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DIVERSITY OF ANCIENT CONIFERS: THE JURASSIC SEED CONE *BANCROFTIASTROBUS DIGITATA* GEN. ET SP. NOV. (CONIFERALES)

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Premise of research. A third genus of anatomically preserved conifer seed cones has been recognized from a Late Jurassic deposit in northeastern Scotland. This cone is described as *Bancroftiastrobus digitata* Rothwell, Mapes, Stockey et Hilton.

Methodology. The cone was sectioned with the classic coal ball peel technique and studied and photographed with transmission light.

Pivotal results. *Bancroftiastrobus digitata* is a cylindrical cone with large, helically arranged ovuliferous scales subtended by short bracts, each bract/scale complex bearing two unwinged inverted seeds on the adaxial surface of the ovuliferous scale. Ovuliferous scales have abaxial plications in the midregion and divide distally, forming up to nine free distal lobes that are vascularized and covered by a dense ramentum of trichomes. The cone axis forms a continuous woody cylinder that surrounds a parenchymatous pith. There are numerous resin canals in the cortex of the cone axis that extend into each bract/scale complex, both abaxial and adaxial to the vascular traces. Vascular tissue to the bract diverges as a prominent terete bundle that separates from the stele immediately below a large inverted-U-shaped scale trace. More distally, the scale trace flattens and divides into a single row of C-shaped woody bundles.

Conclusions. This new genus provides additional evidence for the diversity of stem group conifers that lived during the interval when most crown group conifer families originated. The new species is reminiscent of both Sciadopityaceae and Pinaceae. However, like the three anatomically preserved species of *Pararaucaria* Wieland (Cheirolepidiaceae), this cone does not clearly conform to any family with living species. Rather, these taxa have novel combinations of characters that make fossils vital for resolving deep internal nodes of the seed plant tree and that help to resolve the overall pattern of phylogeny.

Keywords: conifer phylogeny, Coniferales, fossil, Jurassic, seed cone anatomy.

Introduction

Over the past several years there has been significant progress toward the resolution of systematic relationships among living conifers (Quinn et al. 2002; Rai et al. 2008; Rothwell et al. 2009, 2011, 2012; Klymiuk et al. 2011; Leslie et al. 2012; Ryberg et al. 2012) as well as among the most ancient extinct species of conifer plants (Hernandez-Castillo 2005; Rothwell et al. 2005). Organismal and systematic studies of fossil plants have documented the existence of primitive conifers in the Paleozoic and Triassic of both the Northern and Southern Hemispheres (Florin 1951; Archangelsky and Cuneo 1987; Lyons and Darrah 1989; Meyen 1997; Rothwell et al. 1997; Escapa et al. 2008, 2010; Taylor et al. 2009; Serbet et al. 2010; Bomfleur et al. 2013). Such conifer fossils from the Northern Hemisphere are typically assigned to the Voltziales (Rothwell et al. 2005; Bomfleur et al. 2013), whereas a largely disjunct assemblage is preserved in Permian sediments from the Southern Hemisphere (see Serbet et al. 2010 for a comprehensive discussion). A third, distinctly different and more diverse assemblage of stem and crown group conifers is preserved in Jurassic and more recent sediments worldwide (Taylor et al. 2009).

Up to the present, relationships among these geographically and stratigraphically disjunct major groups of conifers have remained elusive. Putative intermediates from Triassic and Jurassic sediments do not clearly fall within any of these groups (Florin 1951; Miller 1977, 1982, 1988; Escapa et al. 2010). However, characterizing such species only as transition conifers perpetuates confusion about organ homologies among crown group conifers and emphasizes that the patterns of both conifer evolution and conifer phylogeny through time are still incompletely understood. Miller (1988) was the first to attempt resolution of the origin of modern conifer families via numerical cladistic analysis of seed cones. At that time, knowledge of both extinct conifer species and systematically informative morphological characters was not yet well enough developed to reveal a clear pattern of relationships.

A paucity of anatomically preserved fossil evidence to de-

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velop whole-plant concepts for Triassic and Jurassic conifer species that display both external morphology and internal anatomy has continued to hamper progress, because most conifer families with living species appear to have originated during those geological periods (Taylor et al. 2009). To help overcome phylogenetic uncertainties resulting from this lack of whole-plant data for conifer species that lived during that crucial time span, when modern families were first appearing in the fossil record, we have initiated a program to use anatomically preserved seed cones as a surrogate or proxy for whole plants in phylogenetic studies (Rothwell et al. 2009). This approach builds on earlier systematic studies of pinaceous conifers (Miller 1988) that continue to be fruitful at the family level (Gernandt et al. 2011; Ryberg et al. 2012), and it has begun to yield encouraging results for resolving deeper internal nodes of the conifer tree (Rothwell et al. 2009). Success of this approach is contingent on a substantial increase in the database for anatomically preserved conifer seed cones from Triassic, Jurassic, and Lower Cretaceous deposits worldwide. Toward that end, several new species have been described recently (Escapa et al. 2010, 2012, 2013; Rothwell et al. 2011, 2012; Ryberg et al. 2012; Stockey and Rothwell 2013), and additional new cones are currently under investigation.

This study provides a new taxon for that database and focuses on the third genus of conifer seed cones that has been discovered in Late Jurassic carbonate marine concretions near Eathie in northeastern Scotland (Miller 1865; Seward and Bancroft 1913; Rothwell et al. 2011, 2012), described here as *Bancroftiastrobus digitata* gen. et sp. nov. Whereas the first two genera represent basal Cupressaceae (i.e., *Hughmillerites juddii* [Seward and Bancroft] Rothwell, Stockey, Mapes et Hilton 2011) and the oldest fossil evidence for Pinaceae (i.e., *Eathiestrobus mackenziei* Rothwell, Mapes, Stockey et Hilton 2012), this new seed cone does not clearly conform to any known family of stem or crown group conifers. Rather, *B. digitata* gen. et sp. nov. displays a novel combination of characters, some of which are reminiscent of Sciadopityaceae while others suggest affinities with Pinaceae.

Material and Methods

The holotype of *Bancroftiastrobus digitata* is a nearly complete seed cone preserved by cellular permineralization within a carbonate marine concretion that had been split open, exposing the specimen in longitudinal view (fig. 1*A*). The nodule is derived from a cobble beach exposure at Eathie on the Black Isle, northeastern Scotland (Miller 1865; Seward and Bancroft 1913; Rothwell et al. 2011). Those sediments are part of the Kimmeridge Clay Formation, which has been biostratigraphically placed within Kimmeridgian Stage of the Upper Jurassic (Riding 2005; Rothwell et al. 2011).

