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ANATOMICALLY PRESERVED *WILLIAMSONIA* (WILLIAMSONIACEAE): EVIDENCE FOR BENNETTITALEAN REPRODUCTION IN THE LATE CRETACEOUS OF WESTERN NORTH AMERICA

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An anatomically preserved ovulate cycadeoid cone has been discovered in Upper Cretaceous (Campanian) sediments of Vancouver Island, British Columbia, Canada. The specimen is preserved by calcareous cellular permineralization and displays diagnostic features of the genus *Williamsonia* Carruthers. The cone consists of a receptacle from which tightly packed interseminal scales and ovulate sporophylls with terminal ovules diverge over an arc of ca. 300°. Adjacent interseminal scales interdigitate and form a continuous tissue. Seeds are erect and more or less round in cross sections at all levels, and a cupule is not produced. The sarcotesta consists of multicellular peglike projections. The nucellus is attached to the integument only at the chalaza and is vascularized by a shallow cup of tracheids. Apically, the nucellus narrows to a solid finger-like projection that fits tightly into the base of the micropylar canal. A pollen chamber is not produced. Nucellar cells are often separated from each other and are associated with large, hollow structures that represent pollen tubes similar to those in living conifers. Cellular megagametophytes and immature embryos are also preserved in some seeds. *Williamsonia bockii* sp. nov. represents the most recent seed cone of the Williamsoniaceae and is the first anatomically preserved reproductive structure of this family to be discovered in western North America. It reveals new features for the family Williamsoniaceae and allows for the interpretation of several additional facets of reproductive biology in the Bennettitales, particularly pollen tube production, pollination biology, and mode of fertilization.

Keywords: Bennettitales, Cretaceous, *Cycadeoidea*, pollen tubes, seed cones, *Williamsonia*.

Introduction

Bennettitalean seed plants formed a major component of Mesozoic vegetation worldwide and have been implicated in the origin of flowering plants for nearly a century (Arber and Parkin 1907; Crane 1985). Plants bore large frondlike leaves similar to those of cycads but produced seeds and pollen in flower-like cones and had syndetocheilic stomata like *Gnetum* L. and many flowering plants. Most bennettitalean genera are assigned either to the Cycadeoidaceae or Williamsoniaceae (Alvin et al. 1967) by characters of vegetative organs, cone position, and cone structure (Rothwell and Stockey 2002). Several species of the Cycadeoidaceae occur in both Jurassic and Cretaceous sediments, but representatives of the Williamsoniaceae are most common in the Jurassic (Sahni 1932; Harris 1932, 1969; Watson and Sincock 1992).

The Williamsoniaceae is well known from both compression and permineralized specimens of vegetative and fertile organs (Sharma 1977). Some genera of the Williamsoniaceae have bisporangiate cones (e.g., *Williamsoniella* Thomas/*Wielandiella* Nathorst; Watson and Sincock 1992), but others bear monosporangiate fructifications. The latter includes the plant *Williamsonia* Carruthers in which the seed cones are assigned to *Williamsonia*, and isolated pollen cones are described as species of *Weltrichia* Braun emend. Harris (Watson and Sincock 1992). Previously described permineralized *Williamsonia* seed cones have provided data about anatomy of the subtending bracts, sporophylls, and interseminal scales, features of the seeds and embryos, as well as information about overall cone structure (Delevoryas and Gould 1973; Sharma 1977).

Recent studies of permineralized fossil plants from Vancouver Island, British Columbia, Canada, have shown a diverse assemblage of Late Cretaceous vascular plants (Ludvigsen and Beard 1997; Rothwell and Stockey 2002; Smith and Stockey 2002). Among these remains are permineralized bennettitalean cones that were probably transported some distance before burial in marine sediments (Rothwell and Stockey 2002). Despite transport, permineralization with marine carbonates produces excellent anatomical preservation and facilitates study using closely spaced cellulose acetate peels. Therefore, this material displays several anatomical features that are not known from the previously studied silicified specimens.

The current investigation focuses on an isolated seed cone assignable to *Williamsonia* from the Brannen Lake locality on Vancouver Island that shows features of the cone receptacle, interseminal scales, seeds, megagametophytes, pollen tubes, and immature embryos. By comparison to diagnostic anatomical structures of living seed plants, this and other well-preserved cycadeoid cone specimens from Vancouver Island (Rothwell and Stockey 2002) help to clarify several facets of

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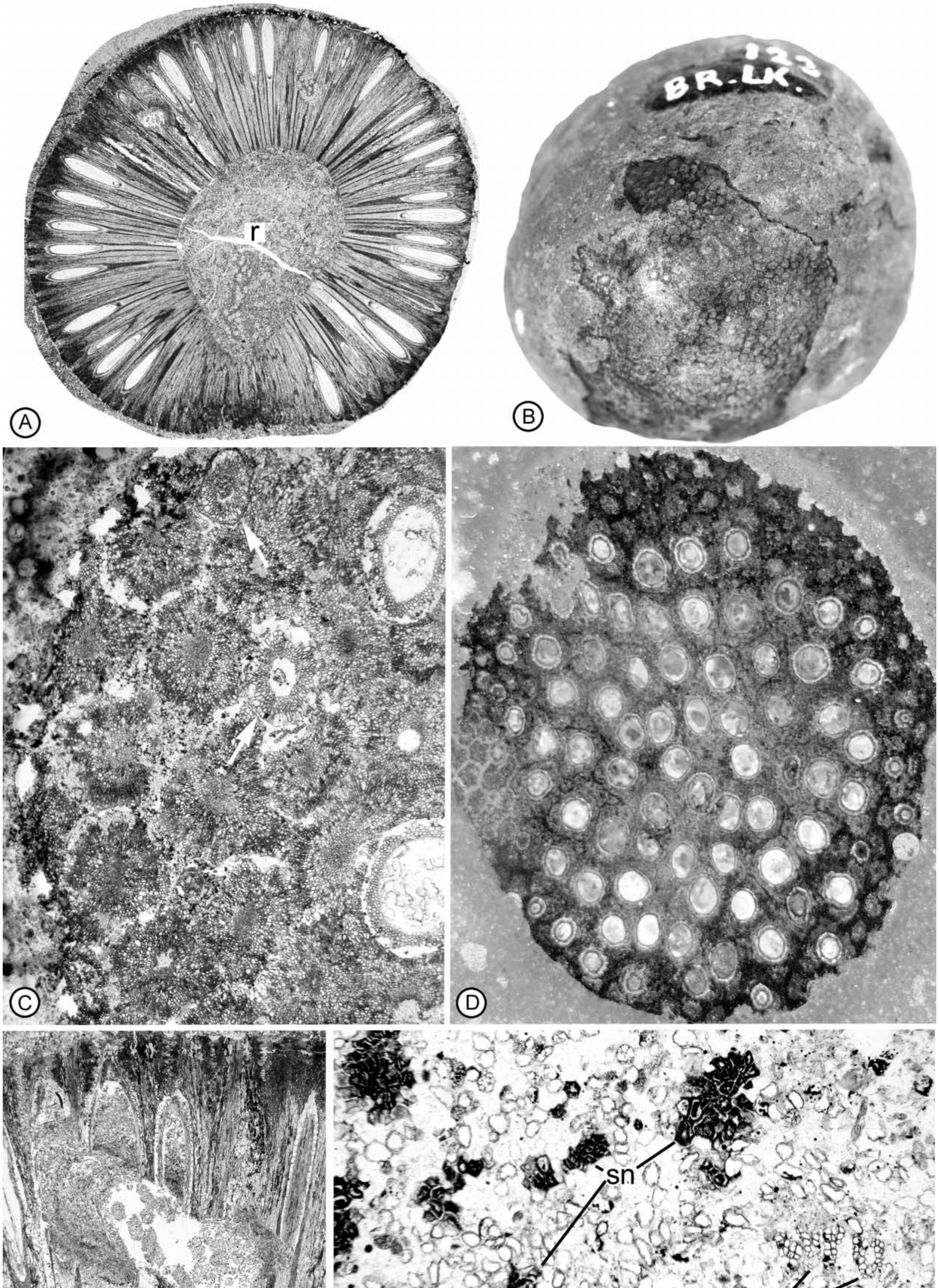
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integument structure, seed vascularization, and nucellus that appear to be common to species of the Bennettitales. The new *Williamsonia* cone reveals several previously unknown facets of pollination and postpollination biology for the Bennettitales, and this provides an opportunity to recognize common modes of pollination, postpollination sealing of the ovules, pollen tube growth, and embryogeny as potential synapomorphies for this order of Mesozoic seed plants. The Vancouver Island seed cone also differs from all previously described species of *Williamsonia* and therefore is described as *Williamsonia bockii* sp. nov.

