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PARALYGODIUM VANCOUVERENSIS SP. NOV. (SCHIZAEACEAE): ADDITIONAL EVIDENCE FOR FILICALEAN DIVERSITY IN THE PALEOGENE OF NORTH AMERICA

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Several fertile pinnules with abaxially borne sporangia have been discovered in calcareous marine nodules from the Middle or Late Eocene Appian Way locality on the east coast of Vancouver Island, British Columbia, Canada. Fertile pinnules are attached in groups of two or three. They are deeply lobed, with each lobe rolled toward the abaxial surface and the entire pinnule rolled toward the abaxial surface to form an irregularly globose structure. Sporangia occur abaxially and form two rows over the entire surface of each pinnule lobe. The midrib of each pinnule lobe is thickened, forming a receptacle from which broadly attached sporangia and numerous paraphyses diverge. As is characteristic of many schizaeaceous ferns, sporangia of the fossil are flask shaped with a short stalk and have a uniseriate, transverse annulus at the apex. Spores are tetrahedral and trilete, like those of the type species for the extinct genus *Paralygodium*. The new specimens are described as *Paralygodium vancouverensis* sp. nov. and are compared to both living genera of schizaeaceous ferns and the extinct species *Paralygodium yezoense* and *Anemia poolensis*. The unique combination of characters displayed by each of the fossil species reveals the presence of several extinct schizaeaceous lineages and supports interpretations that the diversity of Schizaeaceae s.l. was greater during the Cretaceous and Paleogene than it is today.

Keywords: anemia, Eocene, fossil ferns, *Lygodium*, *Paralygodium*, Schizaeaceae, *Schizaeopteris*.

Introduction

The fossil record of leptosporangiate ferns has been substantially enriched by the discovery of increasing numbers of anatomically preserved vegetative and fertile organs in Mesozoic and Tertiary deposits of North America and Japan. Recently discovered specimens have provided crucial information about diversification among several ancient fern families, including Osmundaceae (Serbet and Rothwell 1999; Smith and Stockey 1999; Stockey and Rothwell 2003), anemioid and lygodioid Schizaeaceae (Yoshida et al. 1996, 1997), Cyatheaceae (Smith et al. 2003), Dicksoniaceae (Lantz et al. 1999; Rothwell and Stockey 2003), and Dennstaedtiaceae (Serbet 1997; Serbet and Rothwell 2003), as well as the more highly derived Athyriaceae (Stockey et al. 1999), Blechnaceae (Pigg and Rothwell 2001; Serbet and Rothwell 2006; Smith et al. 2006), Dryopteridaceae (Pigg and Rothwell 2001; Serbet and Rothwell 2006), and possibly Pteridaceae (Rothwell and Stockey 2006). Although the familial relationships among filicalean ferns are not yet fully resolved (Pichi Sermolli 1977; Kramer and Green 1990; Hasebe et al. 1995; Pryer et al. 1995), the discovery of increasing numbers of extinct species is providing a much better picture of leptosporangiate fern diversity through time (Rothwell 1987, 1999; Collinson 2001; Skog 2001), from which the overall pattern of fern phylogeny eventually can be ascertained.

The material described in this study comes from carbonate nodules derived from marine sediments of western North America. Although ferns often form a minor component of the flora of both preangiosperm- and angiosperm-dominated fossil biotas, they clearly were an important component of the floras throughout the late Mesozoic and Paleogene (Collinson 2001; Skog 2001). In this study, we describe a new species of the extinct schizaeaceous genus *Paralygodium* Yoshida, H. Nishida, et M. Nishida. *Paralygodium vancouverensis* sp. nov. emphasizes that species of extinct schizaeaceous genera with novel combinations of characters were present in North America during the Eocene. This discovery also provides an opportunity to expand the range of variation within the genus and to increase our understanding of diversity among living and extinct schizaeaceous ferns.

