

**CYATHEA CRANHAMII SP. NOV. (CYATHEACEAE),
ANATOMICALLY PRESERVED TREE FERN SORI FROM
THE LOWER CRETACEOUS OF VANCOUVER ISLAND,
BRITISH COLUMBIA¹**

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Permineralized cyatheaceous sori occur among remains of conifers, fungi, and other plants in newly discovered calcareous concretions from Early Cretaceous (Barremian) marine sediments of Vancouver Island, British Columbia, Canada. Sori are superficially attached in two rows to narrow pinnules and display a globose sphaeropteroid indusium. Annulate sporangia with multicellular stalks diverge from a basal, vascularized receptacle. The nearly vertical uniseriate annulus is not interrupted by the stalk. The sporangia bear 64 trilete spores with perispore sculpturing that ranges from irregular granulate/echinate to prominent rodlets. These specimens, described as *Cyathea cranhamii* sp. nov., are the first anatomically preserved tree fern sori from the fossil record. They represent the most ancient evidence for fertile structures of the Cyatheaceae and demonstrate that essentially modern species of cyatheaceous tree ferns had evolved by the Early Cretaceous.

Key words: Barremian; British Columbia; Cretaceous; *Cyathea cranhamii* sp. nov.; Cyatheaceae; Filicales.

The fossil record of leptosporangiate tree ferns extends from the Triassic, with dicksoniaceous remains generally appearing earlier than those of the Cyatheaceae (Tidwell and Nishida, 1993; Tidwell and Ash, 1994; Skog, 2001). Most of the material consists of compression remains of vegetative foliage, but there are also a few reports of pinnules with sori (Collinson, 2001; Skog, 2001). Stem remains are by far the most common permineralized fossils, with dicksoniaceous/cyatheaceous species extending from the Jurassic into the Tertiary (Lantz et al., 1999; Skog, 2001). Up to the present only a few species of fertile tree fern foliage have been described, and all of these are from compression material.

In the present study, we describe the first evidence for anatomically preserved sori assignable to the Cyatheaceae and the oldest unequivocal cyatheaceous reproductive structures from the Early Cretaceous of western North America. The specimens are described as *Cyathea cranhamii* sp. nov. and demonstrate that an essentially modern species of the Cyatheaceae had evolved by the early Cretaceous.

MATERIALS AND METHODS

The specimens are from the western shore of Apple Bay, Quatsino Sound, northern Vancouver Island, British Columbia, Canada (50°36'21" N, 127°39'25" W). Small, round calcareous concretions containing permineralized plant remains are embedded in a sandstone (greywacke) matrix. The rocks at this locality are Lower Cretaceous (Barremian) in age, Longarm Formation

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equivalents (Jeletzky, 1976; Haggart and Tipper, 1994), and correspond to Jeletzky's (1976) Barremian variegated clastic unit.

Concretions were slabbed and the specimens serial 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 a Microlumina digital scanning camera (Leaf Systems, Bedford, Massachusetts, USA), and processed with Adobe Photoshop (Adobe, San Jose, California, USA). Specimens, peels, and microscope slides are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA).