Material and Methods

This study is based on an anatomically preserved, Late Cretaceous seed cone collected at the Brannen Lake fossil locality 3 km west of Nanaimo (49°12′16″N, 124°06′01″W; UTM coordinates 10U DK 198495) on Vancouver Island, British Columbia, Canada (Ludvigsen and Beard 1997; Rothwell and Stockey 2002). The single cone comes from the Moto-X Pit west of Brannen Lake. Sediments exposed at this locality are from the Haslam Formation of the Nanaimo Basin, now dated as Upper Cretaceous (early Campanian; Ludvigsen and Beard 1997) on the basis of the occurrence of the ammonite *Sphenoceramus schmidti* (J. Haggert, personal communication).

The cone was photographed and then 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 digital scanning cameras (i.e., Microlumina, Leaf Systems, Bedford, Mass.; PhotoPhase, Phase One A/S, Frederiksberg, Denmark) and processed with Adobe Photoshop. The three-dimensional architecture of the pollen tubes was reconstructed by tracing digital images of serial sections and then stacking the tracings. The specimen and peel preparations are housed in the Vancouver Island Paleontology Museum, Qualicum Beach, British Columbia, Canada.

Systematics

Order—Bennettitales Engler

Family—Williamsoniaceae Carruthers

*Genus—*Williamsonia *Carruthers*

*Species—*Williamsonia bockii *Stockey et Rothwell sp. nov.*

Specific diagnosis. Seed cone subspheroidal, at least 4.4 cm long, 4.3 cm wide without subtending bracts. Receptacle pyriform, 1.8 cm in diameter, with sclerotic nests and small vascular bundles in ground tissue; bearing sporophylls and interseminal scales around arc of 300°. Interseminal scales 12–15 mm long, 2.2 mm in diameter; polygonal outlines of scales forming interdigitating continuous tissue near cone surface; with terete vascular strand, lacking bundle sheath; four to five surrounding each ovule. Sporophylls 6 mm long, 1 mm in diameter, with terete vascular trace and single erect terminal ovule. Seeds ellipsoidal, 8 mm long, 1.7–2.0 mm wide; tapering to elongated micropylar canal; micropyle slightly protruding between scales; circular in cross section at all levels. Sclerotesta of several layers of randomly oriented cells, 32–42 μm in diameter, with simple pits. Sarcotesta formed by multicellular peglike projections. Nucellus attached to integument only at chalaza; forms micropylar plug of tissue; cup-shaped area of vascular tissue at chalaza. Pollen tubes occur between integument and nucellus, concentrated near micropyle, branched, 52–131 μm in diameter.

Holotype hic designatus. Cone specimen BL 123 from Brannen Lake, showing receptacle, interseminal scales, sporophylls, and seeds with megagametophytes, pollen tubes, and immature embryos, is here designated the holotype.

Stratigraphic position and age. Haslam Formation of the Nanaimo Basin (Brannen Lake), lower Campanian Stage of the Late Cretaceous.

Etymology. The epithet *bockii* is proposed for Peter Bock, Nanaimo, British Columbia, who collected and provided the specimen for study.

Description

The specimen of *Williamsonia bockii* consists of approximately one-half of an isolated cone partially embedded in a calcium carbonate nodule (fig. 1*A*, 1*B*). The surface that shows the inside of the cone reveals an oblique longitudinal orientation, with the base of the receptacle just out of view (fig. 1*A*). The external surface of the cone shows a pattern of polygonal interseminal scales (fig. 1*B*, 1*C*). Narrow, round tips of the seed micropyles are not immediately evident among the interseminal scales except in areas where the surface is eroded down to the level of the seed cavities (fig. 1*B*, 1*C*). The cone was apparently nearly spherical in life, and the preserved half is ca. 4.5 cm in diameter.

Interseminal scales and interspersed sporophylls radiate from a central receptacle around an arc of more than 300° (fig. 1*A*). Except at the base of the receptacle, where only interseminal scales are produced, sporophylls are dispersed over the entire surface of the receptacle (fig. 1*A*). There is a small number of galleries through the interseminal scale and seed tissues. These galleries contain coprolites of digested plant tissue (fig. 1*A*, 1*E*). The galleries measure ca. 2–3 mm in di-

Fig. 1 *Williamsonia bockii* sp. nov. Holotype. VIPM 123. *A*, Oblique longitudinal section of cone showing divergence of sporophylls and interseminal scales. Side 46, ×1.8. *B*, External surface of concretion showing somewhat eroded surface of cone with exposed interseminal scales and seeds, ×1.6. *C*, Paradermal section near surface of cone showing interseminal scales and seeds (arrows) in transverse section. Top 32, ×17. *D*, Tangential section of cone showing seeds in midlevel sections at center and more apical sections near periphery. Top 30, ×4.3. *E*, Longitudinal section of seeds and interseminal scales showing herbivore gallery partially filled with coprolites. Side 81, ×6.5. *F*, Transverse section of cone axis showing small vascular strands (*v*) and sclerotic nests (*sn*) embedded in incompletely preserved ground parenchyma. Side 61, ×40.

ameter, with coprolites 0.5 mm that probably represent those of orbatid mites (C. Labandiera, personal communication).