This cone was originally figured as specimen *forma β* of *Conites juddii* by Seward and Bancroft (i.e., text fig. 2*C* of Seward and Bancroft 1913) but not prepared for anatomical investigation. The remaining specimens described as *C. juddii* (Seward and Bancroft 1913) have more recently been renamed *Hughmillerites juddii* (Seward and Bancroft) Rothwell, Mapes, Stockey & Hilton, but the cone described as *forma β* of *C. juddii* sensu Seward and Bancroft (1913) does not conform to that species. We photographed the specimen on both split surfaces of the concretion (fig. 1*A*), made casts of the split concretion, glued the two halves of the concretion back together, and cut the cone into three transverse segments (i.e., slabs A–C). Serial peels were made by the classic cellulose acetate peel technique (Joy et al. 1956) from all surfaces of the cone segments to document cone structure in cross section (fig. 1*B*). Segment B was subsequently reoriented and peeled for longitudinal sections (fig. 1*C*).

Peels for microscopic examination and image capture were mounted on microscope slides with Eukitt (O. Kindler, Freiburg, Germany). Images were captured with Microlumina (Leaf Systems, Bedford, MA) and Photophase (Phase One, Frederiksberg, Denmark) digital scanning cameras and processed with Adobe Photoshop (San Jose, CA). Specimens, specimen casts, peels, and microscope slides are housed at the National Museum of Scotland as specimen NMS 1859.33.4345.

Systematics

Order—Coniferales

Family—indet.

Genus—Bancroftiastrobus *Rothwell, Mapes, Stockey et Hilton gen. nov.*

Generic diagnosis. Cylindrical conifer seed cone with large, helically arranged ovuliferous scales subtended by short bracts, bearing two inverted adaxial seeds per ovuliferous scale; bract free from scale at tip. Ovuliferous scales with abaxial plications in midregion, dividing distally into free lobes. Cone axis continuous woody cylinder surrounding parenchymatous pith; numerous resin canals in cortex, extending into bract/scale complexes both abaxial and adaxial to vascular traces. Vascular tissue to bract diverging as prominent terete bundle, separating from stele immediately below large inverted-U-shaped scale trace; more distally, scale trace flattening and dividing into single row of C-shaped, adaxially convex woody bundles. Seeds oval, unwinged, with apparent 180° rotational symmetry, separated by massive interseminal ridge.

Etymology. *Bancroftiastrobus* (Bancroft plus "*strobus*," or cone) is proposed to honor important contributions to paleobotanical study by the late Nellie Bancroft BSc, FLS, Newnham College, Cambridge.

Type. *Bancroftiastrobus digitata* Rothwell, Mapes, Stockey et Hilton sp. nov.

Species—Bancroftiastrobus digitata *sp. nov. Rothwell, Mapes, Stockey et Hilton* (*Figs. 1–4*)

Specific diagnosis. Seed cone 8.4 cm long, 3.9 cm wide; cone axis 11 mm wide, pith diameter 2 mm. Angle of bract/scale divergence 80°–90°; bracts 8 mm long × 5–6 mm wide, free bract tip 2–3 mm long; bract separating first at margins. Ovuliferous scale ~2 cm long × 2 cm wide, 5 mm wide at base. Resin canals extending into bract and scale and branching distally, one large canal accompanying bract trace; forming one abaxial row and one adaxial row in scale, distributed around margin of free tips; adaxial canals terminate proximal to tips. Pith and cortex parenchymatous, bract and scale tissue

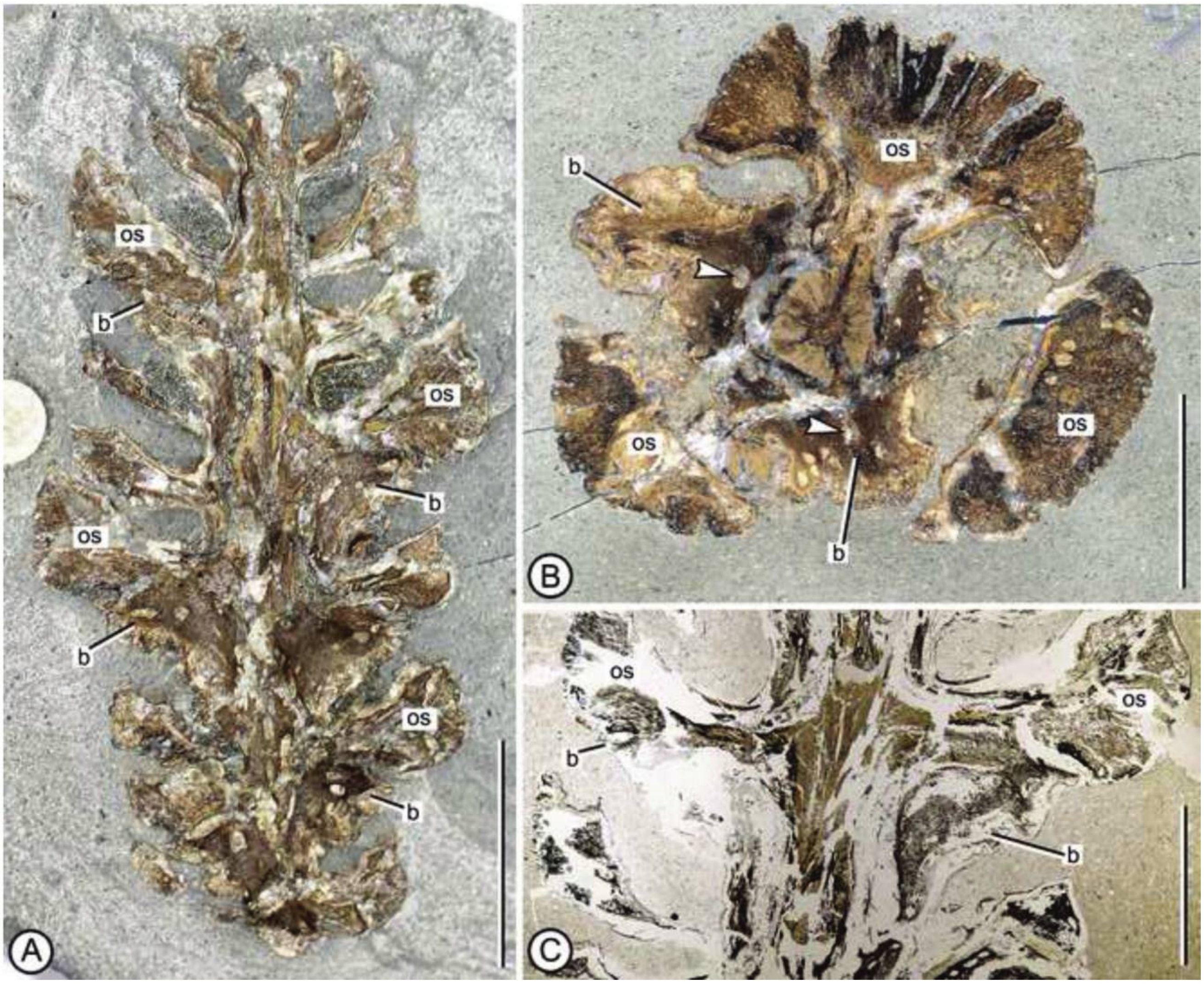

Fig. 1 *Bancroftiastrobus digitata* holotype (NMS 1859.33.4345). *A*, Internal view of cone on surface, showing relatively midlongitudinal section. Cone on split surface; ×1.8. Scale bar = 3 cm. *B*, Cross section of midregion, showing woody axis with resin canals in cortex and helically arranged bract/scale complexes. Arrowheads identify large resin canal accompanying bract trace. Slide B top #26 surface; ×3.0. Scale bar = 1 cm. *C*, Near midlongitudinal section of cone, showing divergence of bract/scale complexes and degree of fusion of bract (b) to scale (os). B_2 side #49; ×2.5. Scale bar = 1 cm. b = bract, os = ovuliferous scale.

parenchymatous, with scattered sclereids and small sclerotic nests. Adaxial periderm present between epidermis and primary ground tissue. Elongated epidermal trichomes forming dense ramentum on adaxial surface of scale. Seeds 3.4 mm wide, 2 mm thick, with thick sarcotesta, prominent nucellus and megaspore membrane.

