

ANEMIA QUATSINOENSIS SP. NOV. (SCHIZAEACEAE), A PERMINERALIZED FERN FROM THE LOWER CRETACEOUS OF VANCOUVER ISLAND

Genaro R. Hernandez-Castillo,* Ruth A. Stockey,^{1,*} and Gar W. Rothwell†

*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and

†Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, U.S.A.

Anatomically preserved schizaeaceous vegetative and fertile organs have been identified from the Apple Bay locality (Lower Cretaceous) of Vancouver Island, British Columbia. Specimens are permineralized in calcareous nodules that contain numerous plants and marine invertebrates. Fertile pinnules are pinnately lobed, with abaxial sporangia and abaxially reflexed laminae. The pyriform sporangia have an apical annulus and occur in two rows on each pinnule lobe. Laminal tissue has wavy, thick-walled, adaxial epidermal cells. Spores are tetrahedral to globose with three sets of obliquely arranged parallel muri and correspond to the *spora dispersae* genus *Cicatricosisporites* Potonié et Gelletich. This fertile material most closely resembles *Anemia* subgenus *Anemiorrhiza* (Schizaeaceae) and is described as a new species, *Anemia quatsinoensis* Hernandez-Castillo, Stockey et Rothwell. Fertile pinnae are associated with an exarch, amphiphloic, solenostelic *Anemia*-like rhizome, with a C-shaped frond trace. Anatomies of the solenostele and frond trace, as well as frond divergence, compare most closely with species of *Anemia* subgenus *Anemiorrhiza* and may represent the vegetative shoot of *Anemia quatsinoensis*. This is the oldest and most complete permineralized fertile material of the genus *Anemia* in North America, and its presence at Apple Bay is consistent with the hypothesis that much of the diversification of Schizaeaceae had already occurred by the beginning of the Cretaceous.

Keywords: *Anemia*, *Cicatricosisporites*, Cretaceous, ferns, fossil, Schizaeaceae.

Introduction

The Apple Bay locality on the northern end of Vancouver Island (fig. 1) is yielding an exceptional flora of permineralized plants (Rothwell and Stockey 2003; Stockey 2004). Seed plants, particularly conifers (Sanders et al. 2004; Stockey and Wiebe 2005), are common at this site, but the locality is most remarkable because of its very large number of small permineralized pteridophytes, bryophytes, and fungi (Smith et al. 2004; Stockey 2004). These include three mosses, a liverwort, *Lycopodium* stems and roots, *Selaginella* stems and megaspores, small *Equisetum* shoots with leaf sheaths, and the oldest remains of polypore fungi (Rothwell and Stockey 2003; Stockey 2004). Such diversity of permineralized pteridophyte remains is unparalleled at other Cretaceous plant localities (Rothwell and Stockey 2003; Stockey 2004).

Ferns are among the most diverse remains at the site. Rhizomes, upright stems, roots, rachides, pinnae of all orders, vegetative pinnules, and fertile frond segments with a variety of solitary sporangia, indusiate sori, and exindusiate sori are common. Even the presence of sporelings or young sporophytes has been recorded (Stockey 2004). The most common of the fern reproductive structures from Apple Bay are the indusiate sori of *Cyathea cranhamii* Smith, Rothwell et Stockey (Cyatheaceae; Smith et al. 2003b). However, several addi-

tional types of indusiate tree fern sori of probable dicksoniacean affinities remain to be described (Smith et al. 2003a). Other families at Apple Bay for which sporangia have been discovered include Osmundaceae (Vavrek et al. 2006), Dipteridaceae (Stockey et al. 2006), Matoniaceae (R. A. Stockey, personal observation, 2005), Schizaeaceae, Dennstaedtiaceae (S. A. Little, personal communication, 2005), and possible Pteridaceae (Rothwell and Stockey 2006).

This article focuses on filicalean remains that conform to the family Schizaeaceae Kaulf. Here we describe *Anemia quatsinoensis* sp. nov., schizaeaceous fertile pinnules with sporangia and spores. We also describe an associated schizaeaceous rhizome with a diverging stipe trace. These newly developed data reveal that *Anemia* subgenus *Anemiorrhiza* Smith was present in western North America by the Lower Cretaceous.

Material and Methods

Fossil specimens were recovered from the Apple Bay locality (fig. 1) on the north shore of Holberg Inlet, Quatsino Sound, on northern Vancouver Island, British Columbia. Abundant permineralized fossil plant remains occur within small, round to ellipsoidal, calcareous nodules embedded in a carbonate-cemented graywacke matrix. The sediments are equivalent to the Lower Cretaceous Longarm Formation (Jeletzky 1976; Haggart and Tipper 1994), corresponding to Jeletzky's Barremian variegated clastic unit (Jeletzky 1976; Sweet 2000). Recent isotope analysis of a measured section

¹ Author for correspondence; e-mail ruth.stockey@ualberta.ca.

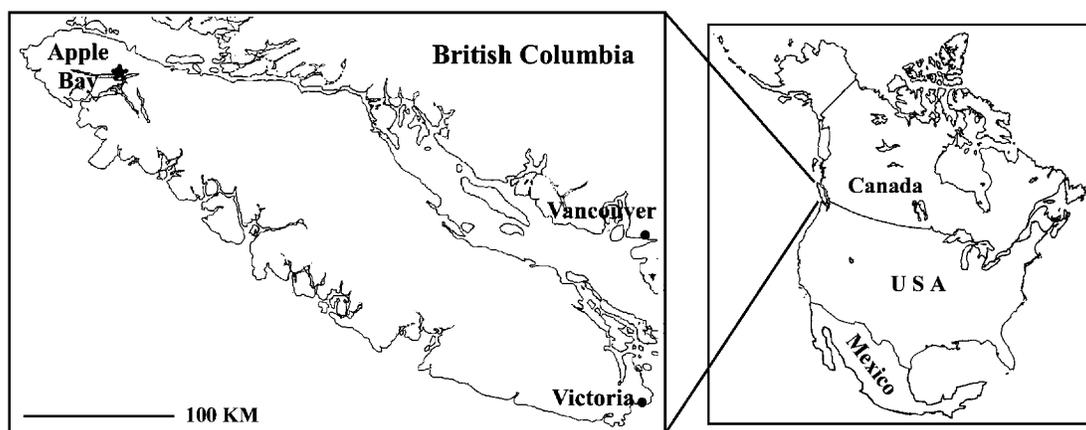


Fig. 1 Map of Vancouver Island showing the Apple Bay locality.

at the locality narrows the deposits to the Valanginian-Hauterivian boundary (D. R. Gröcke, McMaster University, personal communication, 2005).

Nodules were slabbed and studied using the cellulose acetate peel technique (Joy et al. 1956). Peels were mounted on microscope slides in Eukitt mounting medium (O. Kindler, Freiburg, Germany). Spores were extracted using a modified Daghljan and Taylor (1979) technique from deeply etched peels mounted on filter paper by dissolving the peels on a stainless steel Millipore filter (Millipore, Bedford, MA) with acetone under a vacuum. The filter paper with attached spores and the peels with embedded spores were mounted on specimen stubs with double-sided tape and coated with a 100-Å thickness of Au on a Nanotek sputter-coater. Specimens were examined on a JEOL 6301 FXV scanning electron microscope (Japan Electron Optics) at 5 kV.