The receptacle is circular in cross section, measuring 1.8 cm in diameter. Tissue is preserved in only a part of the receptacular region, where it consists of small vascular bundles immersed in loosely arranged ground tissue (fig. 1*F*). Most of the cells of the ground tissue have prominent walls and empty lumens and are separated by spaces that may be taphonomic in origin (fig. 1*F*). Numerous clusters of cells with dark contents occur scattered in the receptacle and appear to be sclerotic nests (fig. 1*F*). The vascular bundles are represented by a small number of radial files of tracheids (fig. 1*F*). The tracheids are angular and measure 15–31 μm in diameter.

The interseminal scales are up to 1.5 cm long and 2.2 mm in diameter at the widest point (at the periphery of the cone). In tangential sections near the surface of the cone, the interseminal scales are polygonal in outline and separated from each other by the carbonate sediment (fig. 1*C*, 1*D*). At more proximal levels, the peripheral cells of adjacent sporophylls interdigitate, forming a continuous tissue (fig. 2*A*, 2*B*). Each scale has a centrally located terete vascular bundle consisting of several tracheids surrounded by a hollow that probably represents unpreserved phloem (fig. 2*C*). Ground tissues of the scale are light colored and show prominent walls except at the periphery, where they form a dark band (figs. 2*A*–2*C*, 3*A*). The dark band is one to three cell layers thick between adjacent interseminal scales and three to five layers thick where the interseminal scale abuts a sporophyll (fig. 2*C*). Near the base of the sporophylls, the dark cells are relatively isodiametric in cross section, but distally they become radially elongated (fig. 2*A*, 2*B*). Except at the periphery of the cone, where the interseminal scales are separated from one another, there is no distinct margin between adjacent scales and no evidence of a cuticle between scales (fig. 2*A*–2*C*). Instead, the interdigitating cells of adjacent interseminal scales form a continuous tissue that completely surrounds the sporophylls with their terminal seeds (figs. 1*D*, 2*A*, 3*B*–3*D*). Cortical cells of the interseminal scales are longitudinally elongated up to the level where the seeds begin to taper toward the micropylar canal (fig. 3*A*). Distally, the cortical cells intergrade with isodiametric, thick-walled sclereids (fig. 3*A*–3*C*, 4*A*).

Sporophylls are more or less straight with a single erect terminal seed (figs. 1*A*, 3*A*). They are 6 mm long from the surface of the receptacle to the base of the seeds. In cross section, sporophylls are up to 1 mm in diameter and can be distinguished from interseminal scales primarily by the thicker zone of dark cells that surrounds each sporophyll (fig. 2*C*). Like the interseminal scales, these sporophylls have a small

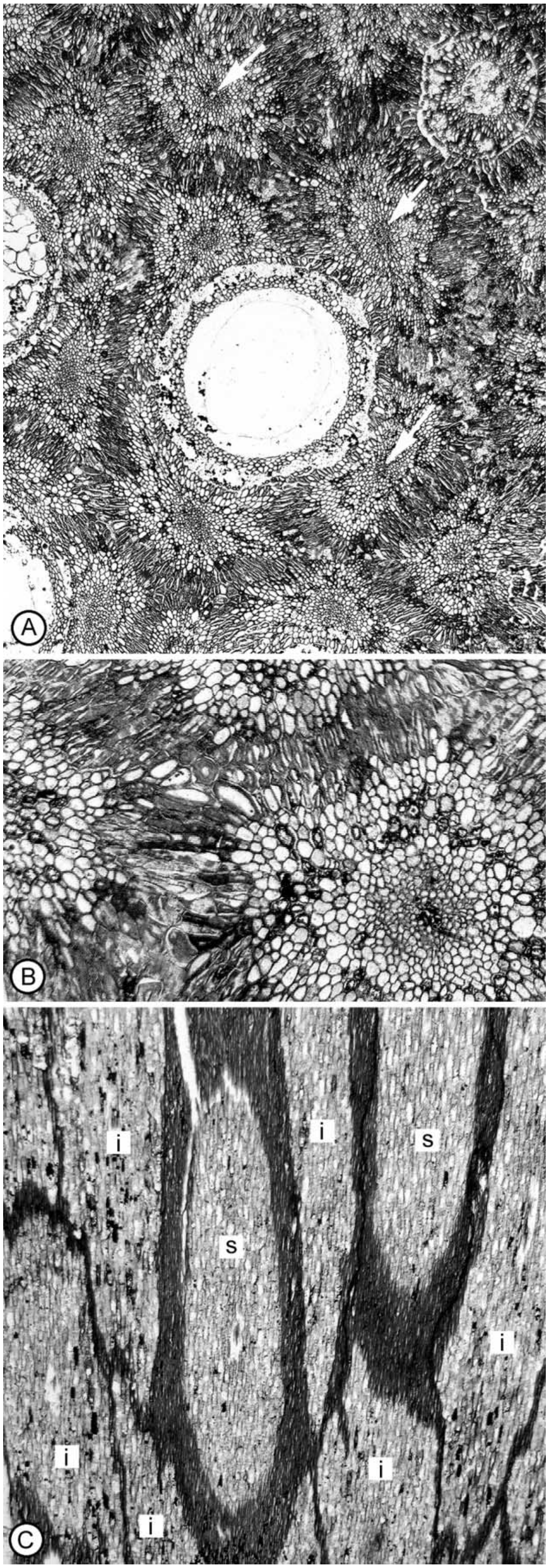


Fig. 2 *Williamsonia bockii* sp. nov. Holotype. VIPM 123. *A*, Transverse section of interseminal scales and seed at midlevel showing radial symmetry of seed, and interseminal scales that form continuous tissue. Arrows indicate vascular bundles. Top 25, × 20. *B*, Enlargement of interseminal scale tissue showing interfingering radially elongate peripheral cells that form a continuous tissue. Top 32, × 55. *C*, Oblique section near base of sporophylls (*s*) and interseminal scales (*i*). Note that dark tissue between interseminal scales is thin; tissue between interseminal scale and sporophyll is thick. Top 6, × 30.