Material and Methods

To date, eight specimens of this fern have been recognized among fossils from the Appian Way locality, located on the eastern shore of Vancouver Island south of Campbell River, British Columbia, Canada (49°56′00″N, 125°11′15″W; UTM 10U CA 433331). They occur among abundant plant remains that are preserved in large calcareous concretions embedded in a sandy-siltstone matrix on the beach. Marine sediments

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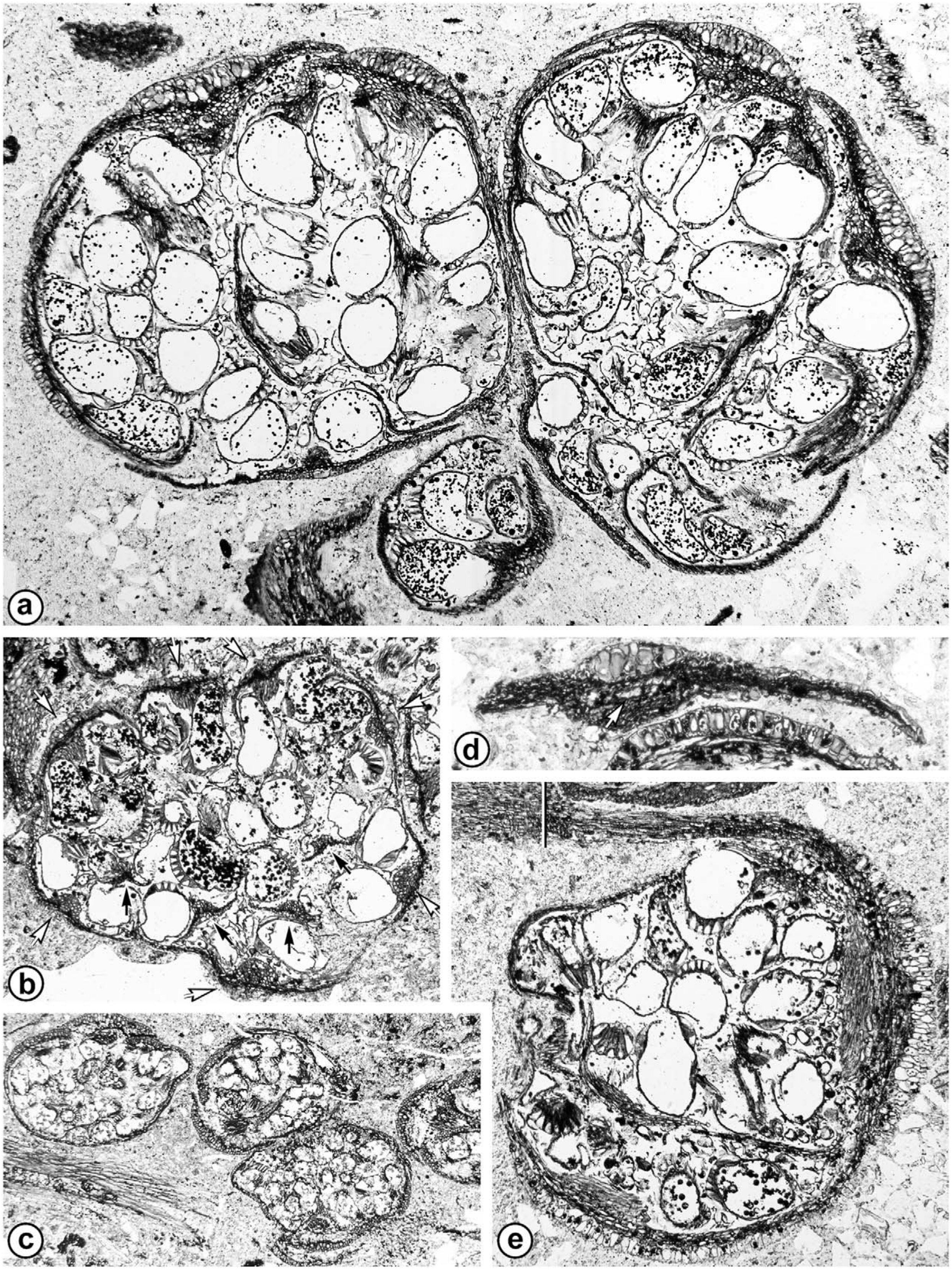

Fig. 1 *Paralygodium vancouverensis* sp. nov. (*a, b, d, e*) and *Paralygodium yezoense* (*c*). *a*, Cluster of three fertile pinnules showing overall shape, general features of pinnule lobes, and sporangia in various planes of section. AW 380 I top 4; ×40. *b*, Cross section of one fertile pinnule

at this locality are Middle or Late Eocene in age (Haggart et al. 1997; J. Haggart, personal correspondence, 2001).