Digital images were obtained with Microlumina (Leaf Systems, Bedford, MA) and PowerPhase (Phase One, Frederiksberg, Denmark) digital scanning cameras. All specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Systematic Description

Order—*Filicales*

Family—*Schizaeaceae* Kaulfuss

Genus—*Anemia* Swartz

Species—*Anemia quatsinoensis* Hernandez-Castillo, Stockey et Rothwell sp. nov. (Figs. 2, 3)

Specific diagnosis. Fertile pinnae with abaxially curved pinnules partly enclosing sporangia. Pinnules 2.0–3.2 mm long, 0.4–0.5 mm wide, each with midvein and branched lateral veins and laminar tissue. Up to eight sporangia in two rows, one on either side of midvein; sessile, pyriform, 286–320 μm long, 130–220 μm in diameter. Annulus uniseriate, apical. Spores 23–50 μm in disto-equatorial view, tetrahedral to globose to slightly ellipsoidal; subtriangular to subcircular amb; interradial sides slightly convex; apices rounded; laesur-

ae raised, two-thirds or more of spore radius; exine of uniform thickness. Sculpture cicatricose with three sets of obliquely arranged, parallel, almost straight muri of uniform width; muri of same set may anastomose; luminae wider than or equal to width of muri; mural sets separated by groove with similar width as luminae; perispore thin and smooth.

Holotype. P 13424 I bot, UAPC-ALTA (figs. 2B, 3).

Paratype. P 13158 C bot, UAPC-ALTA (fig. 2A, 2C–2E).

Locality. Apple Bay locality, Quatsino Sound, northern Vancouver Island, British Columbia (50°36'21"N, 127°39'25"W; UTM 9U WG 951068).

Etymology. The specific epithet refers to the Quatsino Sound collecting locality on the north end of Vancouver Island.

Description

Fertile Pinnae

Anemia quatsinoensis is represented by two segments of fertile pinnae 2.1–3.2 mm long (fig. 2A–2C). Up to six pinnules have been found attached to the pinna fragments (fig. 2A–2C). Pinnule lobes have a rounded tip and abaxially attached sporangia (fig. 2A–2C). Laminar tissues are most evident at the distal end of each pinnule, where the midvein is visible (fig. 2A, 2B, arrows). Laminae curve abaxially to partially cover the sporangia (fig. 2A–2C), and adaxial epidermal cells are rectangular and thick-walled, with wavy margins (fig. 2E). Pinnules show a central vascular bundle at the base that forks distally to vascularize each pinnule lobe (fig. 2D).

Sporangia are attached in two rows on each pinnule lobe, and they may range from one to four per row (fig. 2A–2C). Sporangia are sessile and pyriform, 286–320 μm long and 130–220 μm in diameter (fig. 3C). Cells of the sporangial wall are rectangular and thin-walled (fig. 3A, 3C). The annulus is uniseriate, apical, and composed of eight to 10 cells (fig. 3A–3C). Cells of the annulus are 63–70 μm long and 9–14 μm wide (fig. 3A, 3B).

Spores, preserved in several sporangia, are trilete, tetrahedral to globose, occasionally slightly ellipsoidal, with a

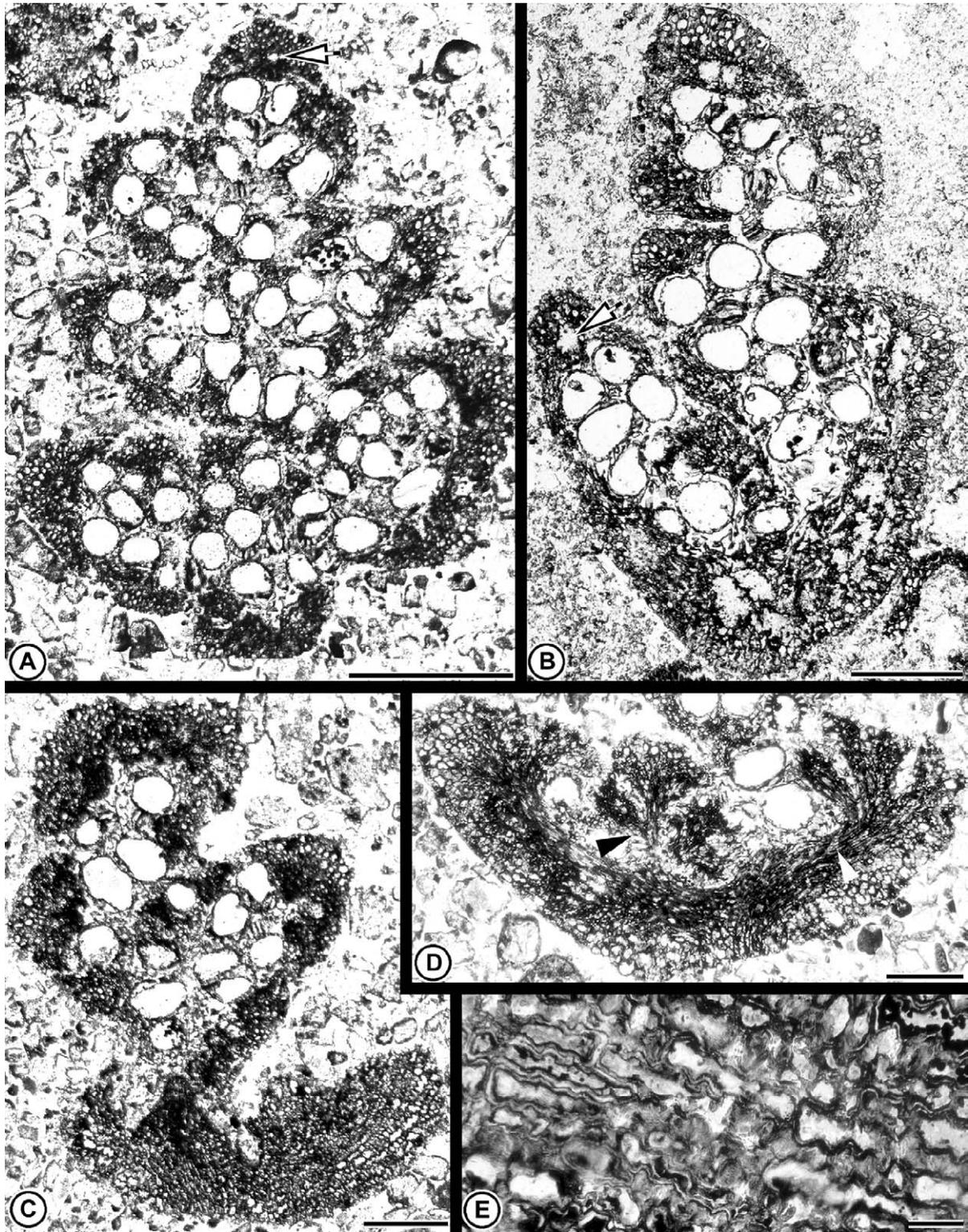


Fig. 2 *Anemia quatsinoensis* sp. nov. fertile pinnules. **A**, General view showing pinnule lobes, sporangia, and arrow indicating former position of phloem in midrib. P13158 C bot #35, scale bar = 1 mm. **B**, Pinnule showing slightly curved lobes with two rows of sporangia each and former position of phloem (arrow). Holotype P13424 I bot #3, scale bar = 500 μ m. **C**, Pinnule lobes abaxially curved showing lamina with epidermal cells. P13158 C bot #18, scale bar = 500 μ m. **D**, Pinnule base showing vascular bundles. Note main bundle (white arrowhead) and secondary bundles of pinnule lobes (black arrowhead). P13158 C bot #25, scale bar = 500 μ m. **E**, Pinnule lamina showing epidermal cells with wavy cell walls. P13158 C bot #2, scale bar = 50 μ m.

