

## PALEOECOLOGICAL AND PHYLOGENETIC IMPLICATIONS OF *SAXICAULIS MECKERTII* GEN. ET SP. NOV.: A BENNETTITALEAN STEM FROM THE UPPER CRETACEOUS OF WESTERN NORTH AMERICA

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A new anatomically preserved bennettitalean stem has been recovered from the Upper Cretaceous (Coniacian) Eden Main locality on Vancouver Island, British Columbia, Canada. The fossil, described as *Saxicaulis meckertii* gen. et sp. nov., is permineralized and consists of a eustelic stem with diverging non-girdling leaf traces, a narrow zone of dense wood, primary cortex, and adventitious roots. Important vegetative characters that differentiate bennettitalean stems from cycad stems are reviewed, and while the anatomy of the stem conforms to Bennettitales, it is not consistent with either the Williamsoniaceae or the Cycadeoidaceae as they are currently understood. This fossil documents greater structural diversity among Cretaceous bennettitaleans than previously known and tentatively documents an additional growth habit (underground stem). Co-occurring fossils and plant structure suggest this plant may have inhabited an environment prone to fires. Additionally, there is evidence for two forms of plant-animal interaction in the fossil. The first is a large gallery in the pith lined with wound reaction tissue and accessed through a 3-mm hole on the surface of the stem that represents a new type of herbivore damage for Bennettitales. Reaction tissue occurs in rings and plates throughout the plant body. Smaller galleries containing coprolites of oribatid mites and lacking wound reaction tissue are present in the cortex. The complexity of Upper Cretaceous bennettitalean plant-animal interactions through herbivory and detritivory is evaluated.

**Keywords:** Bennettitales, borer, Cretaceous, oribatid mites, plant-animal interactions.

### Introduction

The Bennettitales (Cycadeoidales of some authors) is an extinct order of Mesozoic gymnosperms represented by a rich fossil record with worldwide distribution. This group has received considerable attention in studies of seed plant phylogeny and the origin of angiosperms for more than 100 yr because of its unique reproductive structures (Arber and Parkin 1907; Crane 1985; Doyle and Donoghue 1986, 1987, 1992; Donoghue and Doyle 1989; Doyle et al. 1994; Nixon et al. 1994; Rothwell and Serbet 1994; Crane et al. 1995; Doyle 1996; Hickey and Taylor 1996; Hilton and Bateman 2006). Recently, renewed interest in the group has drawn attention to the fact that much remains to be clarified about the anatomy and reproduction of these organisms (Friis et al. 2007, 2009; Ryberg et al. 2007; Crepet and Stevenson 2009; Rothwell et al. 2009).

Upper Cretaceous deposits from Vancouver Island have yielded abundant evidence for a diverse flora including bennettitalean plants (Dawson 1893; Bell 1957; Rothwell and Stockey 2002; Stockey and Rothwell 2003; Rothwell et al. 2009). The subject of this study is a permineralized stem with diverging leaf traces and adventitious roots. The fossil

comes from the Coniacian stage of the Late Cretaceous (fig. 1) and was figured and briefly described by Karafit (2007) as a possible cycadalean. However, the stem conforms to Bennettitales in anatomy of the wood, course of the leaf traces, and histology of the ground tissues. The fossil also displays wound reaction tissue associated with a large gallery in the pith, continuous with an entrance/exit hole on the stem surface. Smaller galleries that lack wound reaction tissue but contain coprolites occur in the cortex near the base of the fossil. Together these features document plant/animal interactions previously unknown in Upper Cretaceous biotas.

### Material and Methods

The specimen was recovered at the Eden Main locality on central Vancouver Island, British Columbia, Canada (Karafit and Stockey 2008). Permineralized plant remains are most commonly preserved at this locality in calcium carbonate concretions (Karafit and Stockey 2008); however, this fossil was not in a nodule. Rather, it was preserved directly in the carbonate cemented sandstone matrix, which is interpreted as representing a shallow marine depositional environment (Karafit and Stockey 2008). The Eden Main deposits were most likely deposited during the early Coniacian stage of the Upper

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Cretaceous and belong to the Dunsmuir Member of the Comox Formation (Karaft and Stockey 2008).

The fossil was broken into two pieces during collection. The surfaces were photographed before the pieces were glued back together with epoxy resin. The specimen was embedded in Durham's Rock Hard Water Putty (Donald Durham, Des Moines, IA) and cut transversely into three slices ~1 cm thick. Surfaces were prepared serially using the well-known cellulose acetate peel technique (Joy et al. 1956). The apical segment was recut in near-radial section, and serial peels were prepared from the longitudinal faces. Peels were mounted on slides using Eukitt xylene-soluble mounting medium (O. Kindler, Freiburg) for examination with light microscopy. Images were captured with Microlumina (Leaf System, Bedford, MA) and Photophase (Phase One A/S, Frederiksberg) digital scanning cameras and processed with Adobe Photoshop (San Jose, CA). Specimens, peels, and microscope slides are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA).