Concretions were slabbed and the specimens serially sectioned by the well-known cellulose acetate peel technique (Joy et al. 1956). Peels for microscopic examination and image capture were mounted on standard microscope slides with Eukitt mounting medium (O. Kindler, Freiburg, Germany). Images were captured with Microlumina (Leaf Systems, Bedford, MA) and PhotoPhase digital scanning cameras (Phase One, Copenhagen) and processed with Adobe Photoshop. Specimens, peels, and microscope slides are housed in the University of Alberta Paleobotanical Collections.

Systematics

Order—Filicales

Family—Schizaeaceae Kaulf.
*s.l. (*sensu *Kramer 1990)*

*Genus—*Paralygodium *Yoshida,*
H. Nishida, et M. Nishida

*Species—*Paralygodium vancouverensis *sp. nov.*
*Trivett, Stockey, et Rothwell (Figs. 1, 2; Fig. 3*a, *3*c*–3*f*)*

Diagnosis. Pinnules attached in clusters of three; palmately lobed, lobes numbering approximately seven; lobes enrolled within tightly rolled pinnules, sporangia covering entire abaxial surface in two rows on each pinnule lobe. Midrib inflated, attaching sporangia by short, broad stalk. Sporangia pyriform, 420–600 μm long, 275–325 μm wide, apical annulus consisting of 14–18 cells. Spores subtetrahedral, 30–48 μm in diameter; interradial sides straight to concave, equatorial flange absent, trilete extending seven-eighths distance to equator; exine psilate with no obvious perispore.

Holotype. AW 52 B top (figs. 1*b*, 2*a*, 3*c*) deposited in the University of Alberta Paleontological Collections, Edmonton, Alberta, Canada, is here designated the holotype.

Paratypes. AW2 I top (figs. 1*e*, 2*b*, 3*a*), AW36 C_2 top (figs. 1*d*, 3*d*), and AW380 I top (figs. 1*a*, 2*e*), also deposited in the University of Alberta Paleontological Collections, are designated as paratypes.

Type locality. Appian Way, beach exposure on the eastern shore of Vancouver Island south of Campbell River, British Columbia, Canada (49°56′00″N, 125°11′15″W; UTM 10U CA 433331).

Age and stratigraphy. Middle or Late Eocene (Haggart et al. 1997; J. Haggart, personal correspondence, 2001).

Etymology. The specific epithet *vancouverensis* refers to the geographic origin of the specimens on the east shore of Vancouver Island.

Description

Specimens of *Paralygodium vancouverensis* consist of closely appressed clusters of usually three connected pinnules forming units that are dispersed in the matrix (fig. 1*a*). Specimens range from 4 to 5 mm in diameter. As in the generitype, *Paralygodium yezoense* Yoshida, H. Nishida, et M. Nishida (fig. 1*c*), each fertile pinnule of *P. vancouverensis* is lobed and circinately coiled, with the sporangia on the abaxial surface, clustered within a subspheroidal space (figs. 1*a*–1*c*, 2*a*). Individual enrolled fertile pinnules range from 2.2 to 3.0 mm in maximum diameter. Pinnules are connected by a short pinnatifid pinna rachis (fig. 1*e*) that is winged in cross sections (fig. 1*d*).