SYSTEMATICS

Order—Filicales

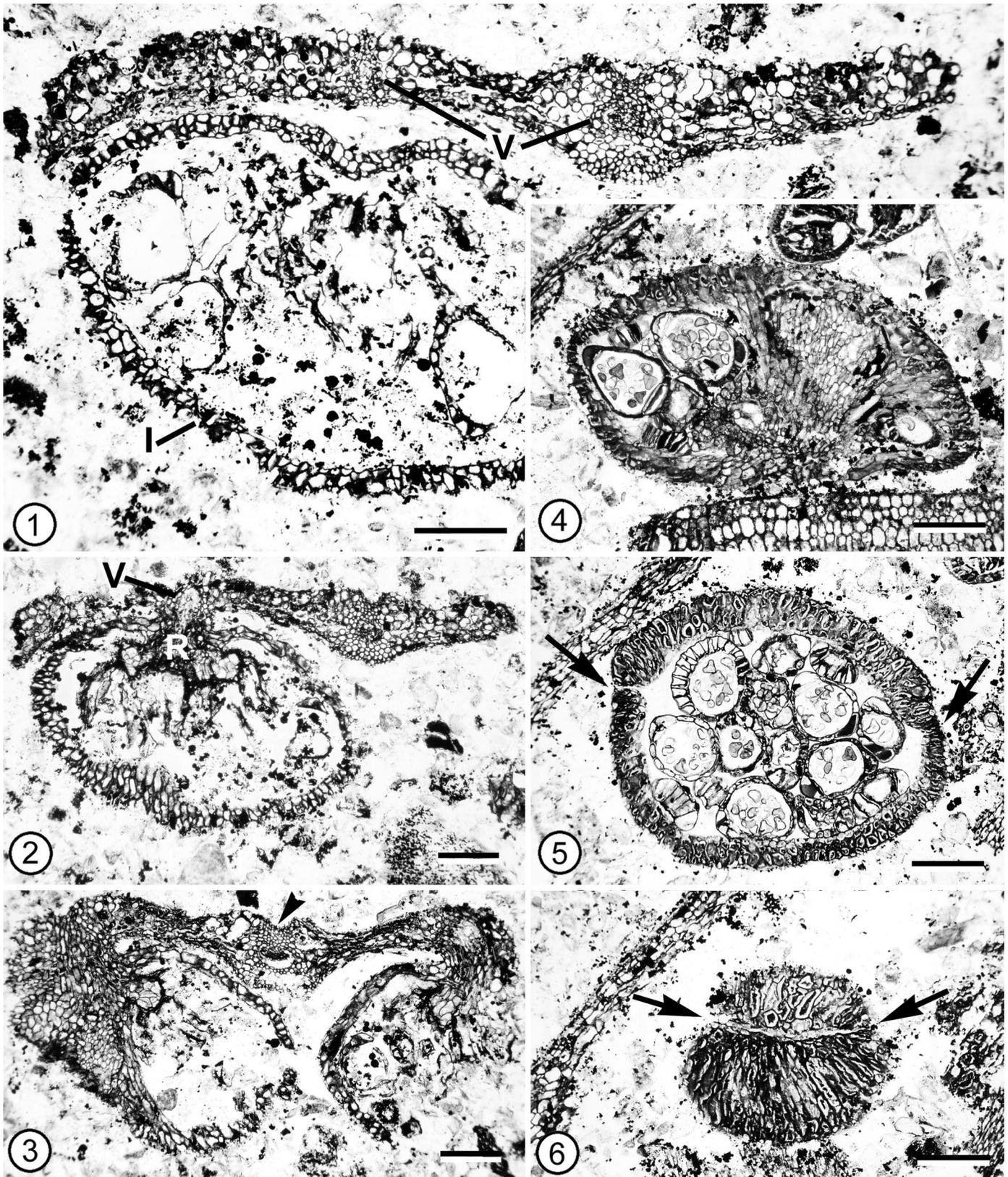
Family—Cyatheaceae Kaulfuss

Genus—*Cyathea* J. E. Smith

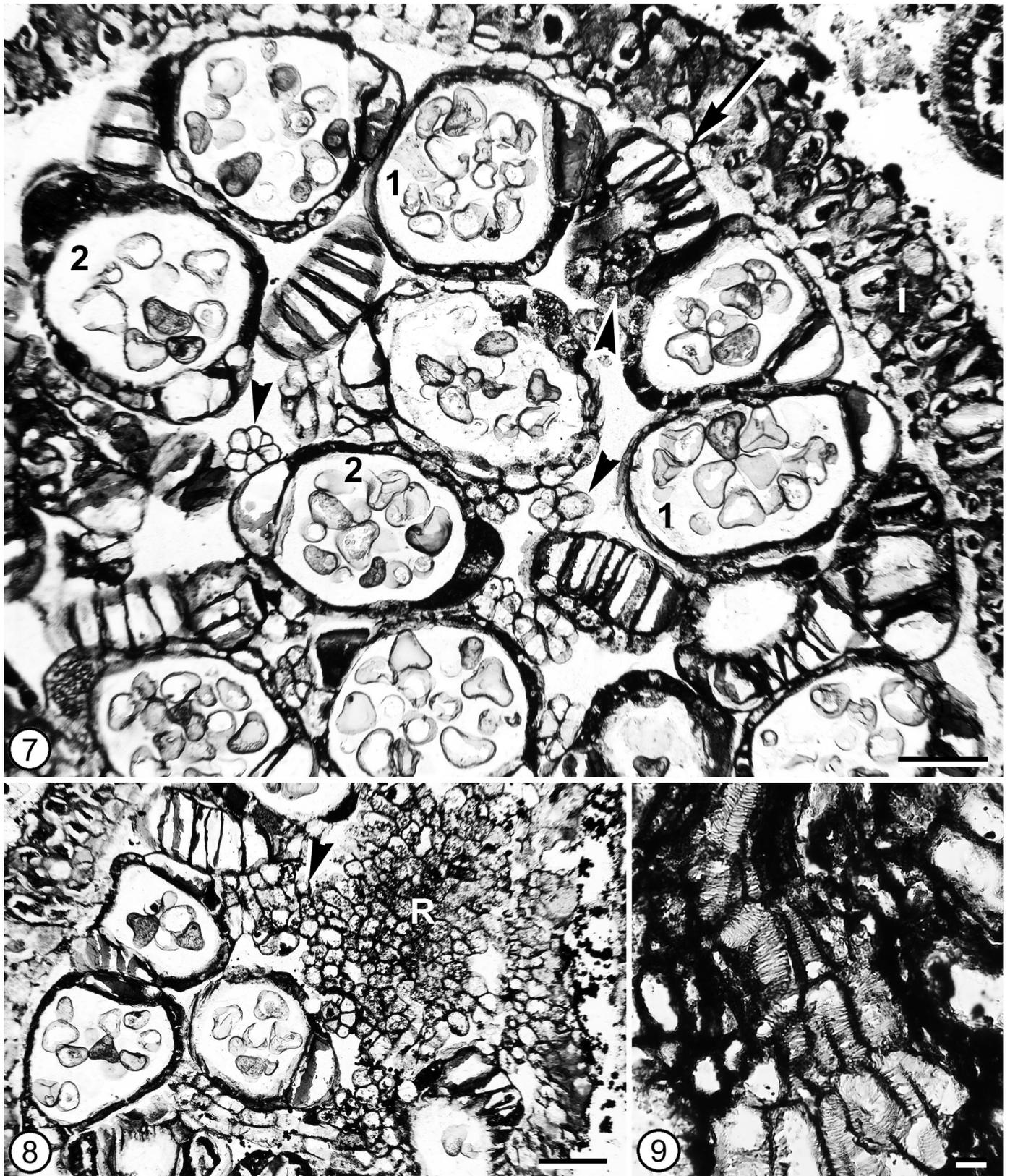
Species—*Cyathea cranhamii* sp. nov.

Specific diagnosis—Tree fern with two rows of superficial sori beneath narrow pinnules. Sori with vascularized receptacle and sphaeropteroid indusium with distal slit-like opening, producing about 35 sporangia. Multicellular sporangial stalks of 5–6 cells in cross section, capsule up to 275–400 μm long, 200–300 μm wide, with annulus of approximately 20 cells and about 64 spores per sporangium. Spores 40–70 μm in diameter, triangular with concave interrational sides and rounded corners; arms of trilete extending three-quarters of the distance to periphery. Exospore approximately 650 nm thick; continuous perispore, with irregular sculpturing ranging from granulate/echinate to distinct rodlets.