Etymology. The specific epithet "*digitata*" refers to the digitate free distal tips of the ovuliferous scales.

Holotype hic designatus. Permineralized slabs, peels, and slides of specimen NMS 1859.33.4345 housed at the National Museum of Scotland, Edinburgh.

Collecting locality. Coastal exposures at Eathie on the Black Isle, northeastern Scotland.

Stratigraphic position and age. Kimmeridge Clay Formation at Eathie, Lower Kimmeridgian Stage, Late Jurassic.

Description

The nearly complete cone of *Bancroftiastrobus digitata* is roughly cylindrical, 8.4 cm long and 3.9 cm in maximum diameter, and is constructed of numerous robust, helically arranged bract/scale complexes (fig. 1). The cone axis has a parenchymatous pith surrounded by a robust cylinder of secondary xylem (figs. 1*B*, 2*A*–2*C*). Bract/scale complexes consist of a large ovuliferous scale that is subtended by a much shorter bract (fig. 1) with a free tip (figs. 1*A*, 1*C*, 2*B*, 2*D*). The robust ovuliferous scales extend from the axis at 80°–90° and bend upward gently (fig. 1*A*, 1*C*). Each ovuliferous scale bears two inverted seeds on the adaxial surface of the midregion (fig. 2*B*). Extending distally, the abaxial surface of the ovuliferous scale becomes plicate in the midregion (figs. 1*B*,

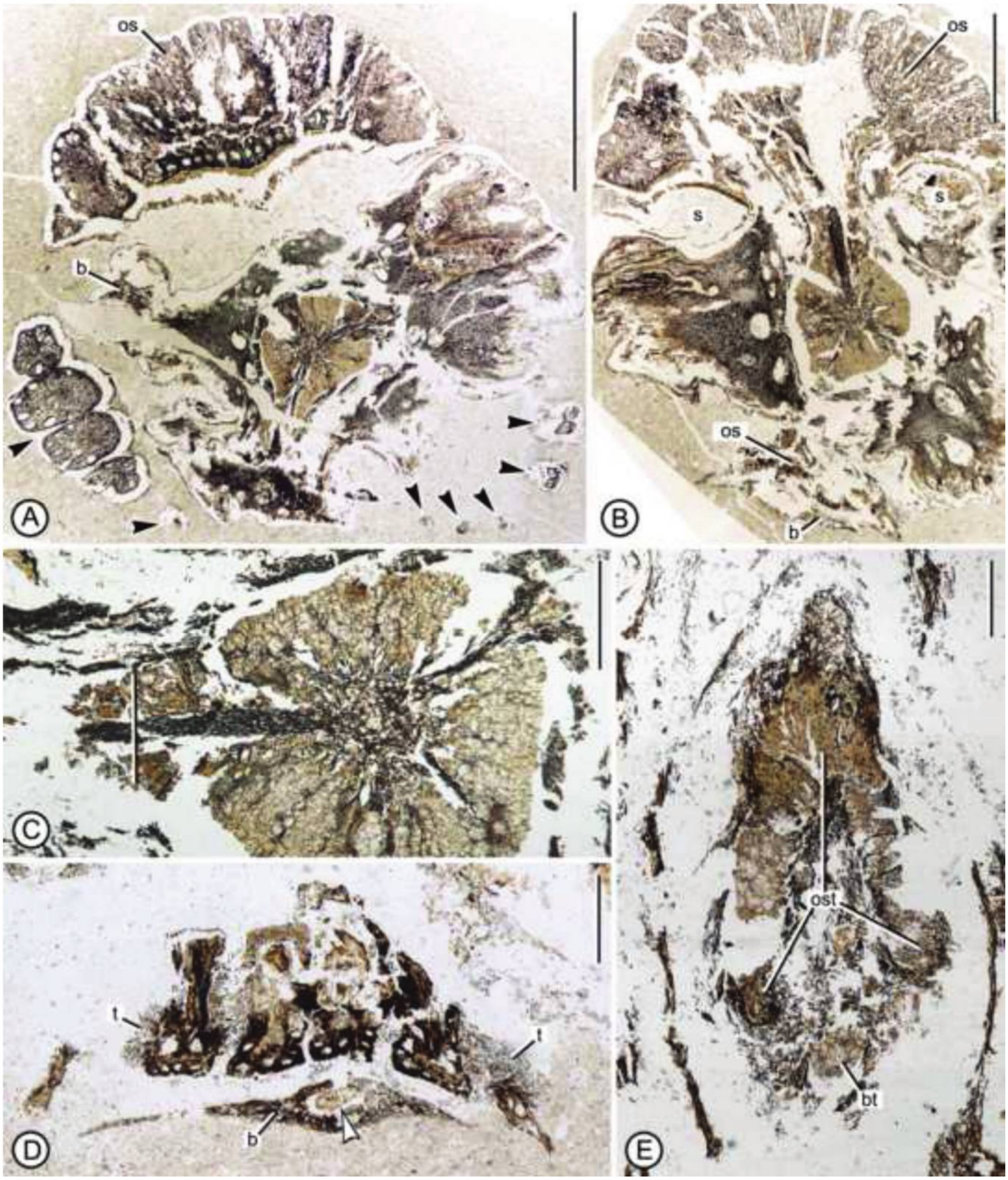

Fig. 2 *Bancroftiastrobus digitata* holotype (NMS 1859.33.4345). *A*, Cross section of cone, showing features of bract/scale complexes at various stages of divergence. Arrowheads identify ovuliferous-scale lobes. Slide A bot #54; ×3.3. Scale bar = 10 mm. *B*, Cross section of cone, showing positions of seeds on ovuliferous scale. Note seeds (s) separated by scale tissue that forms massive interseminal ridge. A bot #47; ×4. Scale bar = 5 mm. *C*, Cross section of cone axis with parenchymatous pith, thick zone of incompletely preserved wood, bract trace divergence (at upper right), and woody ovuliferous-scale trace divergence (at left). Note dark contents of pith cells and pith rays accompanying trace divergences. Line

2*A*) and then divides into seven to nine free distal lobes (fig. 2*A*, 2*D*).