The pinna rachis has an inflated midrib with a single vascular bundle (fig. 1*d*, arrow). Much of the pinnule is constructed of axially elongated cells 15–20 μm in diameter that are often occluded by brown contents (fig. 1*d*, 1*e*). There is a prominent rounded adaxial ridge constructed of two interdigitating layers of large sclereids up to 125 μm long and 60 μm in maximum diameter. Such cells decrease in size and taper to a single layer laterally (fig. 1*d*). Distally, this thick region of adaxial tissue spreads laterally to cover much of the pinna surface at levels proximal to divisions that produce the pinnules (figs. 1*e*, 2*a*).

Paralygodium vancouverensis pinnules typically display seven elongated lobes (fig. 1*b*, white arrows), each of which extends from the base (or center) of the pinnule and imbricates with the adjacent lobes (fig. 1*a*, 1*b*). By comparison with mature, unrolled pinnules of *Anemia adiantifolia* (L.) Swartz (fig. 2*d*) and specimens of *P. yezoense,* the pinnules of *P. vancouverensis* appear to be palmately lobed. In cross sections, the lobes form an overlapping ring that defines the space in which the sporangia are located (fig. 1*a*, 1*b*). More distally, the coiled tips of the lobes curve back into the sporangial cluster, as they do in immature and some more mature fertile pinnules of *A. adiantifolia* (fig. 1*c*). At distal levels of the pinnule, lobes appear as narrow laminae (fig. 1*b*, black arrows). Each lobe has an abaxially inflated midrib (fig. 1*a*, 1*b*; fig. 2*e*). The midrib extends to near the tip of the lobe and forms a receptacle from which two rows of sporangia diverge, one row to each side. There is also an adaxial ridge of thick-walled cells like that of the pinna rachis. Therefore, the structure and histology of each pinnule lobe are similar to but somewhat smaller than those of the pinna rachis in cross sections (figs. 1*a*, 2*e*).

Sporangia of *P. vancouverensis* are arranged in two rows on each pinnule lobe and occur among narrow trichomes or paraphyses that are circular in cross sections (fig. 3*a*, right); they are similar to sporangia of other schizaeaceous ferns (fig. 3*b*, arrows). The sporangia are variously shaped in cross sections (fig. 1*a*, 1*b*, 1*e*; fig. 2*a*, 2*b*; fig. 3*a*, 3*c*), but

showing seven pinnule lobes (white arrows) at periphery and four lobe tips curved around to pass through section again (black arrows) at center. Holotype AW 52 B top 76; ×35. *c*, Four fertile pinnules of *P. yezoense,* Cretaceous of Hokkaido, Japan, for comparison with *P. vancouverensis.* Specimen 101420; ×20. *d*, Cross section of pinnatifid pinna to which sporangial clusters are attached. Note enlarged sclerotic cells at adaxial surface and vascular bundle (at arrow). AW 36 C_2 top 8; ×65. *e*, Longitudinal section of pinna with attached fertile pinnule. Line indicates plane of section in which pinna in *d* is cut (i.e., at right angle to plane of section for *e*). Note numerous paraphyses among sporangia on abaxial surface of pinnule (at right and bottom). AW 2 I top 15; ×40.