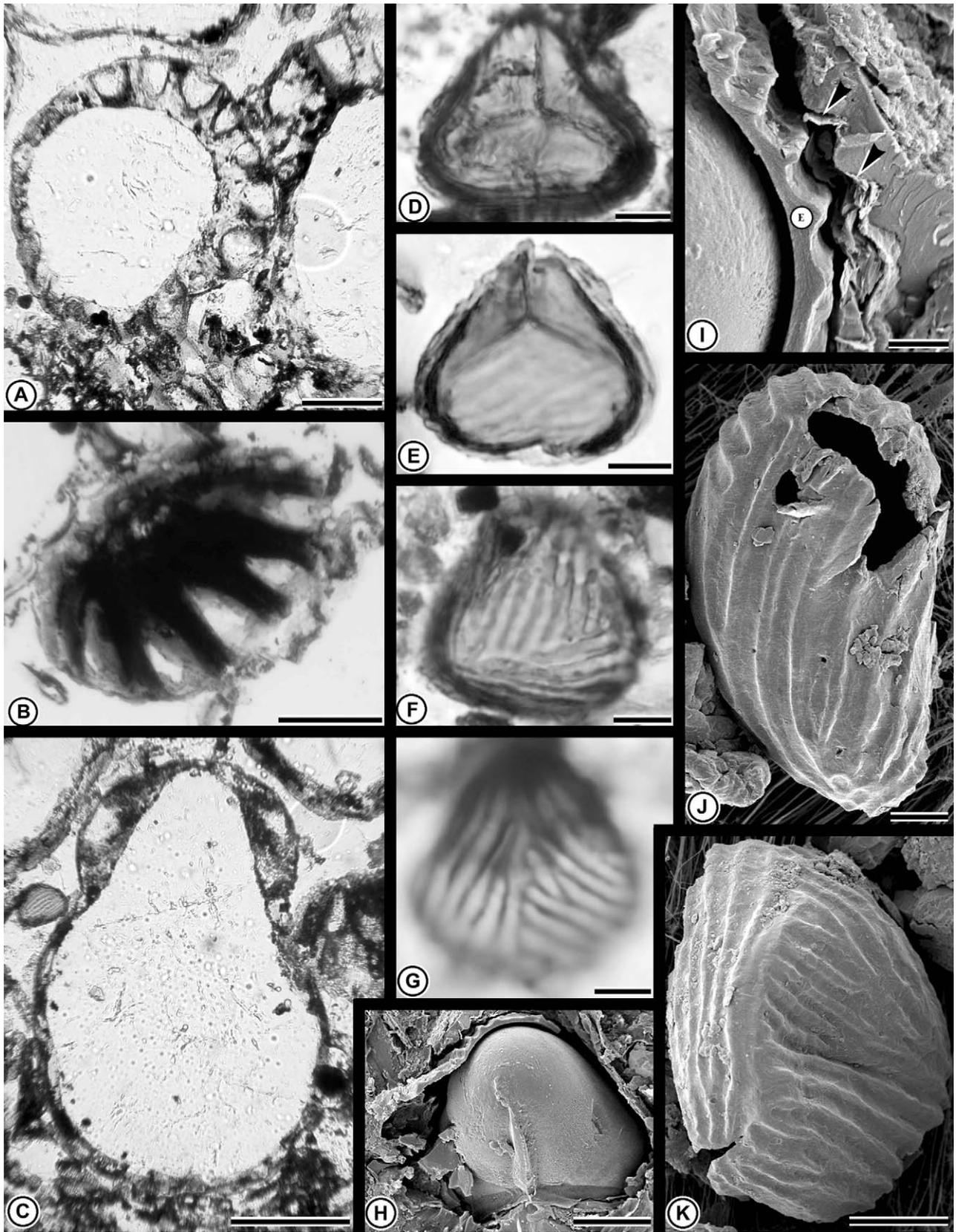


Fig. 3 *Anemia quatsinoensis* sp. nov. sporangia and spores. A, Sporangia in cross section. Holotype P13424 I bot #16, scale bar = 50 μ m. B, Top view of sporangium showing annulus. Holotype P13424 I bot #23, scale bar = 20 μ m. C, Longitudinal section of sporangium showing apical

subtriangular to subcircular amb, and are 23–50 μm in diameter in disto-equatorial view (fig. 3D–3K). Interradial sides are slightly convex, and spores are gently rounded beyond the ends of the laesurae (fig. 3D–3G). Laesurae are raised and cover two-thirds or more of the complete spore radius in proximal view (fig. 3D, 3E). The exine has a uniform thickness (0.3–0.4 μm) and is cicatricose (Dettmann and Clifford 1991), showing three sets of muri (fig. 3D–3K). Muri are parallel and uniform in width, separated by a lumina. Luminae are equal to or somewhat wider than muri and are obliquely arranged in each set (fig. 3E–3G, 3J, 3K). Muri of the same set may anastomose, and anastomosing muri are usually found on the disto-equatorial radial area and are separated by a groove (fig. 3G, 3K). The perispore is thin (0.2 μm) and smooth. These spores correspond to the *sporae dispersae* genus *Cicatricosporites* Potonié et Gelletich (1933).

Associated Rhizome

One small schizaeaceous rhizome, 4 mm long and 2–3 mm in diameter, is also preserved in the nodule matrix (fig. 4A–4D). The central pith region is degraded for the most part (fig. 4A, 4C, 4D), but cells are well preserved in more basal sections (fig. 4B). The pith has two zones, with sclerotic cells in the inner pith and thicker-walled sclerenchyma cells outside (fig. 4B). The rhizome is solenostelic (fig. 4A) and produces a single frond trace over the preserved length (fig. 4B, 4C [at arrows in both], 4E, 4G). The stele is amphiphloic with an inner and outer endodermis, pericycle, phloem, and a cylinder of primary xylem two to four cells thick (fig. 4E). Both inner and outer endodermis can be clearly seen at the level of trace divergence (fig. 4G). Due to incomplete preservation, the inner pericycle and phloem are often missing (fig. 4A–4E). However, some sections show remnants of the outer pericycle and phloem (fig. 4E, at *Pb-Pe*). Protoxylem is relatively inconspicuous, but the presence of smaller tracheids reveals that it is usually exarch with a few strands that are marginally mesarch (fig. 4E).

Inner and outer cortex are present in all sections, but the middle cortex is usually degraded (fig. 4A–4C). The inner cortex is composed of thick-walled sclerenchyma cells, while the middle and outer cortex contain slightly thinner-walled sclerenchyma cells (fig. 4A–4C).