Pith and cortex of the axis consist of parenchyma cells with dark brown walls and internal contents (figs. 1*B*, 2*A*, 2*B*, 3*A*, 3*B*). Prominent resin canals extend through the cortex of the axis and divide to produce resin canals in the bract and ovuliferous scale. The stele forms a continuous cylinder of wood (figs. 1*A*, 2*A*–2*C*). Secondary xylem consists of multiseriate rows of angular tracheids (fig. 4*D*) 9–18 μm in diameter (mean = 13.5 μm), with uniseriate, circular, bordered pits on the radial walls (fig. 4*E*). Distal to the divergence of bract/scale traces, tracheids form swirling patterns that result from polar auxin patterning (Rothwell and Lev-Yadun 2005; fig. 4*F* at left). Rays are primarily uniseriate and homocellular (fig. 4*D*, 4*G*) and one to three cells high. A small number of biseriate rays up to ~15 cells long (fig. 4*G*) are present adjacent to the pith. Individual ray cells typically show dark internal contents (fig. 4*D*, 4*G*).

Bract/scale complexes are robust and are separated from adjacent complexes (fig. 1), giving the cone a rather loose appearance. The bract is much shorter than the ovuliferous scale (fig. 1*A*, 1*C*) and separates first at the margins (fig. 2*A*). More distally, the separation produces a short free bract tip (figs. 1*A*, 1*C*, 2*D*). There is a large central resin canal in each bract that diverges from the axis and subtends the bract trace (figs. 1*B*, 3*A*, 3*B*), as well as two rows of smaller canals. The smaller canals also diverge from the axis, one row extending to the adaxial side and the other to the abaxial tissue of the ovuliferous scale (figs. 1*B*, 2*A*, 2*B*, 2*D*, 3*A*–3*C*). At the level where the free lobes separate, the resin canals are located primarily toward the adaxial side of the ovuliferous scale (fig. 2*A*). Nearer the apex, they extend all the way around the margin of each lobe, with more canals located toward the abaxial side (fig. 2*A*, at left).

Vascular tissue to the bract/scale complex diverges from the stele of the axis as a prominent round to oval bract trace (fig. 3*A*, 3*B*) and a separate inverted-U-shaped scale trace (fig. 2*E*). In cross sections of the cone, dark cells of the ground tissue appear within the inverted U of the ovuliferous-scale trace (fig. 2*C*, 2*E*). Extending distally, the ovuliferous-scale trace flattens and divides into a single row of C-shaped bundles that are each adaxially convex (fig. 3*C*). The lateralmost bundles in each ovuliferous scale become V-shaped in the midregion of the scale (fig. 3*C*, 3*D*) and divide adaxially to produce a bundle that extends toward the base of the seed (fig. 3*D*, arrow).

Ground tissues at the base of the ovuliferous-scale complex are like those of the cortex. Such tissues are largely parenchymatous, consisting of dark, thin-walled cells that often have dark internal contents (figs. 1*B*, 1*C*, 2*A*, 2*B*, 2*D*, 3). At more distal levels (fig. 3*E*), there are small, scattered nests and isolated sclereids located toward the periphery of the ovuliferous-scale tissue (fig. 3*E*, arrows). In some areas there is a thin zone of periderm-like cells between the bract epidermis and the randomly arranged parenchyma of the ground tissue (fig. 4*C*). Similar radially aligned cells that represent secondary ground tissue or periderm occur between the primary ground tissue and the epidermis on the adaxial side of the ovuliferous scale (fig. 3*E*). The epidermis of the bract consists of small, rectangular cells with a thick cuticle (fig. 4*C*). By contrast, on the adaxial and lateral surfaces of the ovuliferous scale and scale lobes, a dense ramentum of elongated, uniseriate trichomes clothes the epidermis (figs. 2*D*, 3*E*), becoming less dense abaxially.

The two seeds per bract/scale complex are typically represented by spaces on the adaxial surface of the ovuliferous scale from which they have been shed (figs. 1, 2*A*). However, a small number of seeds remain in the position of attachment (figs. 2*B*, 4*A*). Individual seeds are oval, 3.4 mm wide, and 2.0 mm thick in cross section, showing 180° symmetry. It is unclear whether the sarcotesta forms a narrow wing in the major plane of seed symmetry. The fleshy sarcotesta forms a thick zone of thin-walled cells (fig. 4*A*, 4*B*). There is a narrow sclerotesta of dark cells and a prominent nucellus surrounding gold-colored fragments of a thick megaspore membrane (fig. 4*A*, 4*B*). No micropyle or pollen chamber has been identified.

Discussion

Examination of *Bancroftiastrobus digitata* has revealed a novel combination of characters that does not clearly conform to any of the large families of stem or crown group conifers, but there are intriguing similarities to Sciadopityaceae, including *Sciadopitys verticillata* Thunberg, *Sciadopitys yezo-koshizakae* Ohsawa, M. Nishida et H. Nishida, and *Sciadopityostrobus kerae* Saiki, and also to the Pinaceae (table 1). These similarities include having a large cylindrical cone with prominent ovuliferous scales subtended by bracts, with each bract/scale complex bearing inverted seeds on the adaxial surface of the ovuliferous scale (table 1).

Bancroftiastrobus can be distinguished from *S. verticillata*, *S. yezo-koshizakae*, and *S. kerae* by its bracts, which are much shorter than the ovuliferous scale, and by having two seeds per ovuliferous scale rather than the larger numbers that characterize the other three species (table 1). Typically, seven to nine seeds characterize *S. verticillata* (Farjon 2005), 9–13 are present in *S. yezo-koshizakae*, and there are five per scale in *S. kerae* (Saiki 1992). Intriguingly, immature ovuliferous scales of *S. verticillata* have a scalloped distal margin (Takaso and Tomlinson 1991; Farjon 2005), similar to the distinctly lobed distal margin of the mature cones of *B. digitata* and *S. kerae*, but in mature cones of *S. verticillata* that feature is much less evident (Takaso and Tomlinson 1991; Farjon 2005). A lobed distal margin has not been described for *S. yezo-koshizakae* (Ohsawa et al. 1991).

The cone axis of all four species forms a stele that surrounds a parenchymatous pith, and the stele forms a continuous woody cylinder (table 1). Vascular tissue to the bract diverges

identifies plane of section shown in *E*. B top #24; ×10. Scale bar = 2 mm. *D*, Cross section of cone, showing bract/scale complex at level distal to attachment of seeds. Note that bract tip has separated from scale at this level and that scale is separating into free distal lobes with prominent resin canals and dense trichomes. Arrowhead identifies large resin canal accompanying bract trace. A bot #35; ×16. Scale bar = 1 mm. *E*, Tangential section of cone axis, showing separate divergence of terete bract trace and woody U-shaped ovuliferous-scale trace. B_2 side #43; ×14. Scale bar = 1 mm. b = bract, bt = bract trace, os = ovuliferous scale, ost = ovuliferous-scale trace, s = seed, t = trichome.