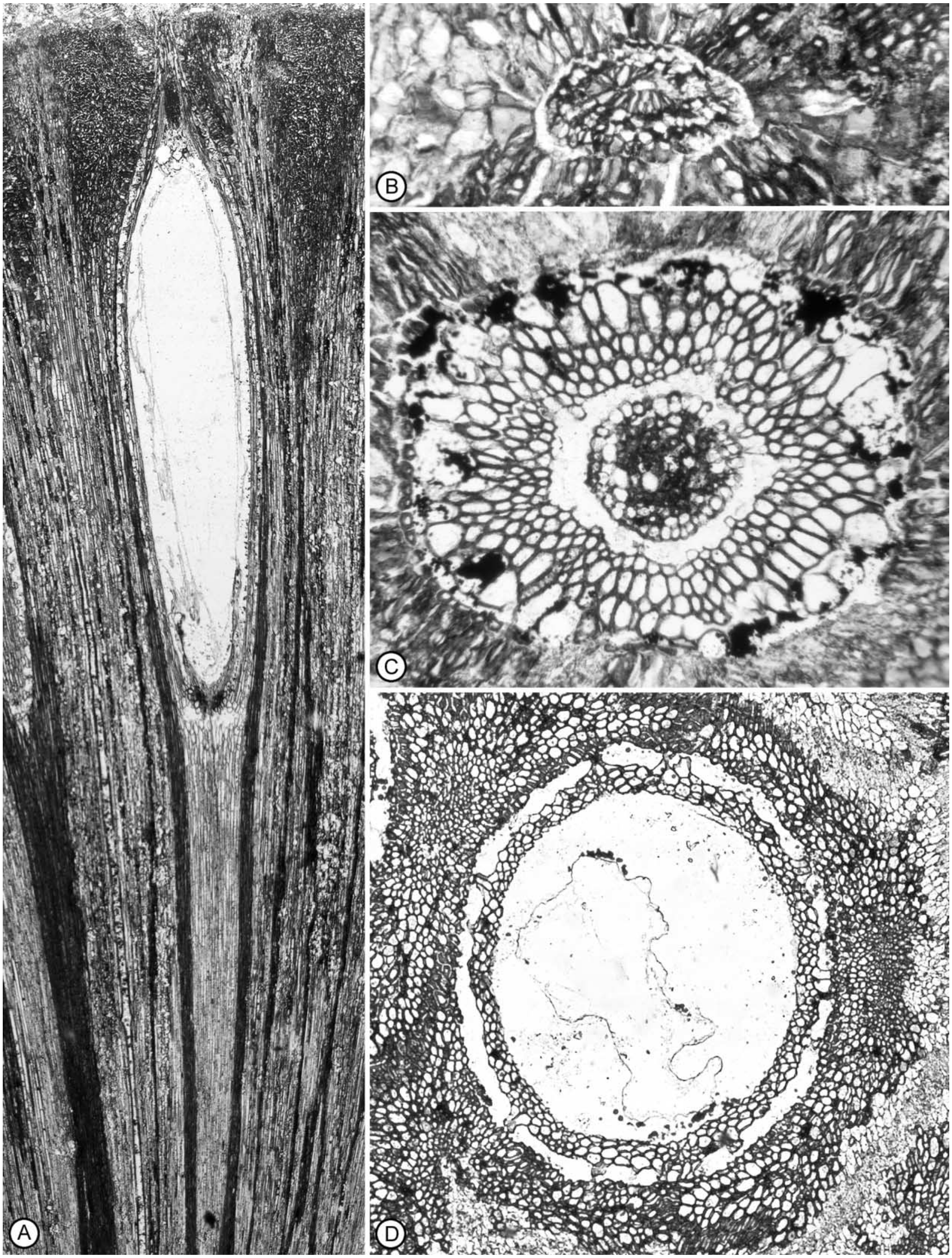
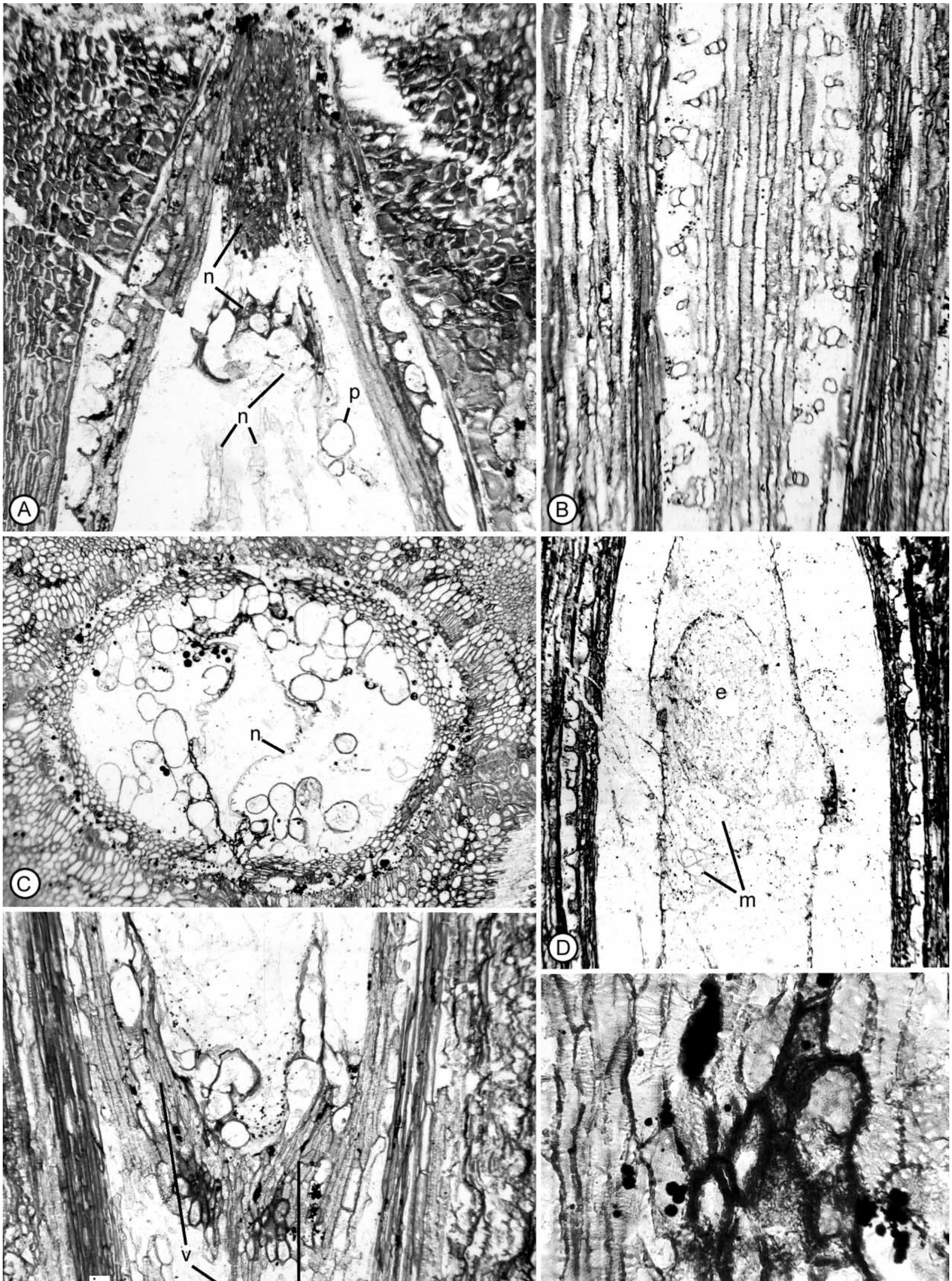


Fig. 3 *Williamsonia bockii* sp. nov. Holotype. VIPM 123. *A*, Longitudinal section of sporophyll with terminal seed, surrounded by interseminal scales. Side 68, × 14.4. *B*, Transverse section near tip of micropylar tube showing small micropylar opening. Top 12, × 117. *C*, Transverse section near base of micropylar tube showing solid nucellar tip (nucellar plug). Top 5, × 121. *D*, Transverse section of seed at midlevel showing sarcotestal pegs and wavy nucellus. Top 30, × 54.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centrally located bundle of tracheids surrounded by a narrow hollow zone (fig. 2*C*). Ground tissue of the sporophyll is similar to the light-colored cortical cells at proximal levels of the interseminal scales (figs. 2*C*, 3*A*).