Serial peels reveal the mode of frond trace divergence (fig. 4A–4C, 4F). In some sections, the frond trace is incompletely preserved, but the outer endodermis usually remains intact, and the outline of the trace can be seen even when preservation of the tracheids is incomplete (fig. 4B). In a series of successively more distal sections, the trace first separates from

one side of the solenostele (fig. 4B) and then becomes completely separated (fig. 4C). The inner endodermis is not continuous between the stele and the trace (fig. 4B [arrowhead], 4E). As the trace diverges, the sclerenchymatous pith expands radially to occupy the leaf gap and the adaxial side of the rachis trace (fig. 4B, 4C, 4F, 4G). Sclerenchyma cells of this tissue (fig. 4G) are similar to those of the inner cortex (fig. 4F).

The frond trace is C-shaped with incurved ends (fig. 4B, 4F). It typically has at least three protoxylem strands, although they are sometimes difficult to identify (fig. 4B, 4F). The middle protoxylem strand is on the abaxial side of the trace, i.e., it shows exarch maturation (fig. 4E, at arrowhead), while the other two protoxylem strands are located at the incurved ends; i.e., maturation is mesarch. Phloem remnants are preserved on the abaxial side of the rachis trace, which is surrounded by endodermis (fig. 4F).

Discussion

Anemia quatsinoensis has pinnately lobed pinnules with two rows of sporangia per lobe. Pinnule lobes curve abaxially to partially enclose the sporangia. Sporangia are similar to those described in living species of *Anemia*, such as *Anemia gardneri* Brade (Mickel 1962). They are sessile and pyriform with an apical and uniseriate annulus. Spores are trilete, tetrahedral to globose, with three sets of obliquely arranged, parallel muri and cicatricose sculpture and an exine of uniform thickness. This combination of characters is diagnostic for the family Schizaeaceae (Bolkhovitina 1961, 1962; Mickel 1962; Tryon and Tryon 1982; Kramer 1990; Dettmann and Clifford 1991).

Within this family, *Lygodium* Swartz has sporangial masses on modified spikelike segments, and each sporangium is covered by a laminar outgrowth (i.e., a flange or indusium; Eames 1936; Gandolfo et al. 2000). *Schizaea* Smith has rows of sporangia on fertile segments that are borne at the apex of pinnately or subdigitately divided pinnae that are simple or dichotomously branched (Tryon and Tryon 1982; Kramer 1990). Sporangial organization in *Lygodium* and *Schizaea* contrasts with that of *Mobria* Swartz and *Anemia* Swartz, which have once pinnate to tripinnate, often pinnatifid, modified fertile fronds with pinnules bearing two to four parallel rows of sporangia on each pinnule lobe (Tryon and Tryon 1982). These lobes are often enrolled and partially cover sporangial rows (Bower 1923, 1926; Mickel 1962; Tryon and Tryon 1982; Kramer 1990). Fertile pinnules of *A. quatsinoensis* resemble those of *Mobria* and *Anemia* in

annulus. Holotype P13424 I bot #19, scale bar = 20 μm . D, Proximal view of tetrahedral-globose spore with trilete mark and several muri (ridges) that give a blurry outline to spore. Note raised laesurae, rounded apices where several muri overlap. Holotype P13424 I bot #18, scale bar = 10 μm . E, Proximal view of spore showing trilete mark, raised laesurae, and obliquely arranged muri below laesurae. Note convex sides and rounded apices. Holotype P13424 I bot #3, scale bar = 10 μm . F, Disto-equatorial view of spore showing two sets of parallel muri running obliquely. Holotype P13424 I bot #23, scale bar = 10 μm . G, Disto-equatorial radial view of spore showing two sets of muri separated by groove that runs along polar axis. Holotype P13424 I bot #16, scale bar = 10 μm . H, SEM of proximal view of spore showing raised laesura on internal cast and exine with muri. Holotype P13424 I bot #14, scale bar = 10 μm . I, Close-up of H showing cross section of exine (E). Note distribution of muri and luminae, and detached perispore (arrowheads). Holotype P13424 I bot #14, scale bar = 1 μm . J, SEM of slightly ellipsoidal isolated spore with two sets of smooth muri. Holotype P13424 I bot #7–8, scale bar = 5 μm . K, SEM of isolated tetrahedral-globose spore showing two sets of muri separated by groove and smooth, anastomosing muri (upper right). Holotype P13424 I bot #7, scale bar = 10 μm .