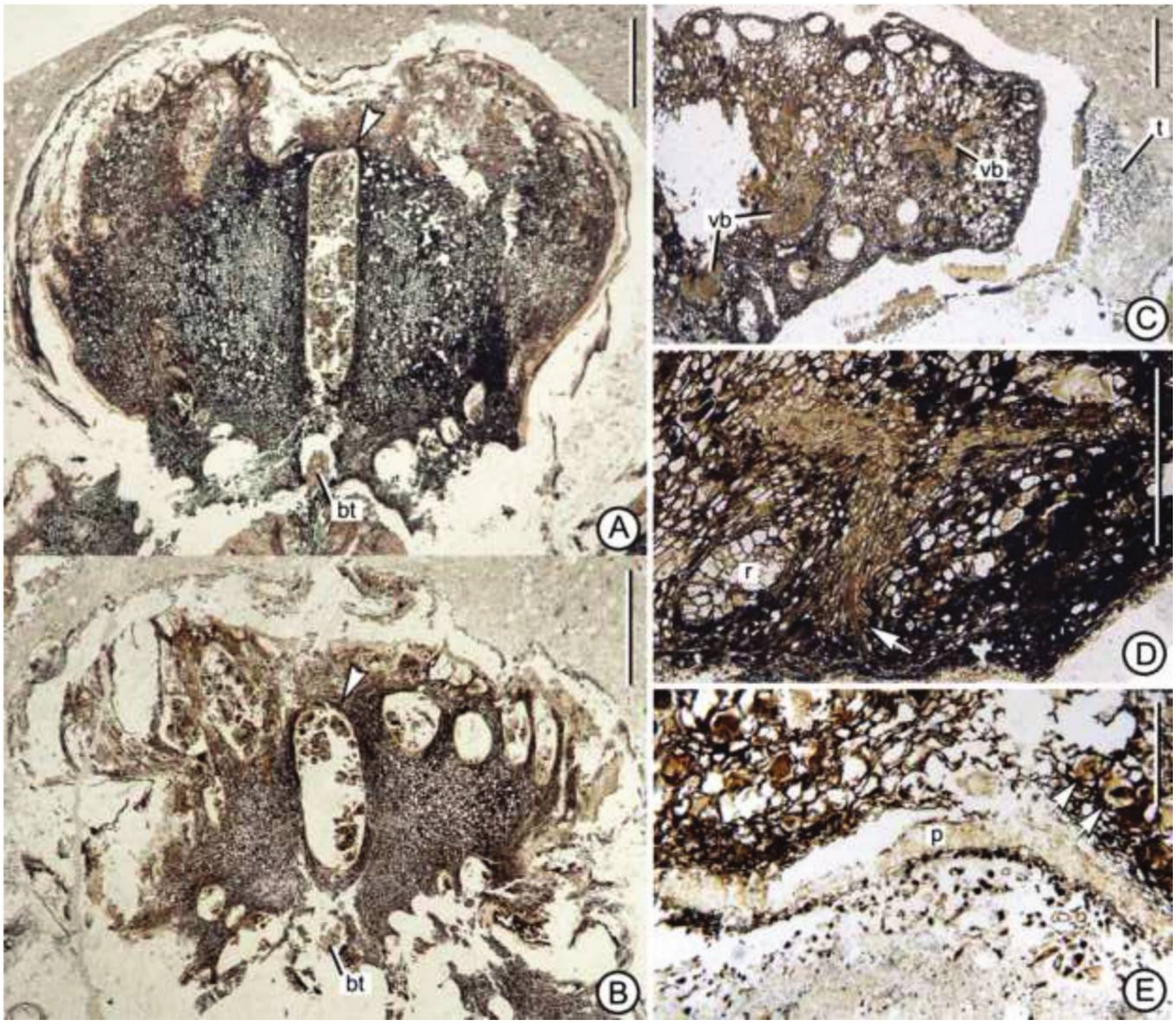

Fig. 3 *Bancroftiastrobus digitata* holotype (NMS 1859.33.4345). *A*, Cross section of cone near base of bract/scale complex, at level of bract trace divergence. Note large central resin canal that accompanies bract trace, and note smaller abaxial and adaxial resin canals diverging from larger cauline resin canals. Arrowhead identifies large resin canal accompanying bract trace. Slide A bot #12; ×7. Scale bar = 2 mm. *B*, Slightly more distal level of bract/scale complex in *A*, showing resin canals somewhat distal to level of bract trace divergence. Arrowhead identifies large resin canal accompanying bract trace. A bot #39; ×9. Scale bar = 2 mm. *C*, Cross section of cone, showing histology of ovuliferous scale at about level of seed attachment. Note vascular bundles of scale, abaxial and adaxial resin canals, parenchymatous ground tissue, and dense epidermal trichomes (t) at right. Note also the V-shaped bundle at level somewhat proximal to where strand diverges to seed. A bot #14; ×11. Scale bar = 1 mm. *D*, Enlargement of region comparable to that in *C*, showing vascular tissue diverging toward seed (arrow) and apparently immature resin canal filled with cells (at left). B top #25; ×28. Scale bar = 1 mm. *E*, Adaxial periphery of ovuliferous scale distal to separation of bract, showing parenchymatous ground tissue, narrow subepidermal zone of periderm, and uniseriate epidermis with dense trichomes (at bottom). Note scattered sclereids in ground tissue (arrows). B_2 side #7; ×83. Scale bar = 0.2 mm. bt = bract trace, p = periderm, r = resin canal, t = trichome, vb = vascular bundle.

from the stele immediately below the scale vasculature as a prominent terete bundle in *B. digitata*, *S. verticillata*, and *S. yezo-koshizakae*, but bract and scale vasculature separates from the cone stele as a single bundle in *S kerae* (table 1). More distally, in *B. digitata* and *S. kerae*, the bract trace separates vertically and the scale vasculature divides horizontally to form a single row of bundles. In *S. verticillata*, some of the ovuliferous-scale bundles divide vertically at about the level of seed attachment. By contrast, with the possible exception of strands that vascularize the seeds, the scale bundles of *B. digitata* do not divide vertically.