### Systematics

Order—Bennettitales Engler

Family—*Incertae sedis*

Genus—*Saxicaulis* gen. nov.

Species—*Saxicaulis meckertii* Jud, Rothwell  
et Stockey sp. nov. (Figs. 1–4E)

**Combined generic and specific diagnosis.** Unbranched stem at least 4.1 cm high and up to 4.0 cm wide with broad pith, eustele, narrow zone of dense secondary vascular tissue, and broad cortex. Secondary xylem is much thicker than secondary phloem. Leaf traces diverge as a single bundle, branching distally to form eight bundles arranged tangentially in a row at periphery of cortex, each bundle crescent shaped, opening abaxially and including secondary xylem. Ground tissues composed of brachysclereids and parenchyma. Cortex containing distally forking secretory canals and narrow zones of traumatic secondary tissues produced by uni- and/or bifacial cambia.

**Holotype hic designatus.** Specimen P14371, consisting of stem base with leaf traces; figures 1–4E; deposited in the University of Alberta Paleobotanical Collections (UAPC-ALTA).

**Etymology.** The genus *Saxicaulis* (Latin *saxeus* = rocky or stony, and Latin *caulis* = the stalk of a plant) refers to the abundance of brachysclereids, or “stone cells,” throughout the ground tissues of this stem. The specific epithet *meckertii* is proposed in honor of Dirk Meckert, Comox, British Columbia, who arranged access to the collecting locality and provided the specimen and additional collecting assistance on Vancouver Island, British Columbia.

**Collecting locality.** Ditch alongside the Eden 400 logging road, located 49°49'38.12"N, 125°26'22.08"W (WGS 84), Vancouver Island, British Columbia, Canada.

**Stratigraphic occurrence.** Dunsmuir Member of the Comox Formation.

**Age.** Early Coniacian, Late Cretaceous (Haggart et al. 2003).

### Description

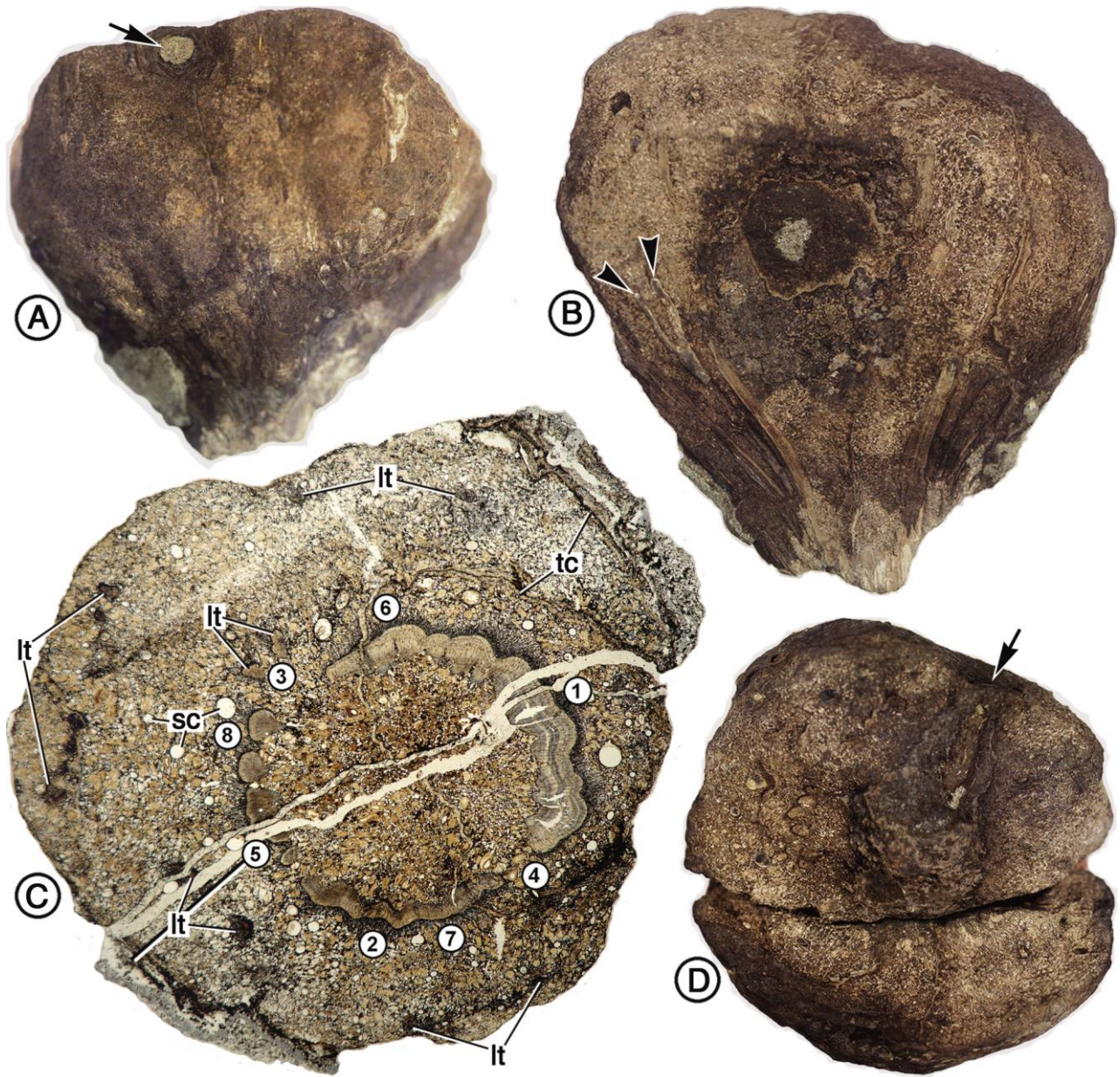
*Saxicaulis meckertii* is represented by an unbranched stem with helically arranged leaf traces and several adventitious root traces (fig. 1). The fossil is 4.1 cm long and roughly conical (i.e., top shaped) and lacks the stem apex. It reaches 4.0 cm at its widest point ~1.6 cm from the distal end (fig. 1A). It is not entirely clear whether the fossil is the base of a large stem or whether it represents a nearly complete, possibly subterranean, stem of a smaller plant. Living cycads with comparable habit include species of *Zamia* Miquel (e.g., *Zamia integrifolia* L. f.), *Cycas* L., *Chigua* Stevenson, and *Bowenia* Hook. The tapering toward the apex in the distal region of the fossil and the absence of preserved resistant leaf bases support the interpretation of a small plant.