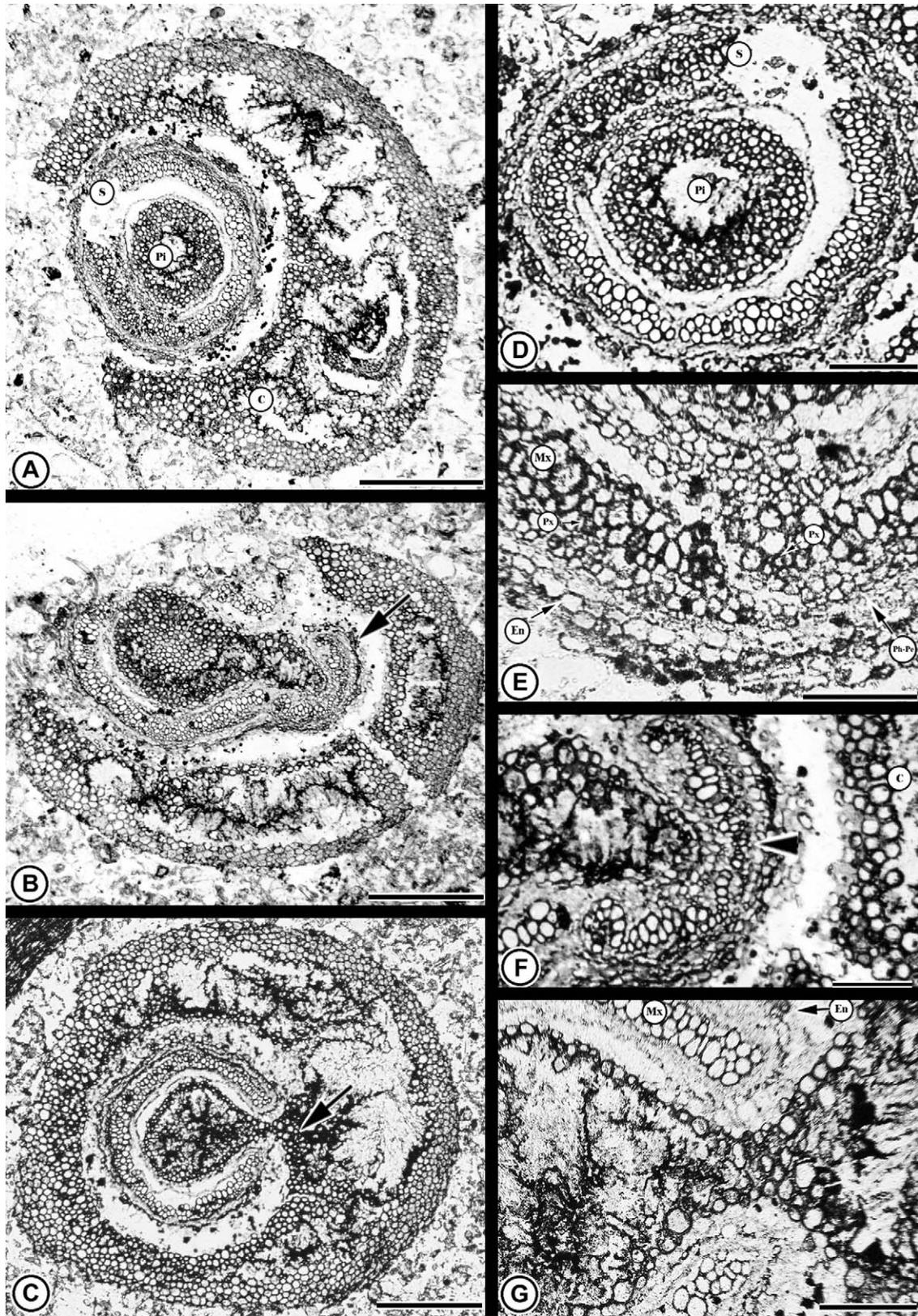


Fig. 4 *Anemia quatsinoensis* sp. nov. associated rhizome. **A**, Cross section showing central pith (*Pi*), solenostele (*S*), and cortex (*C*). P13051 F top #15, scale bar = 0.5 mm. **B**, Cross section showing frond trace divergence. Note pith, outer endodermis (at arrowhead), and frond trace. P13051 E top #4, scale bar = 0.5 mm. **C**, Cross section below frond trace showing open solenostele and frond gap sclerenchyma cells connecting

having two rows of sporangia that are partially covered by abaxially reflexed pinnule lobes.

Sporangia in *Mobria* are short-stalked to sessile, globose, with a subapical, uniseriate annulus, in contrast to the apical annulus of *A. quatsinoensis* (Bower 1926; Kramer 1990). In addition, *Mobria* sporangia are borne in small groups or are solitary near the vein ends (Bower 1926; Tryon and Tryon 1982; Kramer 1990) whereas they are arranged in two rows in *A. quatsinoensis*. The genus *Anemia*, on the other hand, is variable, with species that are more comparable to the fossils. The wavy, thick-walled, adaxial epidermal cells of the lamina in the fossil are similar to those described in living species (e.g., *A. gardneri* Brade) of *Anemia* (Mickel 1962). Like the fossils, sporangia of *Anemia* are sessile and pyriform, with a uniseriate, apical, or subapical annulus, and sporangia in rows on pinnule lobes (Mickel 1962; Tryon and Tryon 1982; Kramer 1990; Skog 1992). *In situ* spores of *A. quatsinoensis* are also most similar to spores in some species of *Anemia*. In both *A. quatsinoensis* and several living species of *Anemia*, the spores are trilete, tetrahedral to globose, with three sets of parallel muri (Bolkhovitina 1961, 1962; Dettmann and Clifford 1991; Tryon and Lugardon 1991). The *in situ* spores of *A. quatsinoensis* correspond to the *spora dispersae* genus *Cicatricosisporites* Potonié et Gelletich (Sweet 2000). Among living species, such spores are most similar to those of *Anemia mexicana* Klotzsch subgenus *Anemiorrhiza* (Dettmann and Clifford 1991, 1992).

The combination of (1) an apical, uniseriate annulus on (2) sessile, pyriform sporangia, (3) borne in two rows flanking the veins of (4) reduced pinnule lobes, (5) *Cicatricosisporites*-type spores, and (6) wavy, thick-walled, adaxial epidermal cells supports assignment of the Apple Bay fossil pinnules to the genus *Anemia*. However, because fossils of *A. quatsinoensis* are quite fragmentary, many characters that are needed in order to assign them to a living species with confidence remain unknown. The spores of *A. quatsinoensis* also have a smaller range of size (23–50 μm) than characterized in most living species (i.e., 40–200 μm ; Mickel 1981; Dettmann and Clifford 1991).

Fossil Record of the Schizaeaceae

The fossil record of the Schizaeaceae includes species that are based on vegetative and fertile remains that range from the Jurassic to the Miocene (Berry 1911; Andrews and Pearsall 1941; Brown 1943; Bolkhovitina 1961, 1962, 1971; van Konijnenburg-van Cittert 1981, 2002; Skog 1982, 1992, 1993, 2001; Manchester and Zavada 1987; Dettmann and Clifford 1992; Rozefelds et al. 1992; Skog and Dilcher 1994; Tidwell and Ash 1994; Collinson 1996, 2001; Deng and Wang 2000; Gandolfo et al. 2000). Some fossils have been

described from foliage with attached fertile pinnae, sporangia, and spores (Raciborski 1890; Seward 1894; Berry 1911; Thomas 1912; Chandler 1955; Boureau 1970; Harris 1977; Skog 1982, 1992, 1993, 2001). Others are isolated sporangia with *in situ* spores (Chandler 1955; Skog 1992), while the remainder are represented by isolated spores (Cookson 1957; Bolkhovitina 1961, 1962; Lukose 1964; Hughes and Moody-Stuart 1966; Wilson 1978; van Konijnenburg-van Cittert 1981; Dettmann 1989). Most fertile fossil remains are preserved as coalified compressions or impressions, but a few species have been described from permineralized or charcoalfied specimens (Stopes and Fujii 1910; Bohra and Sharma 1979; Sharma and Bohra 1980; Yoshida et al. 1996, 1997; Gandolfo et al. 2000; Trivett et al. 2006).

Anatomically preserved (i.e., permineralized or charcoalfied) schizaeaceous fertile remains are known from the Jurassic of India (*Schizaeangium jurassicum* Sharma and Bohra 1980), the Upper Cretaceous of Japan and eastern North America (*Schizaeopteris mesozoica* Stopes et Fujii 1910; *Paralygodium yezoense* Yoshida, H. Nishida et M. Nishida 1997; *Lygodium bierhorstiana* Gandolfo, Nixon, Crepet et Ratcliffe 2000), and the Upper Eocene of western Canada (*Paralygodium vancouverensis* Trivett, Stockey et Rothwell 2006). Among these, *S. jurassicum* and *S. mesozoica* have been compared to living *Anemia* based on the presence of apical annulus and spores with parallel or nearly parallel mural sets (Stopes and Fujii 1910; Sharma and Bohra 1980; Yoshida et al. 1996). *Paralygodium vancouverensis* has been related to *P. yezoense* Yoshida, Nishida et Nishida (1997) and *Anemia poolensis* Chandler (1955) based on the presence of lobed fertile pinnules that are tightly enrolled, forming globose structures that enclose the sporangia and trilete spores with little or no wall sculpturing (Trivett et al. 2006).