There are numerous resin canals in the cortex of the cone

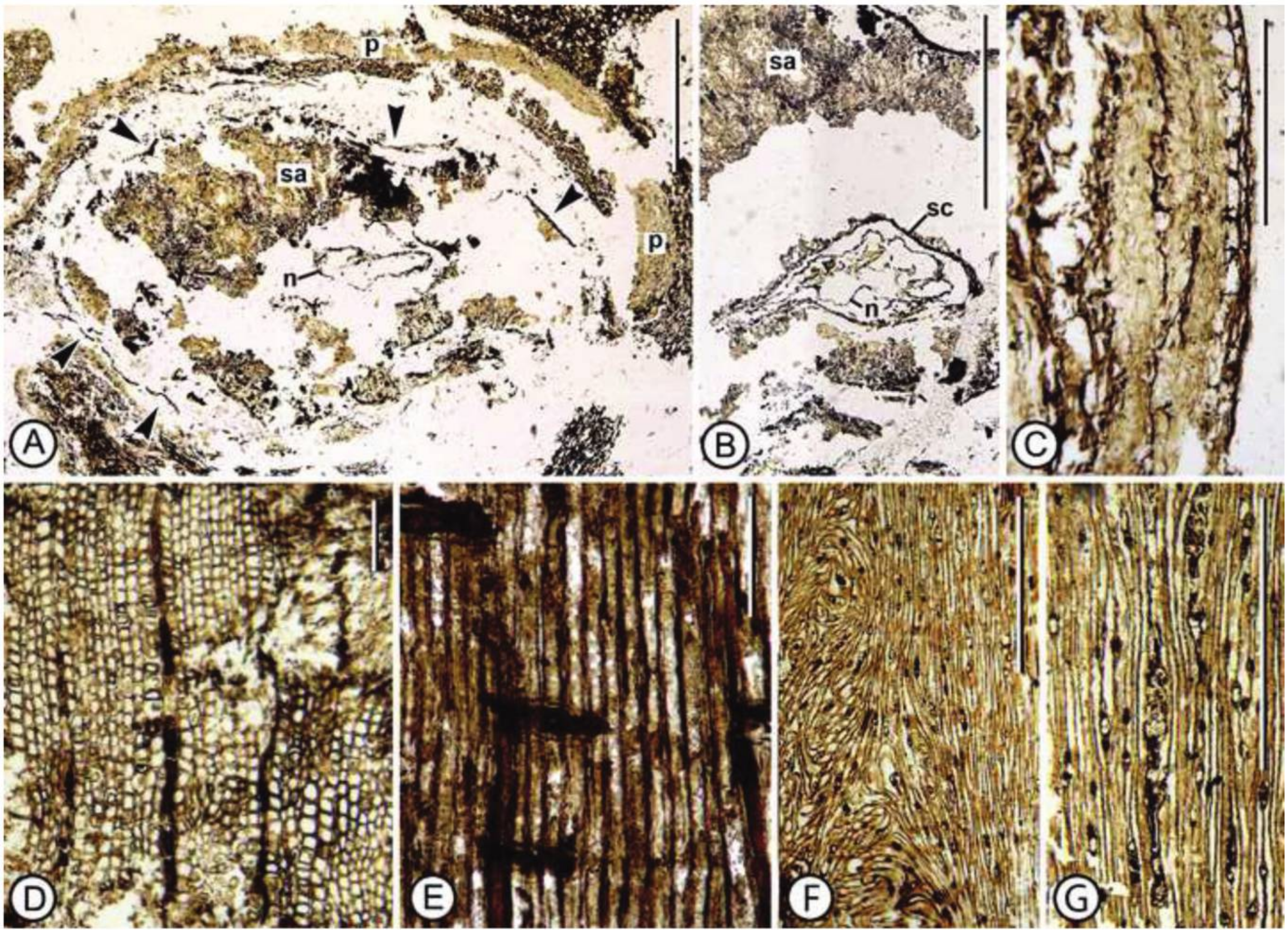

Fig. 4 *Bancroftiastrobus digitata* holotype (NMS 1859.33.4345). *A*, Seed with thick sarcotesta and nucellus in position of attachment to ovuliferous scale. Dark line at arrowheads represents probable thick cuticle of seed epidermis. Ovuliferous scale shows ground tissue (at upper right) and periderm separated from adaxial surface by additional layers of dark primary ground tissue. Slide A bot #49; ×22. Scale bar = 1 mm. *B*, Seed showing sarcotesta, thin sclerotesta, and nucellus surrounding gold-colored fragments of megaspore membrane. B top #8; ×28. Scale bar = 1 mm. *C*, Abaxial surface of bract, showing epidermis with cuticle and one subepidermal cell layer adjacent to periderm-like secondary cortex. A bot #23; ×60. Scale bar = 500 μm. *D*, Cross section of wood, showing multiseriate rows of dense tracheids and uniseriate rays. Note dark contents of ray cells. B top #72; ×100. Scale bar = 100 μm. *E*, Radial section of wood, showing tracheids with uniseriate pits and rays one and two (top left) cells high. B_2 side #67; ×175. Scale bar = 100 μm. *F*, Radial section of wood near divergence of bract and scale traces, showing swirls of tracheids resulting from polar auxin patterning at left and more normal wood at right. B_2 side #53; ×52. Scale bar = 500 μm. *G*, Tangential section of wood, showing tracheids and both uniseriate rays, which are typically one and three cells high, and taller biseriate rays, which occur only adjacent to pith. B_2 side #50; ×77. Scale bar = 500 μm. n = nucellus, p = periderm, sa = sarcotesta, sc = sclerotesta.

axis in all of these cones, but their patterns of distribution vary (table 1). Resin canals diverge to each bract/scale complex both abaxial and adaxial to the vascular traces in *B. digitata* and *S. verticillata*. In *S. yezo-koshizakae* and *S. kerae*, the resin canals enter the base of the scale only on the adaxial side of the scale traces (Ohsawa et al. 1991; Saiki 1992). More distally in all of these species, the resin canals are scattered throughout the ground tissue of the scale.

Bancroftiastrobus digitata, *S. verticillata*, and *S. yezo-koshizakae* are all characterized by prominent trichomes on the bract/scale complex. However, the distribution of trichomes differs in the three species. Those of *B. digitata* occur on the adaxial and lateral surfaces of the ovuliferous scale of mature cones but are absent from the bracts. Trichomes are present on the abaxial surface at the base of immature bracts in *S. verticillata* (Takaso and Tomlinson 1991), whereas in mature cones of *S. yezo-koshizakae* they occur on both the adaxial surface of the bract and the abaxial surface of the ovuliferous scale (Ohsawa et al. 1991). Trichomes have not been described for the bract or scale of *S. kerae* (Saiki 1992).

There also are intriguing similarities between *B. digitata* and the seed cones of Pinaceae (e.g., *Cedrus atlantica* [Endl.] Manetti ex Carrière and *Pinus* L spp.; table 1). All have large cones with numerous bract/scale complexes that consist of a distinct ovuliferous scale and subtending bract. Both have two inverted seeds on the adaxial surface of the scale, but seeds of

Table 1

Comparison of Seed Cones of *Bancroftiastrobus digitata* with Those of Certain Extant and Fossil Conifers