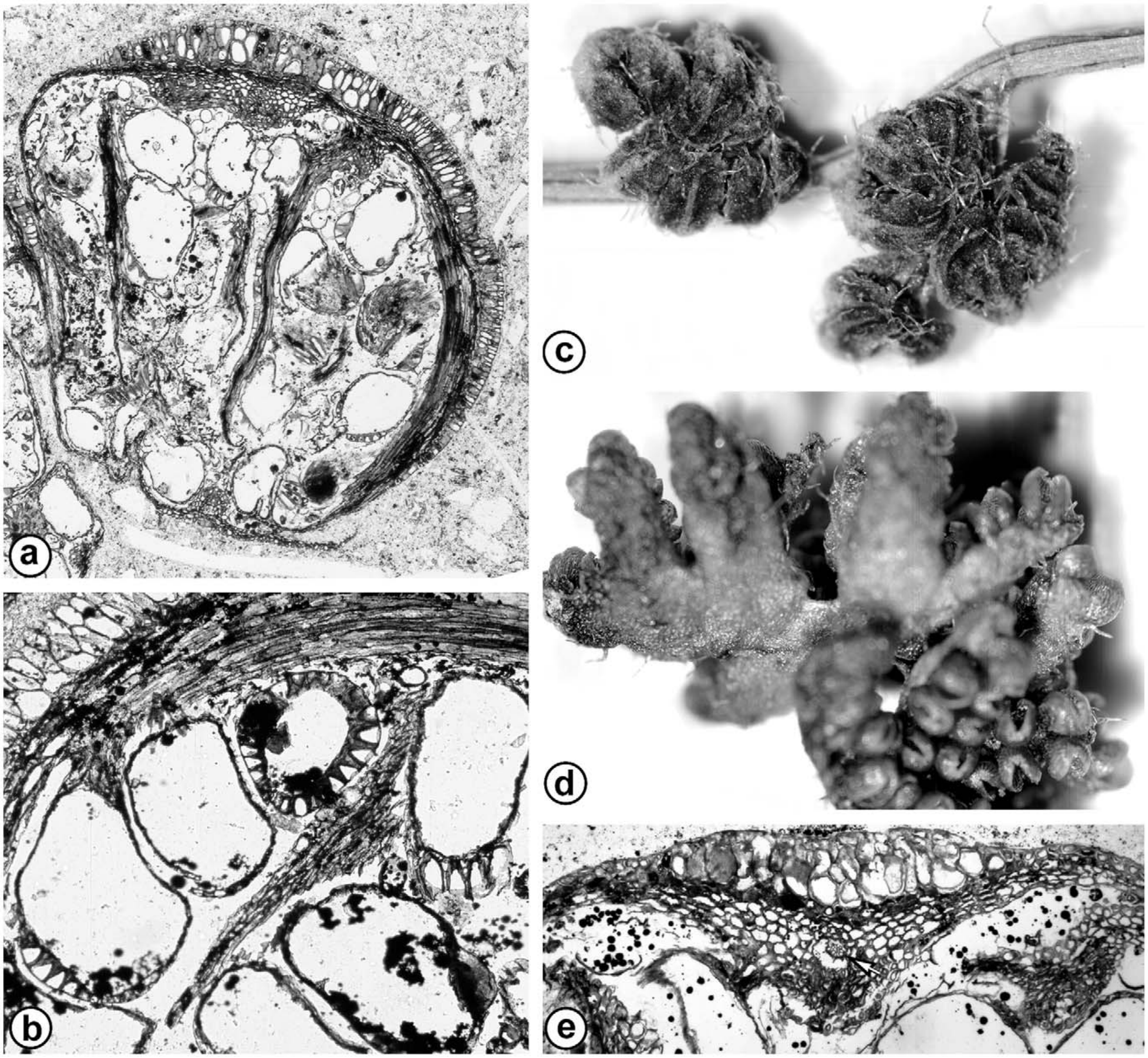

Fig. 2 *Paralygodium vancouverensis* sp. nov. (*a*, *b*, *e*) and *Anemia adiantifolia* (*c*, *d*). *a*, Section of fertile pinnule with pinnule lobes cut in longitudinal section. Internal partitions represent lobes. Holotype AW 52 B top 15; ×40. *b*, Section of interior of pinnule showing sporangia in various planes of section. Note short stalk of attached sporangium (at arrow) and annulus in cross (at top) and longitudinal (at right) planes. AW 2 I top 3; ×85. *c*, Immature *A. adiantifolia* fertile pinnules with pinnule lobes enrolled abaxially, similar to those of fossils. In this view, two short pinnae with small-lobed pinnules are attached alternately to the more proximal frond member. Note numerous trichomes (paraphyses) extending from epidermis. Dried specimen BHO; ×20. *d*, Unrolled fertile pinnules of *A. adiantifolia* showing sporangia attached in two rows (bottom right) to entire abaxial surface of pinnule lobes. Note dehisced sporangia and trichomes (paraphyses) among sporangia. BHO; ×30. *e*, Cross section of pinnule lobe at proximal level, showing terete vascular bundle (at arrow) and disposition of abaxial thin-walled cells and adaxial sclereids restricted to midrib at this level. AW 380 I top 1; ×70.