Among extinct species, *A. quatsinoensis* shows several similarities to *S. mesozoica*, which is represented by a fertile pinnule with deeply dissected segments, each of which is tightly enrolled toward the abaxial surface (Yoshida et al. 1996). In *Schizaeopteris*, each pinnule segment bears several irregularly arranged sporangia that each have a uniseriate apical annulus and *in situ* spores (Yoshida et al. 1996). In contrast, pinnules of *A. quatsinoensis* are abaxially reflexed but not tightly enrolled, and the sporangia are borne in two rows. Furthermore, *S. mesozoica* has a larger number of sporangia per pinnule segment or lobe (13) and spores of the *Ruffordia* type (i.e., *Ruffordiaspora* Dettmann et Clifford; Yoshida et al. 1996), while *A. quatsinoensis* has a smaller number of sporangia (eight) per lobe and spores that correspond to the *spora dispersae* genus *Cicatricosisporites* Potonié et Gelletich (Potonié and Gelletich 1933; Sweet 2000).

to remnants of the frond trace base (at arrow). P13051 E bot #10, scale bar = 0.5 mm. D, Cross section showing solenostele (S), pith (Pi), metaxylem, and exarch protoxylem. Note the lack of inner endodermis, pericycle, and phloem. P13051 F top #14, scale bar = 200 μm . E, Close-up of solenostele. Note outer endodermis (En), pericycle and phloem zone (Ph-Pe), exarch and mesarch protoxylem elements (Px), and metaxylem tracheids (Mx). P13051 F top #18, scale bar = 50 μm . F, Cross section showing diverging frond trace. Note parenchyma cells connecting frond gap (left), exarch protoxylem (at arrowhead), metaxylem, and incurved terminal bundle ends. P13051 E top #4, scale bar = 150 μm . G, Cross section of open solenostele showing cells of frond gap connecting to frond trace. Note endodermis (En) and metaxylem (Mx) delimiting solenostele. P13051 E bot #17, scale bar = 150 μm .

Associated Rhizome

The solenostelic rhizome associated with *A. quatsinoensis* is exarch and amphiphloic, has a zoned sclerotic pith and cortex, and has a C-shaped frond trace with incurved ends and three protoxylem strands. Whereas some solenostelic rhizomes from the fossil record are difficult to identify with genera and families of living ferns (e.g., Sharma and Bohra 1980; Little et al. 2006), others have features that indicate their affinities (e.g., Serbet and Rothwell 2003). General anatomy of the fern rhizome associated with *A. quatsinoensis* resembles that of living Schizaeaceae, particularly the genus *Anemia* (Prantl 1881; Boodle 1901, 1903; Gwynne-Vaughan 1903; Tansley 1907; Bower 1926; Mickel 1962; Ogura 1972; Kramer 1990). The vascular anatomy of schizaeaceous rhizomes ranges from protosteles in *Lygodium* Swartz to medullated protosteles in *Schizaea* Smith, and from solenosteles in some species of *Anemia* to dictyosteles in other species of *Anemia* and *Mobria* (Prantl 1881; Boodle 1901, 1903; Bower 1926; Mickel 1962; Ogura 1972).

In *Anemia*, most solenostelic species are included within the subgenus *Anemiorrhiza* (Boodle 1901, 1903; Mickel 1962, 1981; Ogura 1972). This compares favorably with the rhizome associated with *A. quatsinoensis*, which has a similar stele and frond traces. However, anatomy of most living species is not known in detail. *Anemia mexicana* is by far the most completely studied anatomically among solenostelic species of subgenus *Anemiorrhiza* (Boodle 1901; Mickel 1962). The rhizome of *A. mexicana* is characterized by an amphiphloic solenostele with a sclerotic pith and cortex that may have several zones (Boodle 1899, 1901, 1903; Bower 1926; Ogura 1972). The fossil rhizome associated with *A. quatsinoensis* is also characterized by an amphiphloic solenostele, sclerotic pith, and cortex with several zones. The fossil rhizome differs from *A. mexicana* in a minor way, by a slightly smaller size of the solenostele (i.e., 0.65 mm vs. 1 mm, respectively), metaxylem thickness (i.e., two to four tracheids vs. two to five tracheids, respectively), and pericycle thickness in the solenostele (i.e., one to two cells vs. two to four cells, respectively; Boodle 1901).

The shape of the frond trace in living *Anemia* species ranges from a flattened arch to V-shaped (Mickel 1962). At levels where the trace is diverging, the outer endodermis is continuous around stele and frond trace until the trace is completely separated from the stele (Boodle 1901; Ogura 1972). *Anemia phyllitides* (L.) Swartz frond trace divergence, shape, and position of protoxylem are most similar to that of the fossil rhizome associated with *A. quatsinoensis* (Boodle 1901; G. R. Hernandez-Castillo, personal observation). Although our knowledge of rhizome and frond trace anatomy is incomplete for many living species of *Anemia*, among those species where this information is known, the associated rhizome of *A. quatsinoensis* is most similar to species of the subgenus *Anemiorrhiza*.

Before the discovery of the schizaeaceous rhizome at Apple Bay, no anatomically preserved rhizomes had been assigned to the family on the basis of vascular architecture, frond trace divergence pattern, and histological features. Nevertheless, several other fossil rhizomes share the combination of an exarch solenostele, a C- to V-shaped frond trace, and pith

and cortex differentiated in zones. Such specimens range in age from Upper Jurassic to Upper Cretaceous of North America, India, and Japan and have been described as species of *Solenostelopteris* and *Loxomopteris* (Kershaw 1910; Ogura 1930; Vishnu-Mittre 1958; Sharma and Bohra 1976; Skog 1976; Nishida and Nishida 1982; Tidwell and Skog 1999; Banerji 2000). While the rhizome associated with *A. quatsinoensis* resembles those fossils in general features, it differs from all of them by having the combination of (1) inner and outer pith with sclerenchyma cells of two different thicknesses, (2) sclerotic cortex divided into three zones, and (3) scattered distribution of protoxylem elements on the periphery of the stele (Kershaw 1910; Ogura 1930; Vishnu-Mittre 1958; Skog 1976; Bohra and Sharma 1979; Nishida and Nishida 1982; Tidwell and Skog 1999; Banerji 2000; S. A. Little, personal communication, 2005). Previously described fossil species that compare most closely to the rhizome associated with *A. quatsinoensis* are *Solenostelopteris japonica* Kershaw (1910) and *Solenostelopteris nipanica* Vishnu-Mittre (1958). However, stele shape at levels of frond trace divergence in both *S. japonica* and *S. nipanica* differ from those of the Apple Bay fossil rhizome in the thickness of cauline metaxylem, shape of the frond trace, and position and number of protoxylem strands in the frond trace (Kershaw 1910, pl. 58, figs. 1–3; Ogura 1930, text fig. 5A, 5B; Vishnu-Mittre 1958, pl. 3, figs. 19, 20).

Through the study of extinct filicaleans, it is becoming increasingly clear that living and fossil ferns have a broad range of anatomical diversity and that stelar architecture may be very similar in quite distantly related species, particularly of the second filicalean radiation. These similarities often appear to be more closely associated with the growth habit of ferns than with their phylogenetic relationships (see Boodle 1901, 1903; Gwynne-Vaughan 1901, 1903; Tansley 1907; Kershaw 1910; Bower 1926; Mickel 1962, 1981; Ogura 1972). However, our current knowledge of the range of anatomical diversity among extant ferns remains insufficient either to confidently assign some fossils to known families or to draw conclusions about the ultimate systematic utility of many anatomical characters.

The fertile pinnules with two rows of sporangia and *Cicatricosisporites*-type spores place *A. quatsinoensis* within the Schizaeaceae, possibly within subgenus *Anemiorrhiza*. *Anemia quatsinoensis* is the oldest and most complete permineralized fertile material of the genus *Anemia* in North America and further increases the number of extinct species of Schizaeaceae. This is concordant with the hypothesis that the Schizaeaceae is one of the more basal groups of the second filicalean radiation (Rothwell 1987, 1999).