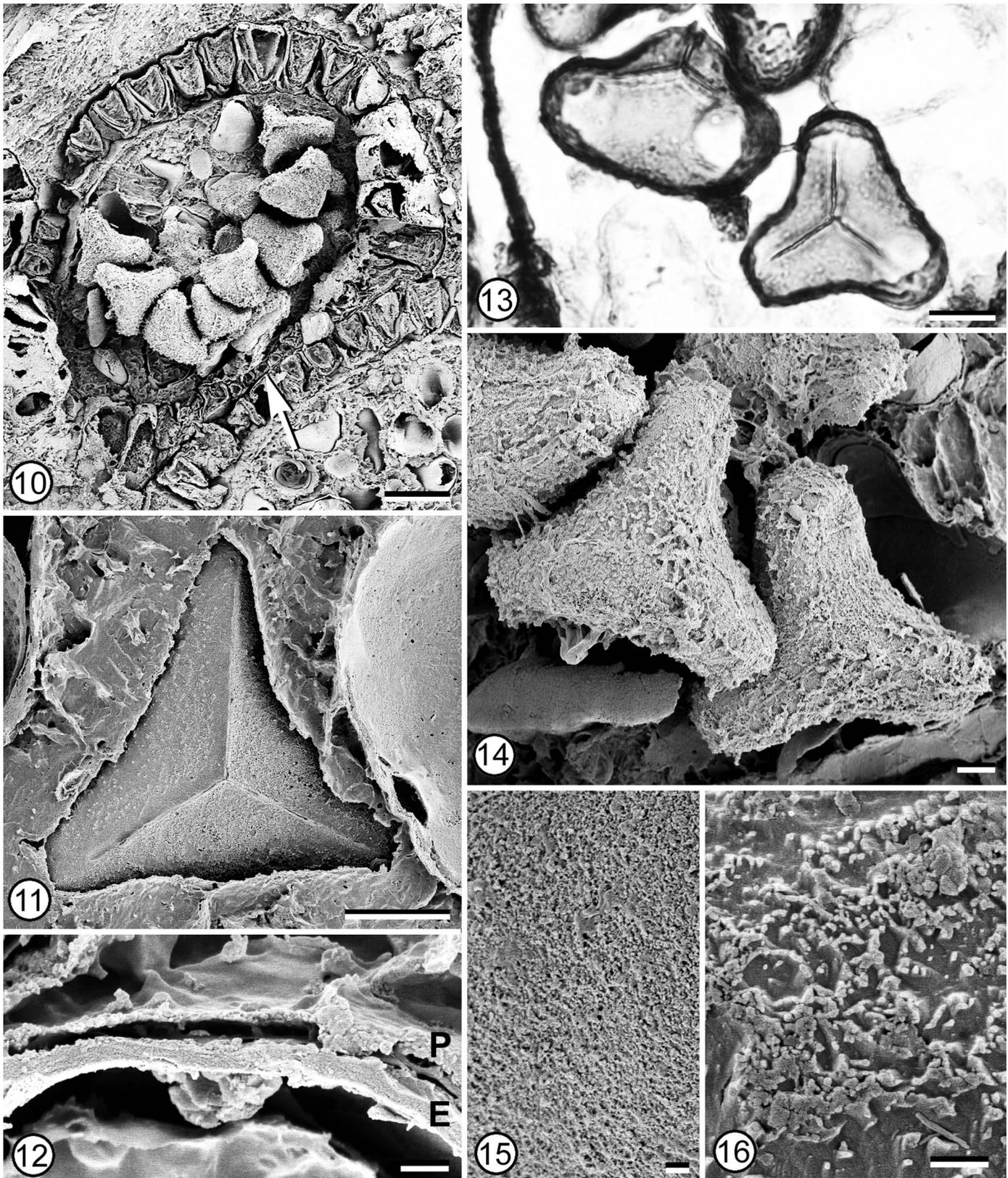
Holotype—Specimen P13021 H_{bot} b, deposited in the University of Alberta Paleobotanical Collections (UAPC-ALTA) is here designated the holotype of *Cyathea cranhamii* (Figs. 4–9, 11–13, 15, and 16).



Figs. 1–6. *Cyathea cranhamii* sp. nov. 1. Cross section of fertile pinnule and indusiate sorus showing anatomical features. Note bundle sheath extensions of mid- and lateral veins (V) and multicellular indusial wall (I). Paratype P13021H_{bot} #107c $\times 85$. Scale = 200 μm . 2. Longitudinal section of sorus attached superficially beneath lateral vein (V) of pinnule. Vascularized receptacle at R. Paratype P13021H_{bot} #114c $\times 46$. Scale = 250 μm . 3. Section of specimen in Figs. 1 and 2 at a level where two sori are attached. Paratype P13021H_{bot} #68c $\times 46$. Scale = 250 μm . Figs. 4–6. Cross sections of one sorus showing features near base (Fig. 4), at mid-level (Fig. 5), and at apex (Fig. 6). Note distal slit that extends basally to mid-region (at arrows). Holotype P13021H_{bot} #91b, 56b, 45b, respectively, all $\times 52$. Scale = 250 μm .