Taxon	Relative size of bract and o.s.	Degree of bract/o.s. fusion	Apical lobes of o.s.	Stele of cone axis	Bract/o.s. trace(s) at divergence from stele	Vasculature of o.s. at divergence	Divergence of resin canals to o.s. complexes	Position of seed attachment	Number of seeds per o.s.	Seed wing
Bancroftiastrobus digitata	Scale larger	To midregion	Present at maturity	Continuous cylinder	Separate	Inverted-U-shape strand	Abaxial and adaxial to traces	Adaxial, surficial	Consistently 2	Small or absent
Sciadopitys verticillata	Relatively equal	To near apex	Absent at maturity (immature only)	Continuous cylinder	Separate	2 strands	Abaxial and adaxial to traces	Adaxial, surficial	Usually 7–9 (1–12)	Small
Sciadopitys yezo-koshizakae	Relatively equal	To near apex	Absent	Continuous cylinder	Separate	Inverted-U-shape strand	Adaxial to trace	Adaxial, surficial	9–13?	?
Sciadopityostrobus kerae	Relatively equal?	To near apex	Present at maturity	Continuous cylinder	Single bundle	Oval	Abaxial to trace	Adaxial, surficial	5	Small or absent
Cedrus atlantica	Scale larger	At base	Absent	Separate bundles	Separate	2 strands	Abaxial and adaxial to traces	Adaxial, surficial	Consistently 2	Single, lateral, of scale tissue
Pinus spp.	Scale larger	At base only	Absent	Continuous cylinder	Single bundle, usually	Usually oval or circular	Abaxial to traces	Adaxial, surficial	Consistently 2	Single, lateral, of scale tissue
Cunninghamia lanceolata	Bract larger	To near apex	Absent	Continuous cylinder	Single bundle	Oval	Adaxial to trace	Adaxial, surficial	2–3	Small
Cryptomeria japonica	Bract larger	To midregion	Present at maturity	Continuous cylinder	Single bundle	2 strands	Absent	Adaxial, surficial	Variable, mostly 3–4	Small or absent
Pararaucaria patagonica	Relatively equal	Free	Absent	Continuous cylinder	Separate	Crescent	Absent	Adaxial, in pocket	1–2 (usually 2)	Absent
Araucaria bidwilli	Bract larger	To near apex	Absent	Separate bundles	Separate	Terete	Abaxial to trace	Adaxial and embedded	1 (rarely 2)	Absent

Note. Underlined characters are those shared with *B. digitata*. o.s. = ovuliferous scale.

B. digitata have little or no lateral wing, whereas those of the Pinaceae typically have a chalazal wing constructed of ovuliferous-scale tissue (table 1). Like that in most genera of the Pinaceae, the bract of *B. digitata* is much shorter than the ovuliferous scale (but see *Pseudotsuga* and some species of *Larix*, *Keteleeria*, and *Tsuga*; Farjon 1990), and it separates distally. Likewise, there is a single vascular trace that enters the ovuliferous scale in both *B. digitata* and most species of the Pinaceae. However, in others (e.g., *C. atlantica*; table 1) there are two separate bundles at the level of trace divergence. Also like *B. digitata*, most seed cones of the Pinaceae have a continuous cylinder of wood in the axis, and the scale trace usually consists of an inverted-U-shaped bundle (Gernandt et al. 2011; Ryberg et al. 2012). Unlike the lobed ovuliferous scales of *B. digitata*, the ovuliferous scales of all pinaceous genera have an entire distal margin.

The large seed cones of other conifer families that consist of numerous bract/scale complexes are more easily distinguished from *B. digitata*. In the taxodioid Cupressaceae (e.g., *Cunninghamia lanceolata* R. Brown and *Cryptomeria japonica* D. Don), the seed cones have a large bract that is typically fused to a much less conspicuous ovuliferous scale (table 1; Farjon 2005; Schultz and Stützel 2007; Rothwell et al. 2011), and there is typically a larger and variable number of seeds per ovuliferous scale (Farjon 2005). However, *C. japonica* is the only living conifer to share with *Bancroftiastrobus* lobed ovuliferous scales in mature cones (Farjon 2005). In the Cheirolepidiaceae (i.e., *Pararaucaria* spp.), the distal margin of the ovuliferous scale is lobed, but unlike those of *B. digitata* the lobes are not all arranged in a single plane (Escapa et al. 2012). Cheirolepidiaceous cones can have either one or two seeds per ovuliferous scale, but unlike those of *B. digitata*, those seeds are more or less enclosed within a diagnostic pocket of ovuliferous-scale tissue (table 1; Escapa et al. 2012). In the Araucariaceae (e.g., *Araucaria bidwilli* Hooker), the bract and scale are fused except at the tip, there typically is only one seed per ovuliferous-scale complex, and the seed of *Araucaria* is largely embedded in ovuliferous-scale tissue (table 1; Wilde and Eames 1948, 1952; Stockey 1982, 1994).

As is characteristic of ancient clades that have experienced high levels of extinction through time (Soltis et al. 2002; Murdock 2008), there is no clear phylogenetic consensus at the base of the conifer tree. Traditional practice has been to assign extinct species of conifer seed cones to crown group families where appropriate and to consider other fossils to be either representatives of the heterogeneous stem group Voltziales or intermediates between the Voltziales and crown group conifers (Miller 1999). This practice has been necessitated by several factors. Important among these are (1) our lack of a clear understanding of which seed cone characters represent synapomorphies and which characters are homoplasious, (2) uncertainties about the relative ages of crown group clades, and (3) the potential relationships of crown group conifers to the various clades of stem group conifers (Miller 1999; Rothwell et al. 2005). We anticipate that the future development of more whole-plant concepts for stem group conifers similar to that of *Telemachus* (Bomfleur et al. 2013) will aid substantially in efforts to resolve the overall pattern of conifer phylogeny.

In the compact nature of its cone and the highly derived structure of its ovuliferous-scale complexes, *Bancroftiastrobus* is more like the seed cones of crown group conifers than like those of voltzialean conifers, but the unique combination of characters displayed by *B. digitata* does not clearly conform to any of the crown group families (table 1). In *B. digitata*, the dissected apical margin of the ovuliferous scale and the absence of a seed wing constructed of scale tissue are more reminiscent of Sciadopityaceae, but the number of seeds per ovuliferous scale and the configuration of the diverging bract and scale traces conform to those of Pinaceae (fig. 1). We do not know which, if any, of those characters are synapomorphies for the clade that includes *Bancroftiastrobus*. Therefore, we have chosen not to assign the genus to a currently recognized crown group family at this time. While this conclusion is, perhaps, emotionally less satisfying than being able to place *Bancroftiastrobus* into a family, the decision emphasizes the important role of fossils with novel combinations of characters for the accurate resolution of deep nodes in the conifer tree (Rothwell et al. 2011; Losos et al. 2012).

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Literature Cited

Archangelsky S, R Cuneo 1987 Feругliocladaceae, a new conifer family from the Permian of Gondwana. Rev Palaeobot Palynol 51:3–30.

Bomfleur B, A-L Decombeix, IH Escapa, AB Schwendemann, B Axsmith 2013 Whole-plant concept and environment reconstruction of a *Telemachus* conifer (Voltziales) from the Triassic of Antarctica. Int J Plant Sci 174:425–444.

Escapa I, R Cúneo, B Axsmith 2008 A new genus of Cupressaceae (sensu lato) from the Jurassic of Patagonia: implications for conifer megasporangiate cone homologies. Rev Palaeobot Palynol 151:110–122.

Escapa IH, NR Cúneo, GW Rothwell, RA Stockey 2013 *Pararaucaria delfueyoi* from the Late Jurassic Cañadón Calcáreo Formation, Chubut, Argentina: insights into the evolution of the Cheirolepidiaceae. Int J Plant Sci 174:458–470.

Escapa IH, A-L Decombeix, EL Taylor, TN Taylor 2010 Evolution and relationships of the conifer seed cone *Telemachus*: evidence from the Triassic of Antarctica. Int J Plant Sci 171:560–573.