undistorted longitudinal sections reveal that they are pyriform (fig. 3*a*, right). They measure 420–600 μm long and 275–325 μm in maximum diameter and have a uniseriate wall. Each sporangium is attached by a short, broad stalk (fig. 2*b*, left) and has an apical annulus (figs. 1*a*, 2*b*; fig. 3*a*, 3*c*) that consists of a uniseriate ring (figs. 1*a*, 2*b*, 3*a*) of 14–18 cells. Cells of the annulus are considerably larger than cells of other sporangial walls (fig. 2*b*; fig. 3*a*, 3*c*) and have cell walls that are thickened on the interior and lateral sides (fig. 3*c*). In these features they compare closely to *A. adiantifolia* (fig. 3*b*) and other schizaeaceous sporangia.

Most sporangia are empty and apparently senescent (fig. 1*a*, 1*b*; fig. 2*a*, 2*b*; fig. 3*a*), but spores remain in a few sporangia (fig. 3*c*) and are scattered among the sporangia within

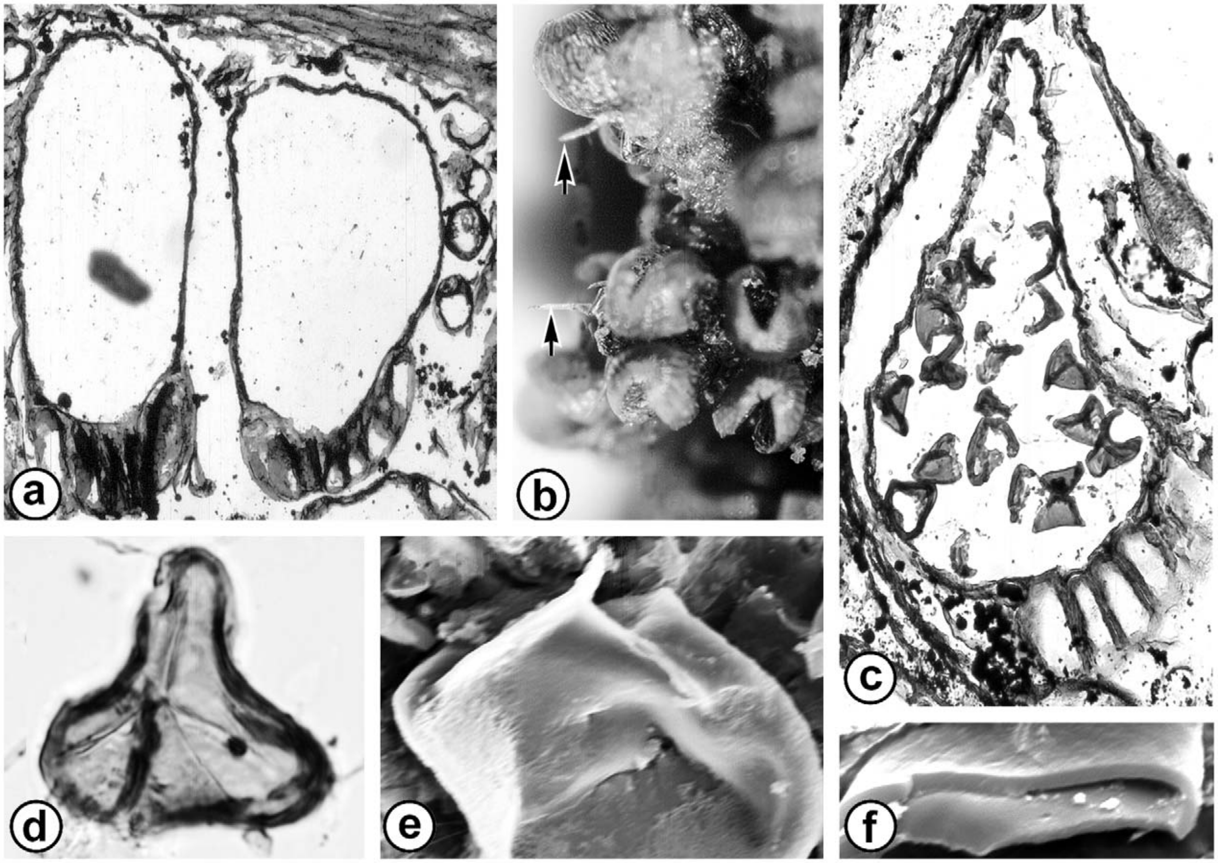

Fig. 3 Sporangia and spores of *Paralygodium vancouverensis* sp. nov. (*a, c–f*) and *Anemia adiantifolia* (*b*). *a*, Longitudinal sections of two sporangia showing apical annulus and cross sections of paraphyses (at right). AW 2 I top 5; ×145. *b*, Mature fertile pinnule of *A. adiantifolia* showing sporangia and trichomes (at arrows); ×40. *c*, Oblique longitudinal section of sporangium with apical annulus (bottom) and enclosed spores. Holotype AW 52 B top 11; ×235. *d*, Proximal view of spore showing overall shape and trilete. AW 36 C_2 top 12; ×835. *e*, SEM of distorted spore showing raised laesurae of prominent trilete. AW 36 C_2 top 16; ×1000. *f*, SEM showing broken section of dense spore wall with psilate surface. AW 36 C_2 top 16; ×2000.

the enrolled pinnule lobes. The spores are radial and trilete, measuring 30–48 μm (mean = 40.32 μm) in diameter. Usually they are collapsed or fragmentary (fig. 3*c*, 3*f*), but when undistorted they are tetrahedral with concave interradial sides and rounded corners (fig. 3*d*). The laesurae of the trilete