Figs. 7–9. *Cyathea cranhamii* sp. nov. 7. Cross section of sorus at mid-level showing structure of indusium wall and characters of sporangia. Multicellular stalks identified by arrowheads. Sporangia cut at level of stomium identified by 1. Sections not at the level of the stomium (i.e., either proximal or distal to stomium) identified by 2. Note base of annulus adjacent to distal end of stalk, at arrow. Holotype P13021H_{bot} #69b $\times 160$. Scale = 100 μm . 8. Cross section of sorus near base showing divergence of sporangial stalk (arrowhead) from receptacle (R). Holotype P13021H_{bot} #81b $\times 134$. Scale = 100 μm . 9. Barrel-shaped tracheids with scalariform secondary wall thickenings in receptacle. Holotype P13021H_{bot} #65c $\times 480$. Scale = 10 μm .



Figs. 10–16. *Cyathea cranhamii* sp. nov. **10.** Scanning electron microscopy (SEM) of sporangium in longitudinal section showing features of annulus, stomium (at arrow), and spores in this view. P13023 A_{bot}#0 $\times 225$. Scale = 55 μm . **11.** Proximal view of exospore showing trilete suture and surface features. Holotype P13021H_{bot} b $\times 1670$. Scale = 10 μm . **12.** Cross section of exospore (E) and perispore (P). Holotype P13021H_{bot} b $\times 9000$. Scale = 1 μm . **13.** Polar and oblique views of spores showing features with light microscopy. Narrow strands extending between spores may represent fungal hyphae. Holotype P13021H_{bot} #53b $\times 1230$. Scale = 10 μm . **14.** Proximal (at lower right) and distal (at left center) views of spores showing surface sculpturing of perispore in SEM, with some probable fungal hyphae. P13023 A_{bot} #0 $\times 950$. Scale = 10 μm . **15.** Exterior surface of exospore. Holotype P13021H_{bot} b $\times 5000$. Scale = 1 μm . **16.** Surface view of perispore showing irregular granulate and echinate sculpturing pattern. Holotype P13021H_{bot} b $\times 1200$. Scale = 1 μm .

Paratypes—P13018 D_{bot} a (not depicted), P13021 H_{bot} c (Figs. 1–3), and P13023 A_{bot} (Figs. 10 and 14) are designated as paratypes.

Collecting locality—Apple Bay, Vancouver Island, British Columbia, Canada.

Stratigraphic position and age—Longarm Formation equivalents, Early Cretaceous (Barremian).

Etymology—The specific epithet *cranhamii* is proposed in recognition of Gerald Cranham, Parksville, British Columbia, Canada, who generously provided numerous plant specimens for study at the University of Alberta.

Discussion—Recent molecular systematic studies reveal five clades within the Cyatheaceae that do not necessarily conform to traditionally recognized genera (Conant and Stein, 2001). Structural characters that could allow assignment of *C. cranhamii* to one of the newly recognized clades are not preserved in the fossils. Therefore, we recognize the fossils as *Cyathea* sensu lato (s.l.) (sensu Holttum, 1963).

DESCRIPTION

The specimens consist of sori with globose indusia, which are attached to the abaxial surface of narrow pinnule segments (Figs. 2 and 3) in two rows (Fig. 3). The pinnules are up to 2 mm wide and 150–200 μm thick, with a midvein, and lateral veins that branch to vascularize each sorus (Figs. 1–3). Vascular bundles consist of several tracheids with helical wall thickenings, surrounded by a narrow poorly preserved area that likely represents phloem. The pinnules have a midrib approximately 300 μm thick with an adaxial furrow (Figs. 1–3). The midvein displays an indistinct bundle sheath with both abaxial and adaxial bundle sheath extensions (Fig. 1). Cells of the bundle sheath extensions range 15–25 μm in diameter and are tightly packed. Mesophyll cells are more loosely arranged and larger, ranging 35–55 μm in diameter, and many contain either amber or black contents. A uniseriate epidermis has also been recognized, but the cells are poorly preserved and are absent from most of the pinnule surfaces.