Seeds are ellipsoidal, up to 8 mm long and 2 mm wide, with a rounded base. Distally, they taper to an elongated micropylar canal (figs. 1*A*, 3*A*, 4*A*; fig. 5*A*, 5*B*). In cross section, the seeds are nearly circular from the base of the seed to the tip of the micropylar canal (fig. 1*C*, 1*D*; figs. 2*A*, 3*B*–3*D*). There are no radiating ribs near the micropyle like those that characterize the genus *Cycadeoidea* Buckland (Rothwell and Stockey 2002). The sclerotesta consists of several layers of thick-walled cells that are 32–42 μm in diameter and randomly arranged in cross sections (figs. 2*A*, 3*D*). In longitudinal sections, these cells are elongated (fig. 4*A*, 4*B*) and display prominent irregularly arranged simple pits (fig. 4*B*, 4*D*). To the inside of the sclerotesta, in some areas, there is a thin line that represents poorly preserved cells of the endotesta (fig. 3*D*). Cells of the sarcotesta have slightly thinner walls than those of the sclerotesta. They form multicellular peglike projections that radiate into the space between the seed and the surrounding interseminal scales (fig. 3*D*; fig. 4*A*, 4*B*, 4*D*).

The nucellus is attached to the integument at the chalazal end of the seed (figs. 3*A*, 4*D*) and is free distally (fig. 3*A*, 3*C*, 3*D*; figs. 4*D*, 5*A*). At the micropylar end, the nucellus narrows and forms a solid plug of tissue that fills the micropylar canal (fig. 3*A*, 3*C*; figs. 4*A*, 5*A*). No pollen chamber is produced. In many seeds, cells of the nucellus cannot be identified to the outside of the megaspore membrane at the level of the seed cavity (fig. 3*D*), but in others, one to four layers of loosely arranged thin-walled cells are preserved. In longitudinal sections at this level, cells of the nucellus are rectangular and longitudinally disposed (figs. 3*A*, 4*B*), measuring 13–39 μm (mean = 28.9 μm). The apical plug consists of tightly packed cells with prominent walls and dark internal contents (fig. 3*C*). In cross sections, the plug shows a distinct epidermis of cells that lack internal contents (fig. 3*C*). Cells toward the base of the plug are larger and often less completely preserved than those within the micropylar canal (fig. 4*A*).

A terete strand of tracheids enters the base of the seed from the sporophyll and expands into a shallow cup at the base of the nucellus (fig. 4*E*). Wall-thickening patterns of the tracheids are scalariform/reticulate (fig. 4*F*, at left). As in *Cycadeoidea* (Rothwell and Stockey 2002), this is the only vascular tissue in the seed, the integument being unvascularized.

The megagametophyte of most seeds is represented only by a megaspore membrane and the hollow that it surrounds (fig. 2*A*; fig. 3*A*, 3*D*), but in some specimens remnants of golden material, including evidence of large thin-walled megagametophyte cells, are preserved (fig. 4*D*, at *m*). A few specimens show two types of cells in this region. In addition to the megagametophyte tissue, there is an ellipsoidal area near one side in the distal third of the seed cavity with smaller cells that represent undifferentiated embryo tissue (fig. 4*D*, at *e*).

Both longitudinal and transverse sections of several specimens show a large number of prominent round or oval structures that occur in the space between the integument and nucellus and within the nucellus (fig. 4*A*, 4*C*; fig. 5*A*). These oval structures measure 52–131 μm in diameter. They are most common in the apical region where they are often crowded (fig. 4*B*), but some extend to the base of the seed cavity (figs. 4*E*, 5*A*). Serial sections reveal that the structures are continuous over some distance and are therefore tubelike. A seed sectioned in longitudinal view shows this continuity. Tracings were made of peels 32–75, and these were superimposed on an outline of the integument and nucellus from peel 43 of this sequence (fig. 5*A*). Figure 5*B* consists of tracings from nine consecutive sections showing continuity of these structures from level to level. When tracings of more sections are added, the continuity of the tubes is further demonstrated, but morphology of the tubes is obscured by the overlapping ovals. Tubes are most common from the base of the micropylar canal (figs. 4*A*, 5*A*) through the midregion (fig. 5*C*), and a few extend to the base of the seed cavity (fig. 5*E*).

Discussion

Nearly all dispersed specimens of anatomically preserved bennettitalean seed cones are thought to represent species of plants assignable to either Cycadeoidaceae (i.e., species of *Cycadeoidea* and *Monanthesia*; Wieland 1906, 1916; Delevoryas 1959) or Williamsoniaceae (i.e., species of *Williamsonia*; Seward 1912; Sahni 1932; Delevoryas and Gould 1973; Sharma 1977). However, specific criteria used in making generic determinations have not been specified in most previous studies. One permineralized cone that could not be correlated with a genus and family of plants has been assigned the morphogenus *Bennetticarpus* Harris (Ohana et al. 1998), along with compression remains (Harris 1969), and the compressed Triassic seed cone *Vardekloeftia* Harris has not been assigned to a family (Pederson et al. 1989). In an attempt to further clarify the relationships of isolated bennettitalean seed cones, a contrasting set of diagnostic characters has recently been developed for relatively complete permineralized specimens, and these provide criteria for distinguishing *Williamsonia* (Williamsoniaceae) from *Cycadeoidea* or *Monanthesia* (Cycadeoidaceae; Rothwell and Stockey 2002).

By virtue of having interseminal scales and sporophylls that diverge around an arc of ca. 300°, seeds that are circular in cross sections at all levels, and sarcotestal cells that form small,

Fig. 4 *Williamsonia bockii* sp. nov. Holotype. VIPM 123. *A*, Longitudinal section of seed apex showing sclerotic tissue of surrounding interseminal scales, nucellar plug, and pollen tubes. Side 60, × 62. *B*, Tangential section of seed showing elongated sclerotestal cells (center) and multicellular sarcotestal pegs. Side 60, × 45. *C*, Transverse section of seed near micropylar end showing abundant pollen tubes between nucellus and integument. Top 32, × 58. *D*, Longitudinal section of seed showing immature embryo (*e*) within megagametophyte (*m*). Side 39, × 35. *E*, Longitudinal section of chalazal end of seed showing vascularized nucellus that is attached to integument only at base. Side 37, × 62. *F*, Enlargement of nucellar vascular tissue in *E* showing scalariform/reticulate pitting of tracheids (left) and simple pitting of ground tissue (right). Side 37, × 290. Abbreviations: *is* = interseminal scale, *n* = nucellus, *p* = pollen tube, *v* = vascular tissue.