At the proximal end, the fossil is less than 2 mm wide (fig. 1A, 1B). Transverse sections reveal relatively wide pith surrounded by a relatively narrow ring of secondary vascular tissue (figs. 1C, 2A) and a relatively broad cortex (fig. 1C). Leaf traces diverge from the stele as a single bundle that divides repeatedly in the cortex to form a row of up to eight small bundles (figs. 1C, 3). A large sediment-filled gallery replaces the pith in the distal half of the fossil (fig. 1B, at center; fig. 4A–4C) and is continuous with an entrance/exit hole on the stem surface (fig. 1A, 1D, at arrows). The gallery is lined with conspicuous wound reaction tissue (fig. 4A–4C). Coprolites occur in small galleries in the cortex near the base of the stem (fig. 4E). No epidermis or leaf bases are preserved.

The pith is relatively wide and increases in diameter apically (fig. 1B). Pith tissue consists of stone cells having thick walls and distinct pit canals and parenchyma (figs. 1C, 2A). Secretory canals are absent.

Primary xylem occurs as an endarch eustele (figs. 1C, 2A) that produces leaf traces in a helical sequence (fig. 1C). Cauline bundles of the stele are small, as in figure 2A, where a few metaxylem cells are visible in the lower left. Helically thickened protoxylem, or possibly metaxylem with loose scalariform thickenings, is visible in longitudinal views as well (fig. 2F). A narrow zone of dense wood surrounds the primary xylem (figs. 1C, 2A, 3C). Toward the distal end of the specimen, the intrafascicular cambium is incompletely developed such that woody bundles are separate (fig. 1C, at left; fig. 3A; fig. 4A, at left). Complete growth rings are absent; however, some apparently traumatic rings occur in some areas of the wood (fig. 1C, at right; fig. 2A) without extending all the way around the stem (fig. 1C). Some can be seen ending abruptly, as in figure 2A.