Sori are delimited by a globose indusium approximately 1.3 mm diameter (Figs. 1–3 and 5). In longitudinal section sori are oval and vary from laterally to vertically elongated (Figs. 2 and 3). The differences probably result from a combination of distortion during fossilization and natural variation. The indusial wall ranges from one to three layers of tightly packed cells with dark contents that are shrunken away from the wall. Cells are vertically elongated and measure 22–55 μm in diameter. A vertically oriented dehiscence slit extends across the distal surface and extends basally into the midregion of the indusium (Figs. 5 and 6, at arrows), and this reveals that the indusium opened into two valves. Each sorus has a basal vascularized receptacle (Figs. 2, 3, and 8) from which approximately 35 sporangial stalks radiate. Tracheids of the receptacle are barrel-shaped, 10–25 μm in diameter, and display scalariform secondary wall thickenings (Fig. 9).

Sporangia consist of a multiseriate stalk and a capsule with a vertical or slightly oblique annulus (Figs. 5, 7, 8, and 10). In cross section sporangial stalks are terete and consist of 5–6 cells (Fig. 7, at arrowheads). Sporangial capsules are 275–400 μm long and 200–300 μm wide. In cross section they are

oval in shape with the long axis of the oval corresponding to the plane of the annulus. Sporangial walls are one cell layer thick (Fig. 7). The annulus consists of a ring of approximately 20 cells interrupted on one side by a stomium of five or six cells (Fig. 10, at arrow). As is characteristic of cyatheaceous sporangia, the annulus is not interrupted by the stalk. Rather, it extends around the base of the capsule where it lies adjacent to the position of stalk attachment (Fig. 7, at arrow). Cross sections of the capsule that pass through the level of the stomium display only one cell of the annulus (Fig. 7, at 1), whereas sections that do not pass through the level of the stomium (i.e., are either proximal or distal to the stomium) show two cells of the annulus (Fig. 7, at 2).

Many sporangia are apparently senescent (Figs. 1–3) but others contain approximately 64 spores (Figs. 7 and 10). Spores are radial and trilete, with a relatively unornamented exospore and a continuous perispore (Figs. 7 and 10–14). Individual spores are roughly triangular, with concave interradian sides and rounded corners (Figs. 10, 13, and 14). Measurements of 107 spores range from 40 to 70 μm in diameter (mean = 53.5 μm). The trilete suture extends approximately 3/4 of the distance to the margin of the spore (Figs. 11 and 13) and is obscured by sculpturing of the perispore (Fig. 14, at right). The exospore is approximately 650 nm thick with a smooth to scabrate surface (Figs. 11 and 15). The perispore displays irregular granulae and coarse echinae that sometimes form slender rodlets (Figs. 14 and 16).

DISCUSSION

Cyathea cranhamii displays an informative combination of characters, including abaxially borne sori with globose indusia, annulate sporangia with multiseriate stalks and vertical annuli that are not interrupted by the stalk, and about 64 radial trilete spores, diagnostic of the Cyatheaceae (Kramer, 1990a). A similar combination of characters also occurs in the Dicksoniaceae and related genera (Tryon and Tryon, 1982), but sori of the latter are born at the margin of the pinnule (Kramer, 1990b). Also, the pinnule margin and the indusium, or an outer and inner indusium, typically form a marginal pocket or two-valved enclosure for each sorus (Tryon and Tryon, 1982; Kramer, 1990b) that is quite different from the globose indusium of *Cyathea cranhamii* and many other cyatheaceous ferns (Tryon and Feldman, 1975; Tryon and Tryon, 1982). Although compressed tree fern foliage of probable dicksoniaceae affinities occurs from the Middle Triassic onward (Skog, 2001) and permineralized dicksoniaceae/cyatheaceous stems have been described from Lower Cretaceous and Tertiary deposits, *C. cranhamii* represents the oldest unequivocal evidence of the genus *Cyathea*.