Fig. 5 *Williamsonia bockii* sp. nov. Holotype. VIPM 123. Longitudinal sections of one seed reconstructing morphology of pollen tubes from serial sections. *A*, Midlongitudinal section of seed showing relative positions of integument, nucellus, and pollen tubes in one section. Side 43, × 19. *B*, Tracing of integument and nucellus from section in figure 5*A* (in black), with tracings of pollen tubes from nine consecutive sections (in red), × 19.

horizontally elongated pegs, the cone described in this study is clearly assignable to *Williamsonia* of the Williamsoniaceae. Contrasting characters of *Cycadeoidea* and *Monanthesia* (Cycadeoidaceae) include interseminal scales and sporophylls that diverge parallel to each other, seeds that are distinctly stellate at the base of the micropylar canal, and sarcotesta made up of axially elongated tubelike cells (table 1 of Rothwell and Stockey 2002). Late Cretaceous *Williamsonia bockii* is by far the geologically youngest species of permineralized Williamsoniaceae thus far described (table 1); the other species of seed cones are all from Jurassic strata (table 1). *Williamsonia bockii* is also the only species of the genus to display interdigitating cells of adjacent interseminal scales that form a continuous tissue (table 1). This latter feature results in a unique fusion of adjacent interseminal scales that has not been reported previously for bennettitalean cones.

Like *Williamsonia bucklandii* (Unger) Saporta and *Williamsonia diquiyui* Delevoryas and Gould, *W. bockii* is an isolated specimen, so its position on the plant is unknown. However, the other species of *Williamsonia* seed cones either have elongated receptacles or are known to terminate branches (Sahni 1932; table 1). Bracts are absent from the *W. bockii* cone (fig. 1*A*, 1*B*; table 1). This is probably because the bracts abscised as interpreted by Sharma (1970*b*) for *Williamsonia* cones. Alternatively, the bracts could have been lost while *W. bockii* was transported into the marine environment before deposition. Like *Williamsonia gigas* Carruthers, *W. bockii* has a pyriform receptacle, and this contrasts with the conical, hemispherical, or dome-shaped receptacles of the other known species (table 1). Whereas *W. gigas* and *W. diquiyui* produce only interseminal scales at the cone apex, *W. bockii*, *W. bucklandii*, *Williamsonia scotica* Seward, *Williamsonia sewardiana* Sahni, and *Williamsonia harrisiana* Bose have sporophylls in this region (table 1). Interseminal scales in *W. bockii* are longer than those of most *Williamsonia* species, and they lack a bundle sheath like that preserved in *W. diquiyui* (table 1). The number of interseminal scales surrounding the seeds of *W. bockii* (i.e., four to five) is the smallest known for *Williamsonia* species; either the other species have ranges that overlap with *W. bockii* or the numbers are consistently larger (table 1).

The relative lengths of interseminal scales and sporophylls vary from species to species in the genus *Williamsonia*, such that the seed micropyles protrude from the cones of some species, are flush with the tips of the interseminal scales in other species, and are sunken below the tips of the interseminal scales in still others (table 1). Like *W. bucklandii*, *W. bockii* has slightly protruding seed micropyles. This character may reflect structural differences among the species, but it could also be related to pollination biology or to the developmental stage at which some cones were preserved (e.g., *W. scotica* appears to be either an immature or abortive cone; Seward 1912).

Structure of the Nucellus

The nucellus of *W. bockii* and other bennettitalean species for which such features are known is attached to the integument only at the base of the ovule and is vascularized by a shallow cup of tracheids at the chalaza. In the micropylar region, the nucellus tapers to a narrow plug of solid tissue that extends into the micropylar canal. Such nucellar plugs have been figured and/or reported in virtually all species of bennettitalean cones for which such data are available. However, this feature has not been widely recognized as characterizing the clade, and the nucellus has been interpreted differently for *Williamsonia*, *Bennetticarpus yezoites* Ohana, Kimura and Chitaley, and *Vardekloeftia* (Sharma 1976; Pedersen et al. 1989; Ohana et al. 1998; see also Rothwell and Stockey 2002). Contrary to the interpretations by Sharma (1976) and Ohana et al. (1998) for *Williamsonia* sp. and *B. yezoites*, respectively, there is no evidence for a pollen chamber in either taxon. Rather, photographs and drawings of these two previously

Table 1

Comparison of Permineralized *Williamsonia* Carruthers emend. Harris Cones

	W. bockii sp. nov.	*W. bucklandii* (Unger) Saporta	*W. gigas* Carruthers	*W. scotica*	*W. sewardiana*	*W. harrisiana*	*W. diquiyui*
Source		Buckland 1836; Seward 1917; Harris 1969	Lignier 1903	Seward 1912	Sahni 1932	Bose 1968	Delevoryas and Gould 1973
Geographical source	Brannen Lake, Vancouver Island, British Columbia	Charmouth Dorset, England	France	Southerland, England	Rajmahal Hills, India	Rajmahal Hills, India	Oaxaca, Mexico
Stratigraphy and age	Cretaceous	Jurassic	Jurassic	Jurassic	Jurassic	Jurassic	Jurassic
Position on plant	?, isolated specimen	?, isolated specimen	Among bracts at branch apex	Among bracts at apex of slender branching shoot	Among bracts at apex of slender branch	Among bracts at apex of slender branch	?, isolated specimen
Elongated peduncle	?	?	Yes?	Yes	Yes	Yes	?
Cone shape (without bracts)	Subspheroidal	Ovoid-oblate spheroidal with bluntly pointed apex	Pyriform	?	Broadly ovoid	Broadly ovoid-oblate spheroidal	Broadly ovoid
Cone size, L × W (mm)	44 × 43	30 × 38[a]	Ca. 70 × 50	10+ × 12	15 × 15	30–38 × 28–36	23 × 34
Subtending bracts	?	Present	Present	Present	Present	Present	Present
Peduncle diameter (mm)	?	?	Ca. 15	Ca. 7	Ca. 20	8–9	9
Receptacle	Pyriform		Pyriform	Conical	Hemispherical	Dome shaped	Conical
Ovules at apex	Yes	Yes	No	Yes?	Yes	Yes	No
Interseminal scales:							
L × W (mm)	12–15 × 2.2	?	8–12 × 0.5–0.7	2/0.2	1.5–3.0 × 0.9	7–10 × 0.9–1.2	6–10 × 0.5–1.0
Fused at apex	Yes	?	No?	No	No?	No?	?
Bundle sheath	No	?	?	No	No?		Yes?
No. around seeds	4–5	4–6	?	5–6	Usually 5–6	5–7	Usually 6
Seed:							
Micropyle	Slightly protruding	Slightly protruding	Flush, slightly sunken	Flush with apex of interseminal scales	Slightly sunken	Protruding	Protruding
Near apex in X.S.	Round	Angular-stellate[b]	?	Round	Round	Round	Round
L × W (mm)	8 × 1.7–2	7.5 × 2	Ca. 1 × 0.5	1.8 × 0.25	2.6 × 0.3	8 × 1.5–2.0	6.0–7.5 × 1.0–1.3
Sarcotestal cells	Short pegs	?	?	Short pegs	?	?	?

