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. Laminar 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 sporae 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 solenosteles 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 (Cyatheaaceae; Smith et al. 2003b). However, several addi-

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

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

Nodules were slabbed and studied using the cellulose ace-
tate 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
Daghlian 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 speci-
men stubs with double-sided tape and coated with a 100-A˚
thickness of Au on a Nanotek sputter-coater. Specimens were
examined on a JEOL 6301 FXV scanning electron micro-
scope (Japan Electron Optics) at 5 kV.

Digital images were obtained with Microlumina (Leaf Sys-
tems, Bedford, MA) and PowerPhase (Phase One, Frederiks-
berg, 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 lat-
eral 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-

Fig. 1 Map of Vancouver Island showing the Apple Bay locality.
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 μm. C, Pinnule lobes abaxially curved showing lamina with epidermal cells. P13158 C bot #18, scale bar = 500 μm. 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 μm. E, Pinnule lamina showing epidermal cells with wavy cell walls. P13158 C bot #2, scale bar = 50 μm.
Fig. 3 *Anemia quatsinoensis* sp. nov. sporangia and spores. 

A, Sporangia in cross section. Holotype P13424 I bot #16, scale bar = 50 μm. 

B, Top view of sporangium showing annulus. Holotype P13424 I bot #23, scale bar = 20 μm. 

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 laesaeae (fig. 3D–3G). Laesaeae 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 Cliftord 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 Cicatricosistorites Potonie et Geltelich (1933).

**Associated Rhizome**

One small schizaeaceae 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], 4F, 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. 4F, 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 trilette, 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 (Bolkovitina 1961, 1962; Mickel 1962; Tryon and Tryon 1982; Kramer 1990; Dettmann and Cliftord 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 Mohria 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 Mohria and Anemia in

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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 laesaeae, rounded apices where several muri overlap. Holotype P13424 I bot #18, scale bar = 10 μm. E, Proximal view of spore showing trilete mark, raised laesaeae, and obliquely arranged muri below laesaeae. 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 laesaeae 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 elliptoid 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 (P), 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 *Mohria* 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, *Mohria* 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 sporules of *A. quatsinoensis* are also most similar to sporules 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* sporules of *A. quatsinoensis* correspond to the sporae 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 1993, 2001; Manchester and Zavada 1987; Dettmann and Konijnenberg-van Cittert 1981, 2002; 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 charcoalified 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 charcoalified) schizaeaceous fertile remains are known from the Jurassic of India (*Schizaengium jurassicum* Sharma and Bohra 1980), the Upper Cretaceous of Japan and eastern North America (*Schizaceopteris mesozoica* Stopes et Fuji 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 trilette spores with little or no wall sculpture (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 *Schizaecopteris*, each pinnule segment bears several irregularly arranged sporangia that each have a uniseriate apical annulus and *in situ* sporules (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 sporules 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 *sporae 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 (*P*), 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 (*Pe*), 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 medulated protosteles in *Schizaea* Smith, and from solenosteles in some species of *Anemia* to dicotystes in other species of *Anemia* and *Mohria* (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 solenostele species of subgenus *Anemiorrhiza* (Boodle 1901; Mickel 1962). The rhizome of *A. mexicana* is characterized by an amphiphloic solenosteole 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 solenosteole, 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 solenosteole (i.e., 0.65 mm vs. 1 mm, respectively), metaxylen thickness (i.e., two to four tracheids vs. two to five tracheids, respectively), and pericycle thickness in the solenosteole (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 solenosteole, 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-Mitre 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-Mitre 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-Mitre (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 metaxyylem, 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-Mitre 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 *Cicatricisporites*-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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