolar, extremely short antennae)	*Convolutispora*	Jennings and Eggert 1977
Senftenbergia saxonica			+	Multiseriate	.5–.7	.5	?	*Raistrickia*	Barthel 1976; M. Barthel, personal communication, 2011
Tedelea glabra	Surficial		+[c]	Multiseriate	.35	.2	Anchor shaped (thin apolar, long and thin antennae)	*Raistrickia*	Eggert and Taylor 1966
Ankyropteris brongniartii	Surficial		+[c]	Multiseriate	.3–.6	.2–.3	Anchor shaped (thin apolar, long and thin antennae)	*Raistrickia*	Mickle 1980

[a] Thickness and length of antennae are distinctive for species and are intermediate between those of *Senftenbergia* sp. and those of *T. glabra* and *A. brongniartii* (which are virtually identical).

[b] Spores globose and trilete, with smooth, thin wall.

[c] Rare solitary sporangia are reported.

[d] Andrews (1943) describes sporangia as marginal and densely covering the pinnules. However, his figs. 1–3 show what appear to be dense clusters of surficial sporangia near the margin of the pinnules, an interpretation also supported by Eggert and Taylor (1966).

[e] Close spacing of sporangial clusters gives pinnules an acrosticoid appearance.

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