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Literature Cited

- Andrews HN, CS Pearsall 1941 On the flora of the Frontier Formation of southwestern Wyoming. *Ann Mo Bot Gard* 28:165–192.
- Banerji J 2000 Occurrence of angiosperm remains in an Early Cretaceous intertrappean bed, Rajmahal Basin, India. *Cretac Res* 21:781–784.
- Berry EW 1911 A Lower Cretaceous species of Schizaeaceae from eastern North America. *Ann Bot* 24:193–198.
- Bohra DR, BD Sharma 1979 Jurassic petrified filician plants from the Rajmahal Hills, India. *Ann Bot* 44:749–756.
- Bolkhovitina NA 1961 Studies of recent and fossil spores of the family Schizaeaceae. *Tr Geol Inst Akad Nauk SSSR* 40:1–176. (In Russian.)
- 1962 History of Schizaeaceae family in the geological past on the basis of spore studies. *Pollen Spores* 4:334–335.
- 1971 Distribution of schizaeaceous spores in Jurassic and Lower Cretaceous deposits of Eurasia. *J Palynol* 7:9–15.
- Boodle LA 1899 Stem-structure in Schizaeaceae, Gleicheniaceae, and Hymenophyllaceae. *Ann Bot* 13:624.
- 1901 Comparative anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae. II. On the anatomy of Schizaeaceae. *Ann Bot* 15:359–421.
- 1903 Comparative anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae. IV. Further observations of *Schizaea*. *Ann Bot* 17:511–537.
- Boureau E 1970 *Traité de paléobotanique. Filicophyta. Tome 4, fascicle 1.* Masson, Paris. 519 pp.
- Bower FO 1923 *The ferns (Filicales). Vol 1. Analytical examination of the criteria of comparison.* Cambridge University Press, Cambridge. 306 pp.
- 1926 *The ferns (Filicales). Vol 2. The Eusporangiate and other relatively primitive ferns.* Cambridge University Press, Cambridge. 344 pp.
- Brown RW 1943 A climbing fern from the upper Cretaceous of Wyoming. *J Wash Acad Sci* 33:141–142.
- Chandler ME 1955 The Schizaeaceae of the south of England in early Tertiary times. *Bull Br Mus (Nat Hist) Geol* 2:291–314.
- Collinson ME 1996 “What use are fossil ferns?”—20 years on: with a review of the fossil history of extant pteridophyte families and genera. Pages 349–394 in Camus JM, M Gibby, RJ Johns, eds. *Pteridology in perspective.* Royal Botanic Gardens, Kew.
- 2001 Cainozoic ferns and their distribution. *Brittonia* 53: 173–235.
- Cookson IC 1957 On some Australian Tertiary spores and pollen grains that extend the geological and geographical distribution of living genera. *Proc R Soc Vic* 69:41–53.
- Daghlian CP, TN Taylor 1979 A new method for isolating pollen and spores from acetate peels for scanning electron microscopy. *Rev Palaeobot Palynol* 27:85–89.
- Deng S, S Wang 2000 *Klukiopsis jurassica*, a new Jurassic schizaeaceous fern from China. *Sci China, Ser D*, 43:356–363.
- Dettmann ME 1989 Antarctica: Cretaceous cradle of austral temperate rainforests. *In* JA Crame, ed. *Origins and evolution of the Antarctic biota, special issue, Geol Soc Spec Publ* 47:89–105.
- Dettmann ME, HT Clifford 1991 Spore morphology of *Anemia*, *Mobria*, and *Ceratopteris* (Filicales). *Am J Bot* 78:303–325.
- 1992 Phylogeny and biogeography of *Ruffordia*, *Mobria*, and *Anemia* (Schizaeaceae) and *Ceratopteris* (Pteridaceae): evidence from *in situ* and dispersed spores. *Alcheringa* 16:269–314.
- Eames AJ 1936 *Morphology of vascular plants, lower groups.* McGraw-Hill, New York.
- Gandolfo MA, KC Nixon, WL Crepet, GE Ratcliffe 2000 Spores of *Lygodium* Sw. (Schizaeaceae) from the Late Cretaceous of New Jersey. *Plant Syst Evol* 221:113–123.
- Gwynne-Vaughan DT 1901 Observations on the anatomy of solenostelic ferns. *Ann Bot* 17:689–742.
- 1903 Observations on the anatomy of solenostelic ferns. I. *Loxosoma*. *Ann Bot* 14:71–98.
- Haggart JW, HW Tipper 1994 New results in Jura-Cretaceous stratigraphy, northern Vancouver Island, British Columbia. *Geol Surv Can Curr Res* 1994E:59–66.
- Harris TM 1977 Notes on two of Raciborski’s Jurassic ferns. *Acta Palaeobot* 18:3–12.
- Hughes NF, J Moody-Stuart 1966 Descriptions of schizaeaceous spores taken from early Cretaceous macrofossils. *Palaeontology* 9: 274–289.
- Jeletzky JA 1976 Mesozoic and Tertiary rocks of Quatsino Sound, Vancouver Island, British Columbia. *Geol Surv Can Bull* 242:1–243.
- Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in paleobotany. *Ann Bot, NS*, 20:635–637.
- Kershaw EM 1910 A fossil solenostelic fern. *Ann Bot* 24:683–691.
- Kramer KU 1990 Schizaeaceae. Pages 258–263 in K Kubitzki, ed. *The families and genera of vascular plants. KU Kramer, PS Green, vol eds. Pteridophytes and gymnosperms. Vol 1.* Springer, Berlin.
- Little SA, RA Stockey, GW Rothwell 2006 *Stramineopteris aureopilosus* gen. et sp. nov.: reevaluating the role of vegetative anatomy in the resolution of the leptosporangiate fern phylogeny. *Int J Plant Sci* 167:683–694.
- Lukose NG 1964 New species of *Schizaea* spore from the upper Mesozoic of Kashmir, India. *Nature* 204:566–567.
- Manchester SR, MS Zavada 1987 *Lygodium* foliage with intact sorophores from the Eocene of Wyoming. *Bot Gaz* 148:392–399.
- Mickel JT 1962 A monographic study of the fern genus *Anemia*, subgenus *Coptophyllum*. *Iowa State J Sci* 36:349–382.
- 1981 Revision of *Anemia* subgenus *Anemiorrhiza* (Schizaeaceae). *Brittonia* 33:413–429.
- Nishida M, H Nishida 1982 Histology of the rhizome of *Loxosomopsis* and affinity of *Solenostelopteris loxosomoides* Ogura. *Acta Phytotaxon Geobot* 33:302–307. (In Japanese; English summary.)
- Ogura Y 1930 On the structure and affinities of some Cretaceous plants from Hokkaido. *J Fac Sci Imp Univ Tokyo Sect III Bot* 2: 381–412.
- 1972 Comparative anatomy of vegetative organs of the pteridophytes. *Encyclopedia of plant anatomy. Vol 7.* Borntraeger, Berlin. 502 pp.
- Potonié R, J Gelletich 1933 Über Pteridophytensporen einer eocänen Braunkohle aus Dorog in Ungarn. *Sitzungsber Ges Naturforsch Freunde Berl* 33:517–526.
- Prantl K 1881 Vorläufige Mitteilung über die Morphologie, Anatomie und Systematik der Schizaeaceen. *Bot Jahrb* 2:297–303.
- Raciborski M 1890 Über die Osmundaceen und Schizaeaceen der Juraformation. *Bot Jahrb* 13:1–9.
- Rothwell GW 1987 Complex Paleozoic Filicales in the evolutionary radiation of ferns. *Am J Bot* 74:458–461.
- 1999 Fossils and ferns in the resolution of land plant phylogeny. *Bot Rev* 65:188–218.
- Rothwell GW, RA Stockey 2003 Anatomically preserved vascular and nonvascular cryptogams from the Lower Cretaceous of western North America. *Botany* 2003—Aquatic and wetland plants: wet and wild. *Mobile, AL. Abstracts* 232:62.
- 2006 Combining characters of Pteridaceae and tree ferns: *Pterisorus radiata* gen. et sp. nov., a permineralized Lower Cretaceous filicalean with radial sori. *Int J Plant Sci* 167: 695–701.
- Rozefelds AC, Christophel DC, NF Alley 1992 Tertiary occurrence of the fern *Lygodium* (Schizaeaceae) in Australia and New Zealand. *Mem Queensl Mus* 32:203–222.