Systematic relationships among cyatheaceous ferns are the subject of ongoing discussion and debate. Although some authors have recognized as many as six genera in the family (i.e., *Alsophila* R. Brown, *Cnemidaria* Presl, *Cyathea*, *Nephelea* Tryon, *Sphaeropteris* Bernhardt, *Trichipteris* Presl) (Tryon, 1970; Tryon and Tryon, 1982; Tryon and Lugardon, 1990), others have recognized four (Lellinger, 1988), three (Domin, 1929, 1930), or only one (Holttum, 1963). Some authors place all the species within the single genus *Cyathea*, which is subdivided into subgenera and sections that correspond to some of the genera of other authors (Kramer, 1990a). Although recent molecular analyses by Conant and others (Conant et al., 1994, 1995, 1996; Conant and Stein, 2001) suggest that there

are five clades within the family, the morphological characters needed to assign *C. cranhamii* to one of these clades are not preserved in the fossils. Therefore, recognition of a single genus within the Cyatheaceae is the practice we are following in this paper.

Species of *Cyathea* have superficial sori and display a variety of indusial morphologies (Tryon and Feldman, 1975). Hemitelioid indusia only partly surround the base of the receptacle, whereas the other forms are radial, extending all the way around the receptacle. Among the latter, meniscoid indusia are discoid or saucer-shaped. Cyathiform indusia are somewhat deeper, forming a cup, whereas urceolate indusia envelop more than half of the sorus. The most complete indusia, the sphaeropteroid form including that of *C. cranhamii*, are more or less globose and completely envelop the sorus. Some sphaeropteroid indusia have a distal "umbo," whereas others have either a small irregular opening or a distal slit, such as that in *C. cranhamii*. Among those authors who recognize six genera of Cyatheaceae, sphaeropteroid indusia are produced by *Alsophila*, *Cyathea*, and *Sphaeropteris* (Tryon and Feldman, 1975). Therefore, this character appears to occur in several groups of cyatheaceous species and is not considered to be a systematically informative character (Kramer, 1990a).

Although there are some variations among the spores of cyatheaceous ferns, all are radial and trilete with a perispore that adheres tightly to the exospore. Large, prominent pits occur in the exospore of species assignable to the *Cyathea* clade (sensu Conant and Stein, 2001), but these structures are not present in *C. cranhamii*. Many species including *C. cranhamii* have a relatively smooth exospore surface with most of the sculpturing being produced by the perispore. The rodlets and irregular granulate/echinate sculpturing of the perispore of *C. cranhamii* is quite similar to that seen in several species of *Cyathea*, *Trichopteris*, and *Sphaeropteris*, including *T. costaricensis* (Kuhn) Barrington and *C. fulva* (Mart. & Gal.) Fée. (Tryon and Lugardon, 1990). Other species have a relatively thin and/or incomplete perispore, and most of the sculpturing is produced by the exospore.

Taxonomy among living cyatheaceous species relies heavily upon either characters of multicellular scales that occur on several organs of the plant (Tryon and Tryon, 1982), or molecular characters (Conant and Stein, 2001). Lack of preservation of scales on the pinnules and indusia of *C. cranhamii* makes determination of relationships to other species of the family difficult. At the present time, we do not know if this absence is due to the lack of production of such structures or to a lack of preservation. However, we suspect that the latter is most probable. Although *C. cranhamii* currently cannot be related to a particular living species or group of living species of Cyatheaceae, it does display all of the diagnostic characters found in modern species of the family. These include structure of the indusium, morphology and orientation of the sporangial annulus, number of spores per sporangium, and fine structure of the spore wall and perispore.

Cyathea cranhamii represents the first unequivocal evidence for the Cyatheaceae in Mesozoic deposits. It is also the first anatomically preserved cyatheaceous species from the fossil record to display characters of the fertile pinnules, sori, sporangia, and spores. This demonstrates that essentially modern species of *Cyathea* s.l. had evolved by Early Cretaceous time

and complements data from compression fossils and several permineralized species of stems that suggest that the tree fern clade consists of a dicksoniaceae grade from which the Cyatheaceae clade was derived (Lantz et al., 1999). There are additional, apparently dicksoniaceae, fern sori in the calcareous marine nodules from Apple Bay. These are currently under investigation for publication elsewhere. Together with *C. cranhamii* these hold great promise for improving our understanding of tree fern diversity in the Early Cretaceous and for clarifying both the sequence of character evolution and pattern of diversity among ancient representatives of the dicksoniaceae/cyatheaceous clade.

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