Note. L = length, W = width.

[a] *Williamsonia bucklandi* is described as being 30 × 38 mm (Buckland 1836), but measurements of the specimen as figured by Wieland (1906) and Seward (1917) are 80 × 96 mm. We suspect that the magnification is incorrect in Wieland and Seward.

[b] This species is based on one specimen, originally described by Buckland (1836). It is apparently well preserved, but many characters are not known. It is badly in need of reinvestigation, and Seward (1917) suggests that it could be a *Cycadeoidea* cone. The stellate shape of the seeds supports this interpretation. If reinvestigation reveals that the seeds also display tubular sarcotestal cells, this will confirm Seward's supposition.

described taxa clearly show a solid nucellar plug in both *Williamsonia* sp. (i.e., plate 2, fig. 4 of Sharma 1976) and *B. yezoites* (i.e., figs. 2.4, 2.5, 3.1 of Ohana et al. 1998) that is comparable to that of *W. bockii* and other permineralized bennettitalean seeds (e.g., *Cycadeoidea maccafferyi*; Rothwell and Stockey 2002).

The apical region of the nucellus is more difficult to interpret from the compressed cuticular remains of *Vardekloeftia sulcata* Harris. Pederson et al. (1989) illustrate carefully prepared macerations of *V. sulcata* that show several distinct layers of cuticular envelopes that are interpreted by those authors to represent nucellus, integument, and cupule (fig. 2 of Pederson et al. 1989). By comparison to other gymnospermous seeds that typically display a pollen chamber, this interpretation is quite reasonable. However, by comparison to permineralized bennettitalean seeds that lack a pollen chamber, an alternative interpretation now appears to be more probable (Rothwell and Stockey 2002). The more recent interpretation regards the cuticular envelopes of *V. sulcata* as representing a nucellar plug surrounded by integumentary cuticles (Rothwell and Stockey 2002). Photographs of *V. sulcata* cuticles (i.e., plate III, 6; plate V, 3; plate V, 4 of Pederson et al. 1989) clearly show a centrally located, solid-appearing, elongated structure that is structurally indistinguishable from the nucellar plug of permineralized bennettitalean seeds (Crepet and Delevoryas 1972; Rothwell and Stockey 2002; fig. 3*A*, 3*C*; fig. 4*A*), thus suggesting that an apical nucellar plug may be a synapomorphy for Bennettitales.

Pollen Tubes

The circular to oval structures that occur in peel sections of several *W. bockii* seeds (figs. 4*A*–4*C*, 5*A*) are essentially identical to anatomical sections of pollen tubes produced by both living and fossil araucarian conifers (Eames 1913; Stockey et al. 1994; Owens et al. 1995*a*, 1995*b*). In the araucarians, pollen tube growth is invasive, extending both through the tissues of the nucellus and between the nucellus and integument (Thomson 1907; Eames 1913; Haines 1981; Owens et al. 1995*a*, 1995*b*). This corresponds precisely with the positions and sizes of the structures in *W. bockii* (figs. 3*A*, 4*A*–4*C*, 5*A*). In addition, the tubelike nature of the structures in *W. bockii* has been confirmed from serial sections of peels (e.g., fig. 5*B*), revealing an overall form and disposition within the seeds that are comparable to the pollen tubes of the living araucarians (Eames 1913; Owens et al. 1995*a*, 1995*b*).

While the preservation of pollen tubes in fossil seeds or ovules is rare, two previous examples have been documented. These include the Paleozoic seed fern *Callistophyton* (i.e., in an ovule of *Callospermarion* Eggert and Delevoryas; Rothwell 1972) and the Jurassic conifer *Araucaria nipponensis* (Stockey et al. 1994), thus demonstrating the potential for similar preservation in *W. bockii*. While one might suspect that the structures in W. *bockii* are either remnants of the nucellus or fungal hyphae, these alternatives are far less probable. The size of the tubes in *W. bockii* is similar to the comparable structures in the living araucarians (i.e., 50–120 μm in *W. bockii*; Eames 1913; Owens et al. 1995*a*, 1995*b*) and much larger than known for fungal hyphae. Also, there is no evidence of fungi elsewhere in the cone. The possibility that the structures in *W. bockii* represent some form of nucellar proliferation as seen in extant *Araucaria angustifolia* (Burlingame 1914) and fossil *Araucaria mirabilis* (Stockey 1978) also has been considered. Such nucellar proliferation is known to occur in aborted ovules and consists of a dense tissue of small cells rather than the large tubes found in *W. bockii*.

Pollination and Fertilization Biology

Both outcrossing via wind pollination and self-pollination by an insect vector (possibly a beetle) have been proposed for members of the Cycadeoidaceae (Delevoryas 1968; Crepet 1972, 1974), but the position of the grains following pollination, postpollination microgametophyte development, and mode of fertilization have not been addressed for species of the Bennettitales. Pollination in *Williamsonia* may have been by wind, since the cones that have been found attached occur on slender branches without tightly adhering microsporangiate structures. Moreover, bracts that surround the cones at early stages of development were apparently abscised during cone development (Sharma 1970*b*). This contrasts with the axillary reproductive structures of *Monanthesia* or *Cycadeoidea*, many of which are known to be deeply embedded among the leaf bases near the trunk of the plant (Wieland 1906). Some cones of the Cycadeoidaceae also have seeds that are tightly enclosed by both microsporangiate structures and bracts (Delevoryas 1968), and this has led Crepet (1972, 1974) to hypothesize that such species may have been pollinated by insects.

The absence of microsporangiate structures from *Williamsonia* seed cones bolsters hypotheses of outcrossing and supports suggestions of wind pollination for the genus. Seward (1912) describes a slightly funnel-shaped apex to the micropylar region of the seed in *W. scotica*, where the micropyle is flush with the interseminal scales (table 1). Sahni (1932) reports a similar seed apex in *W. sewardiana* where the micropyle is slightly sunken. Both of these morphologies are consistent with outcrossing by wind pollination. We have been unable to see a funnel-shaped apex in *W. bockii* in which the micropylar ends of seeds are slightly protruding, but this cone may have undergone some abrasion before deposition. Although *W. bockii* does have coprolite-filled galleries somewhat similar to those of cones in which insect pollination has been hypothesized for *Cycadeoidea* (Crepet 1972, 1974), the galleries in *W. bockii* are located in positions that are more indicative of destructive herbivory than pollination biology (i.e., through the sporophylls and the basal region of the seeds; fig. 1*E*).