Secondary xylem tracheids are 10–32.5  $\mu\text{m}$  in diameter and typically display uniseriate circular bordered pits (fig. 2D, 2E) with narrow apertures (fig. 2D), but infrequent biseriate pitting has also been found. Pit pores are circular in radial sections (fig. 2E). Fungal hyphae extend through much of the wood (fig. 2D, at arrowhead) occluding pit pores and in some cases creating the appearance of a torus (fig. 2E, at top center). Rays are uniseriate or, less often, biseriate (fig. 2A–2C) and range 1–30 cells high. Ray cells are procumbent and radially elongated in tangential sections (fig. 2B). The zone of secondary phloem is much narrower than the wood, and it is difficult to distinguish sieve cells from thick-walled



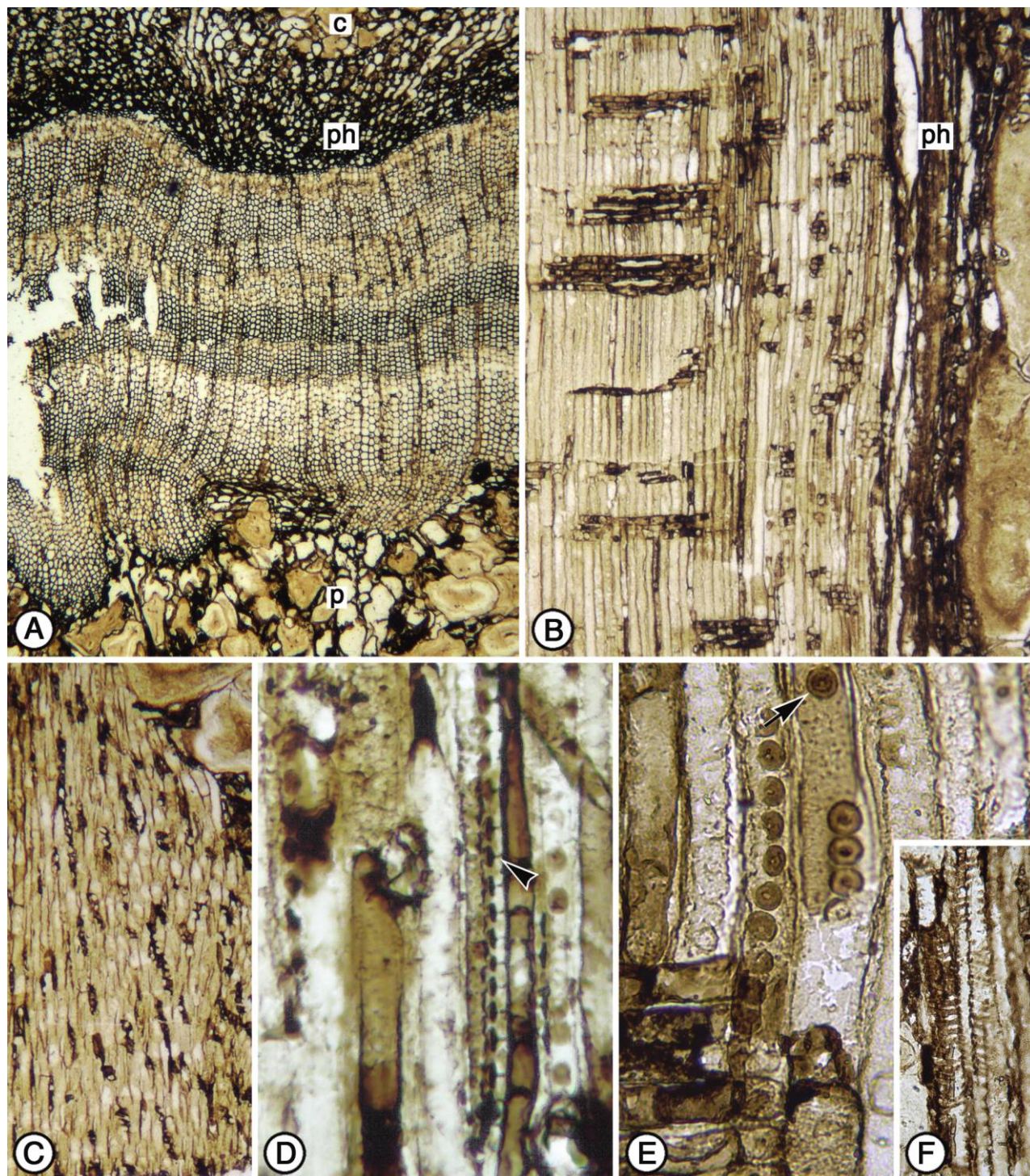
**Fig. 1** *Saxicaulis meckertii* Jud, Rothwell et Stockey gen. et sp. nov. Holotype (P14,371 UAPC-ALTA); stem base showing borer wound, stele, leaf traces, and ground tissues. A, Exterior surface of stem base showing rapid increase in diameter from base toward apex and wound entrance/exit hole at arrow,  $\times 1.8$ . B, Interior broken surface of stem in near-longitudinal section showing gallery in center, narrow zone of wood and leaf trace bundle at lower left, and forking secretory canal at arrowheads,  $\times 2.0$ . C, Transverse section of stem near base showing wide pith lacking secretory canals, relatively narrow ring of dense wood, phloem and broad cortex containing secretory canals (sc), diverging leaf traces (lt), and zones of traumatic cellular proliferation (tc). Eight orthostichies marked with numbers. Note abundance of sclereids in ground tissues, and note only half of wood displays discontinuous growth rings. B bot no. 82,  $\times 4.7$ . D, Top surface of fossil with apex broken off showing large gallery in center continuous with wound entrance/exit hole at arrow,  $\times 1.6$ .