are narrow and raised (fig. 3*d*, 3*e*) and extend seven-eighths of the distance to the equator. The spore surface is psilate, and edge views of broken spores reveal a dense sporoderm ca. 0.8 μm thick (fig. 3*f*). Spores of this type are comparable to the sporae dispersae genus *Cyathidites* R. A. Couper (Balme 1995).

Discussion

Abaxially borne pyriform sporangia, each with a short, broad stalk and terminal uniseriate annulus, are diagnostic of the family Schizaeaceae Kaulf. s.l. (*sensu* Eames 1936; Kramer 1990). Croziers that are rolled with the abaxial surface oriented inward are also unique to the family (Rothwell 1999). Therefore, *Paralygodium vancouverensis* can be assigned to the Schizaeaceae with a great deal of confidence. Among living schizaeaceous genera, exindusiate sporangia with narrow skeletonized pinnule lobes like those of *P. vancouverensis* are found only in the genus *Anemia* Sw. (Kramer 1990). However, *P. vancouverensis* has psilate spores, whereas the spores of *Anemia* are characterized by coarse ridges that may be echinate and/or reticulate (Tryon and Lugardon 1990). Also, the fertile pinnules of many *Anemia* species and most other schizaeaceaous ferns typically unroll from croziers (fig. 2*c*) as they mature (fig. 2*d*) rather than remaining tightly rolled to senescence, as the fertile pinnules of *P. vancouverensis* do. However, species of *Anemia* subgenus *Coptophyllum* do retain various degrees of coiling in their mature fertile pinnules (Collinson 2001).

Among extinct schizaeaceous ferns, several have mature fertile segments in which the pinnule lamina is abaxially rolled around the sporangia to varying degrees. These include the Cretaceous species *Anemia fremonti* (Knowlton) forma *fertilis* Andrews (Andrews and Pearsall 1941; Collinson 2001), *Anemia sphenopteroides* (Fontaine) Skog (1992), *Anemia dicksonioides* (Fontaine) Skog (including *Pelletixia amelguita* Skog; *sensu* Skog 1992), *Schizaeopteris mesozoica*