Pollen grains are almost always absent from the interior of Bennettitalean seeds, even when embryos are present (Wieland 1906; Rothwell and Stockey 2002). However, grains do occur in a Middle Jurassic specimen of *Williamsonia* sp. that was probably immature (Sharma 1977). This pollen is preserved in the most apical sections of the micropylar canal, distal to the apex of the nucellar plug. At this level, elongated epidermal cells line the micropylar tube, suggesting to us that they had a secretory function. Grains also occur within seed cuticles of *V. sulcata* (Pedersen et al. 1989). They are located between what we interpret to be the nucellar plug and the inner integumentary cuticle (i.e., plate V of Pedersen et al. 1989; Rothwell and Stockey 2002). However, whether these grains have filtered down between the integument and nucellar plug during fossilization and/or preparation (as interpreted by us) or were located within a pollen chamber (as interpreted by Pederson et al. 1989) cannot be determined from available specimens. New preparations of *Vardekloeftia* seed cuticles may help clarify this point.

As stressed above, pollen grains have not been reported in the seed cavities of most bennettitaleans. This correlates well with the lack of a pollen chamber from bennettitalean ovules but does not explain the mode of fertilization biology in this clade. However, the numerous pollen tubes that extend from the base of the micropylar plug to the chalaza of several *W. bockii* seeds may provide new insights into bennettitalean microgametophyte development and fertilization biology. The pollen tubes in *W. bockii* are virtually identical to those of living *Agathis australis* and other araucarian conifers in morphology, size, and distribution within the seed cavity (fig. 5; Eames 1913; Stockey et al. 1994; Owens et al. 1995*a*, 1995*b*). In both the Araucariaceae and *W. bockii*, pollen tubes occur between the integument and nucellus and within the nucellus from the base of the micropylar canal to the chalaza, but they are most numerous at the micropylar end of the ovules (figs. 5–9, 10 of Eames 1913; fig. 29 of Owens et al. 1995*a*; fig. 6 of Owens et al. 1995*b*). In araucarian conifers, this distinctive pollen tube structure is correlated with a unique pollination mechanism in which there is no pollen chamber, and the pollen grains do not enter the seed cavity (Berg 1950). Instead, the pollen grains land on the cone scale, and pollen tubes grow into the seed cavity through nucellar tissue that extends out of the micropyle.

Bennettitalean seeds are not borne on cone scales and do not have the tip of the nucellus that extends outside the micropyle. However, the combination of pollination that places grains distal to the nucellar plug in the micropylar canal of one species of *Williamsonia* (Sharma 1970*a*) and pollen tubes with distinctly araucarian morphology in *W. bockii* suggests that pollination brought grains into only the distalmost part of the micropylar canal in most Bennettitalean ovules. If pollination of this type were followed by pollen tube growth past the nucellar plug and into the seed cavity, this would account both for the paucity of grains found within seed cavities of Bennettitalean seeds and for the distinctive pollen tube morphology that is identical for araucarian conifers and *W. bockii*. As in most living gymnospermous species, the pollen tube of *W. bockii* probably developed within the seed cavity for some time before fertilization took place. Growth of the megagametophyte and embryo probably pressed the nucellar plug tightly into the micropylar tube after the tube had grown into the ovule, thus achieving postpollination sealing of the pollen chamber and explaining the absence of pollen grains in the seed cavity of most species.

Among living seed plants, pollen tube structure of araucarian conifers is extremely distinctive and is diagnostic of microgametophytes that produce a haustorial pollen tube that grows extensively before facilitating siphonogamous fertilization (Eames 1913; Owens et al. 1995*a*, 1995*b*, 1997). If form/function relationships are comparable in the living araucarian conifers and *W. bockii*, then at least one species of Bennettitales had siphonogamous pollination from highly branched microgametophytes with pollen tubes that also had a haustorial function. The absence of a pollen chamber and the paucity of pollen grains from bennettitalean seeds (as interpreted by us) indicates that such a pollination/fertilization mechanism may characterize reproduction in Bennettitales as a whole. If, however, *Vardekloeftia* had a pollen chamber (as interpreted by Pedersen et al. 1989), then the distinctive pollination biology of Cycadeoidaceae and Williamsoniaceae may have evolved within the benettitalean clade.

The preservation of megagametophyte and embryo tissues is relatively common in the seeds of *Williamsonia* and other genera of permineralized bennettitaleans, where dicotyledonary embryos with fully developed and apparently quiescent embryos are commonly present (Lignier 1894; Seward 1917; Sharma 1977; Rothwell and Stockey 2002). By contrast, the small, undifferentiated embryos of *W. bockii* suggest that preservation occurred closer to the time of pollination than to seed dispersal, and this accounts for the well-preserved pollen tubes in this cone.

Summary of Bennettitalean Reproduction

If the absence of a pollen chamber, the presence of a solid nucellar plug, highly branched pollen tubes, and siphonogamous fertilization are characteristic of Bennettitales as a whole, then these features can be added to the large body of data about seed development, pollen, pollination, megagametophytes, postpollination sealing of the seeds, and embryos that has accumulated over the past 175 yr (e.g., Carruthers 1870; Lignier 1894; Seward 1917; Crepet and Delevoryas 1972; Taylor 1973; Crepet 1974; Rothwell and Stockey 2002) to provide the most complete understanding of reproductive biology yet achieved for an extinct clade of seed plants. As with living plants, bennettitaleans underwent meiosis to produce a linear tetrad when the ovules were extremely small, and the tip of the nucellus was a solid mound of tissue (Crepet and Delevoryas 1972).

Some bennettitalean species were apparently inbreeding, with bisporangiate cones and pollination effected by an insect vector. Others, including *W. bockii*, had monosporangiate cones and appear to have been outcrossing and wind pollinated. In some species, pollination was apparently aided by micropyles that protruded beyond the tips of the interseminal scales, and in one species, the pollinated ovules were retracted between the interseminal scales by a contractile mechanism similar to that of some roots (Rothwell and Stockey 2002). Pollination placed the microgametophytes into the tip of the micropylar canal, and the pollen tubes grew into the seed cavity. Postpollination sealing of the seeds was effected by a solid plug of tissue that occurs in the position where a pollen chamber is found in most other groups of nonflowering seed plants.

Megagametophyte tissue became cellular after filling the seed cavity, and archegonia formed toward the micropylar end. Embryogeny led to the production of dicotyledonous embryos that are common to many species. The predominance of these embryos, all with a comparable and apparently mature structure, reveals the occurrence of postzygotic quiescence (Mapes et al. 1989) in the Bennettitales and suggests that seed dormancy mechanisms were well developed in the clade. This highly sophisticated mode of reproductive biology undoubtedly contributed significantly to Bennettitales being among the most widely distributed and successful clades of Mesozoic seed plants.

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