- Sanders H, GW Rothwell, RA Stockey 2004 Diversity of Cretaceous conifers: a species with pollen cones that bear adaxial pollen sacs. Botany 2004—Alpine diversity: adapted to the peaks, Snowbird, UT. Abstracts 344:89.
- Serbet R, GW Rothwell 2003 Anatomically preserved ferns from the Late Cretaceous of western North America: Dennstaedtiaceae. Int J Plant Sci 164:1041–1051.
- Seward AC 1894 The Wealden flora. I. Thallophyta-Pteridophyta. Catalogue of the Mesozoic plants in the Department of Geology. Br Mus Nat Hist 1:1–179.
- Sharma BD, DR Bohra 1976 Petrified solenostelic rhizomes from the Jurassic of Rajmahal Hills, India. Phytomorphology 26: 411–414.
- 1980 Schizaeaceous spores *in situ* from the Jurassic rocks of Rajmahal Hills, India. Adv Pollen-Spore Res 5–7:257–264.
- Skog JE 1976 *Loxomopteris anasilla*, a new fossil fern rhizome from the Cretaceous of Maryland. Am Fern J 66:8–14.
- 1982 *Pelletexia amelguita*, a new species of fossil fern in the Potomac Group (Lower Cretaceous). Am Fern J 72:115–121.
- 1992 The Lower Cretaceous ferns in the genus *Anemia* (Schizaeaceae), Potomac Group of Virginia. Rev Palaeobot Palynol 70:279–295.
- 1993 The relationship of the fossil fern *Schizaeaopsis* Berry to modern genera in the Schizaeaceae. Am Fern J 82:20–29.
- 2001 Biogeography of Mesozoic leptosporangiate ferns related to extant ferns. Brittonia 53:236–269.
- Skog JE, DL Dilcher 1994 Lower vascular plants of the Dakota Formation in Kansas and Nebraska, USA. Rev Palaeobot Palynol 80:1–18.
- Smith SY, RS Currah, RA Stockey 2004 Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. Mycologia 96:180–186.
- Smith SY, GW Rothwell, RA Stockey 2003a Anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island. Botany 2003—Aquatic and wetland plants: wet and wild. Mobile, AL. Abstracts 234:63.
- 2003b *Cyathea cranhamii* sp. nov., anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. Am J Bot 90:755–760.
- Stockey RA 2004 Anatomically preserved pteridophytes: unexpected diversity for the early Cretaceous. Pages 25–26 in Abstracts from Ferns for the 21st Century, an International Symposium on Pteridophytes, Royal Botanic Gardens, Edinburgh. Symposium 4: Fossils.
- Stockey RA, GW Rothwell, SA Little 2006 Relationships among fossil and living Dipteridaceae: anatomically preserved *Hausmannia* from the Lower Cretaceous of Vancouver Island. Int J Plant Sci 167: 649–663.
- Stockey RA, NJ Wiebe 2005 Taxodiaceous pollen cones from the Lower Cretaceous of Vancouver Island, Canada. Botany 2005—Learning from plants. Austin, TX. Abstracts 273:87.
- Stopes MC, K Fujii 1910 Studies on the structure and affinities of Cretaceous plants. Philos Trans R Soc Lond B 201:1–90.
- Sweet AR 2000 Applied research report on two samples of Cretaceous age from Vancouver Island, British Columbia, as requested by J. Haggart (GSC Pacific, Vancouver). Geol Surv Can Paleontol Rep 2:1–3.
- Tansley AG 1907 The Schizaeaceae. Lecture V: the evolution of the solenostele. Lectures on the evolution of the filicinean vascular system. New Phytol 6:148–155.
- Thomas MA 1912 *Stachypteris hallei*: a new Jurassic fern. Proc Camb Philos Soc 16:610–614.
- Tidwell WD, SR Ash 1994 A review of selected Triassic to early Cretaceous ferns. J Plant Res 107:417–442.
- Tidwell WD, JE Skog 1999 Two new species of *Solenopteris* from the upper Jurassic Morrison Formation in Wyoming and Utah. Rev Palaeobot Palynol 104:285–298.
- Trivett ML, RA Stockey, GW Rothwell, G Beard 2006 *Paralygodium vancouverensis* sp. nov. (Schizaeaceae): additional evidence for filicalean diversity in the Paleogene of North America. Int J Plant Sci 167:675–681.
- Tryon AF, B Lugardon 1991 Spores of Pteridophyta. Springer, New York. 648 pp.
- Tryon RM, AF Tryon 1982 Ferns and allied plants. Springer, New York. 857 pp.
- Van Konijnenburg-van Cittert JHA 1981 Schizaeaceous spores *in situ* from the Jurassic of Yorkshire, England. Rev Palaeobot Palynol 33: 169–181.
- 2002 Ecology of some late Triassic to early Cretaceous ferns in Eurasia. Rev Palaeobot Palynol 119:113–124.
- Vavrek MJ, RA Stockey, GW Rothwell 2006 *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. Int J Plant Sci 167:631–637.
- Vishnu-Mittre 1958 Studies on the fossil flora of Nipania, Rajmahal Series, India: Pteridophyta, and general observations on Nipania fossil flora. Paleobotanist 7:47–66.
- Wilson MA 1978 Palynology of three sections across the uppermost Cretaceous/Paleocene boundary in the Yukon Territory and District of Mackenzie, Canada. Palaeontogr Abt B 166:99–183.
- Yoshida A, H Nishida, M Nishida 1996 Permineralized schizaeaceous fertile pinnules from the Upper Cretaceous of Hokkaido, Japan. I. *Schizaeopteris*. Res Inst Evol Biol Sci Rep 8:85–94.
- 1997 Permineralized schizaeaceous fertile pinnules from the Upper Cretaceous of Hokkaido, Japan. II. *Paralygodium yezoense* gen. et sp. nov. Res Inst Evol Biol Sci Rep 9:1–10.