Stopes et Fujii from the Upper Cretaceous of Japan (Stopes and Fujii 1910; Yoshida et al. 1996), *Anemia poolensis* Chandler from the Eocene and Paleocene-Eocene boundary of England (review in Collinson 2001), and *Paralygodium yezoense* Yoshida, H. Nishida, et M. Nishida (Yoshida et al. 1997) from the Upper Cretaceous of Japan. Among these, *A. fremonti* and *S. mesozoica* have pinnules that are somewhat less tightly coiled than the others, and they display spores with distinct ridges (Andrews and Pearsall 1941; Yoshida et al. 1997). The spores of *A. sphenopteroides* and *A. dicksonioides* also have ridges, making them quite distinct from the smooth spores of *P. vancouverensis* (Skog 1992), and their preservational mode (i.e., coalified compression) precludes closer comparisons to the anatomical and histological characters of *P. vancouverensis*.

Paralygodium vancouverensis, *P. yezoense*, and *A. poolensis* all have lobed fertile pinnules that are tightly enrolled to form subglobose structures that enclose the sporangia. Moreover, all have sporangia that are borne in two rows along the abaxial surface of pinnule lobes, and all have trilete spores that show little or no wall sculpturing (Chandler 1955, 1962; Yoshida et al. 1997; Collinson 2001).

Specimens of *A. poolensis*, like those of *P. vancouverensis*, are from Eocene deposits. Both species consist of subspheroidal, enrolled, lobed fertile pinnules that bear two rows of pyriform sporangia with a terminal annulus on the enrolled pinnule lobes, and both bear smooth, trilete spores (Collinson 2001). In all of these features, *A. poolensis* and species of *Paralygodium* could represent extremely similar plants, but they cannot be compared more closely because they are preserved by different modes. We concur with past practice (Yoshida et al. 1997; Collinson 2001) and recognize *A. poolensis* and species of *Paralygodium* as distinct at the generic level.

Among all currently known schizaeaceous ferns, *P. vancouverensis* compares most closely to *P. yezoense* (Yoshida et al. 1997). Both consist of subglobose fertile pinnules that bear two rows of pyriform sporangia with a terminal annulus on pinnule lobes, and both have smooth trilete spores. Fertile pinnules of *P. yezoense* (1.5–2.0 mm in diameter) are somewhat smaller than those of *P. vancouverensis* (2.2–30 mm in diameter), as are the sporangia (280–350 μm long for *P. yezoense* and 420–600 μm long for *P. vancouverensis*). *Paralygodium yezoense* has 15–24 cells in the annulus, whereas *P. vancouverensis* has only 14–18 cells. In most other features, including sporangial position and shape, presence of paraphyses among the sporangia, and histology, pinnules of the two species are extremely similar. However, pinnules of *P. yezoense* are borne in an alternate pinnate arrangement on a terete pinna rachis (Yoshida et al. 1997), whereas those of *P. vancouverensis* occur as groups of usually three pinnules attached to a pinnatifid (i.e., with narrow lamina) pinna rachis. Another difference between these species is the number of lobes per pinnule (seven in *P. vancouverensis* and nine to 13 in *P. yezoense*). The spores of *P. yezoense* (33–40 μm) are similar in size to those of *P. vancouverensis* (30–48 μm), but they can be distinguished by a prominent equatorial flange that is absent from spores of *P. vancouverensis*. The Eocene specimens of *P. vancouverensis* are also younger than those of those of the Upper Cretaceous *P. yezoense*.

The discovery of *P. vancouverensis* extends the range of the genus from the Upper Cretaceous of eastern Asia (Hokkaido Island, Japan) to the Eocene of western Canada (Vancouver Island), thus revealing that the genus had a circumpolar distribution that extended well into the Tertiary. Likewise, the new species reveals that the rich diversity of extinct schizaeaceous genera (Collinson 2001; Skog 2001) continued well into the Paleogene of the Tertiary. Together with other components of the extraordinarily diverse flora present at the Appian Way locality on Vancouver Island, *P. vancouverensis* helps illuminate the dynamic floristic turnover that was underway during the Eocene and further emphasizes the continuing success of homosporous pteridophytes long after the rise to dominance of the flowering plants (Rothwell 1996).

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