Escapa IH, GW Rothwell, RA Stockey, NR Cúneo 2012 Seed cone anatomy of Cheirolepidiaceae (Coniferales): reinterpreting *Pararaucaria patagonica* Wieland. Am J Bot 99:1058–1068.

Farjon A 1990 Pinaceae, drawings and descriptions of the genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. Koeltz, Champaign, IL.

——— 2005 A monograph of Cupressaceae and *Sciadopitys*. Royal Botanic Garden, Kew.

Florin R 1951 Evolution in cordaites and conifers. Acta Bergiana 15: 286–388.

Gernandt DS, CS León-Gómez, S Hernández-León, ME Olson 2011 *Pinus nelsonii* and a cladistics analysis of Pinaceae ovulate cone characters. Syst Bot 36:583–594.

Hernandez-Castillo GR 2005 Systematics of the most ancient conifers. PhD diss. University of Alberta, Edmonton.

Joy KW, AJ Willis, S Lacey 1956 A rapid cellulose peel technique in palaeobotany. Ann Bot, NS, 20:635–637.

Klymiuk A, RA Stockey, GW Rothwell 2011 The first organismal concept for an extinct species of Pinaceae: *Pinus arnoldii* Miller. Int J Plant Sci 172:294–313.

Leslie AB, JM Beaulieu, HS Rai, PR Crane, MJ Donoghue, S Mathews 2012 Hemisphere-scale differences in conifer evolutionary dynamics. Proc Natl Acad Sci USA 109:16217–16221.

Losos JB, DM Hillis, HW Greene 2012 Who speaks with a forked tongue? Science 338:1428–1429.

Lyons PC, WC Darrah 1989 Earliest conifers of North America: upland and/or paleoclimatic indicators? Palaios 4:480–486.

Meyen SV 1997 Permian conifers of western Angaraland. Rev Palaeobot Palynol 96:351–447.

Miller CN 1977 Mesozoic conifers. Bot Rev 43:218–280.

——— 1982 Current status of Paleozoic and Mesozoic conifers. Rev Palaeobot Palynol 37:99–144.

——— 1988 The origin of modern conifer families. Pages 448–486 *in* CB Beck, ed. Origin and evolution of gymnosperms. Columbia University Press, New York.

——— 1999 Implications of fossil conifers for the phylogenetic relationships of living families. Bot Rev 65:240–277.

Miller H 1865 Testimony of the rocks. Gould & Lincoln, Boston. 502 pp.

Murdock A 2008 Phylogeny of marattioid ferns (Marattiaceae): inferring a root in the absence of a closely related outgroup. Am J Bot 95:626–641.

Ohsawa T, M Nishida, H Nishida 1991 Structure and affinities of the petrified plants from the Cretaceous of northern Japan and Saghalien. IX. A petrified cone of *Sciadopitys* from the Upper Cretaceous of Hokkaido. J Phytogeogr Taxon 39:97–105.

Quinn CJ, RA Price, PA Gadek 2002 Familial concepts and relationships in the conifers based on *rbcL* and *matK* sequence comparisons. Kew Bull 57:513–531.

Rai HS, PA Reeves, R. Peakall, RG Olmstead, SW Graham 2008 Inference of higher-order conifer relationships from a multi-locus plastid data set. Botany 86:658–669.

Riding JB 2005 Middle and Upper Jurassic (Callovian–Kimmeridgian) palynology of the onshore Moray Firth Basin, northeast Scotland. Palynology 29:87–142.

Rothwell GW, WL Crepet, RA Stockey 2009 Is the anthophyte hypothesis alive and well? new evidence from the reproductive structures of Bennettitales. Am J Bot 96:296–322.

Rothwell GW, S Lev-Yadun 2005 Evidence of polar auxin flow in 375 million-year-old fossil wood. Am J Bot 92:903–906.

Rothwell GW, G Mapes, GR Hernandez-Castillo 2005 *Hanskerpia* gen. nov. and phylogenetic relations among the most ancient conifers (Voltziales). Taxon 54:733–750.

Rothwell GW, G Mapes, RH Mapes 1997 Late Paleozoic conifers of North America: structure, diversity and occurrences. Rev Palaeobot Palynol 95:95–113.

Rothwell GW, G Mapes, RA Stockey, J Hilton 2012 The seed cone *Eathiestrobus* gen. nov.: fossil evidence for a Jurassic origin of Pinaceae. Am J Bot 99:708–720.

Rothwell GW, RA Stockey, G Mapes, J Hilton 2011 Structure and relationships of the Jurassic conifer seed cone *Hughmillerites juddii* gen. et comb. nov.: implications for the origin and evolution of Cupressaceae. Rev Palaeobot Palynol 164:45–59.

Ryberg PE, RA Stockey, J Hilton, G Mapes, JB Riding, GW Rothwell 2012 Reconsidering relationships among stem and crown group Pinaceae: oldest record of the genus *Pinus* from the Early Cretaceous of Yorkshire, UK. Int J Plant Sci 173:917–932.

Saiki K 1992 A new sciadopityaceous seed cone from the Upper Cretaceous of Hokkaido, Japan. Am J Bot 79:989–995.

Schulz C, T Stützel 2007 Evolution of taxodiaceous Cupressaceae (Coniferopsida). Org Divers Evol 7:124–135.

Serbet R, I Escapa, TN Taylor, EL Taylor, NR Cúneo 2010 Additional observations on the enigmatic Permian plant *Buriadia* and implications on early coniferophyte evolution. Rev Palaeobot Palynol 161:168–178.

Seward AC, N Bancroft 1913 Jurassic plants from Cromarty and Sutherland, Scotland. Trans R Soc Edinb 48:876–888.

Soltis PS, DE Soltis, V Savolainen, PR Crane, TG Barraclough 2002 Rate heterogeneity among lineages of tracheophytes: integration of molecular and fossil data and evidence for molecular living fossils. Proc Natl Acad Sci USA 99:4430–4435.

Stockey RA 1982 The Araucariaceae: an evolutionary perspective. Rev Palaeobot Palynol 37:133–154.

——— 1994 Mesozoic Araucariaceae: morphology and systematic relationships. J Plant Res 107:493–502.

Stockey RA, GW Rothwell 2013 *Pararaucaria carrii* sp. nov., anatomically preserved evidence for the conifer family Cheirolepidiaceae in the Northern Hemisphere. Int J Plant Sci 174:445–457.

Takaso T, PB Tomlinson 1991 Cone and ovule development in *Sciadopitys* (Taxodiacee-Coniferales). Am J Bot 78:417–428.

Taylor TN, EL Taylor, M Krings 2009 The biology and evolution of fossil plants. Elsevier, Amsterdam.

Wilde MH, AJ Eames 1948 The ovule and "seed" of *Araucaria bidwilli* with discussion of the taxonomy of the genus. I. Taxonomy. Ann Bot 12:311–326.

——— 1952 The ovule and "seed" of *Araucaria bidwilli* with discussion of the taxonomy of the genus. II. Taxonomy. Ann Bot 16: 27–47.