phloem fibers that occur immediately outside the wood in transverse section (fig. 2A). Individual phloem cells appear to be up to  $38.4\ \mu\text{m}$  in diameter and up to  $500\ \mu\text{m}$  long (fig. 2B).

Leaf trace divergence appears to approach a  $3/8$  phyllotaxis, with the leaf traces following a direct radial path outward through the cortex (fig. 1C). Diverging leaf traces

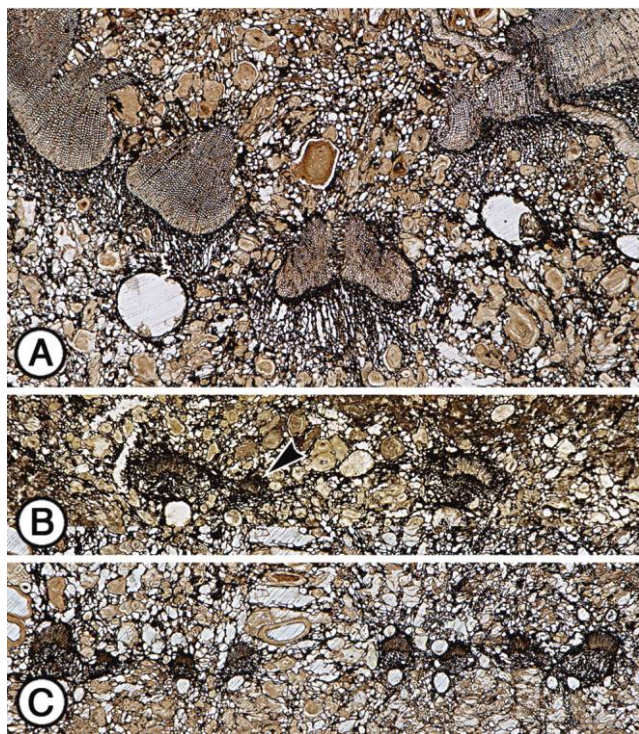
separate from the stele as a single crescent-shaped bundle. That bundle divides almost immediately in the inner cortex to form a pair of crescent shaped bundles (fig. 3A). The pair then extends radially and distally through the cortex. About halfway through the cortex, each bundle divides to produce a smaller bundle toward the other peripheral bundle (fig. 3B, at arrowhead), which produces a tangentially oriented row





**Fig. 2** *Saxicaulis meckertii* Jud, Rothwell et Stockey gen. et sp. nov. Holotype (P14,371 UAPC-ALTA) showing details of the vascular tissues. A, Transverse section of stem showing, from top to bottom, cortex (*c*), phloem (*ph*), wood with traumatic growth rings, primary xylem bundles, and pith (*p*). B bot no. 72,  $\times 45$ . B, Near-radial longitudinal section of wood showing rays, narrow zone of phloem (*ph*), and sclereids in cortex at right. A side A no. 20,  $\times 70$ . C, Tangential section of wood showing rays 2–18 cells high and 1–2 cells wide. P14,371 A side B no. 17,  $\times 71$ . D, Tangential section of wood showing pits with fungal hyphae at arrow. A side B 41,  $\times 543$ . E, Near-radial longitudinal section of wood showing circular bordered pits. Note torus-like appearance of some pits, probably caused by fungal infection or incomplete preservation (at arrow). A side A no. 20,  $\times 430$ . F, Near-radial longitudinal section of wood showing scalariform secondary wall thickening pattern. A side B no. 26,  $\times 200$ .





**Fig. 3** *Saxicaulis meckertii* Jud, Rothwell et Stockey gen. et sp. nov. Holotype (P14,371 UAPC-ALTA) showing leaf trace divergence. A, Transverse section showing leaf trace just distal to divergence from stele and first division. Note that weakly crescent-shaped bundle has just divided into two bundles. B bot no. 72,  $\times 13$ . B, Transverse section showing leaf trace bundle configuration in midcortex. Note pair of crescent-shaped bundles. Bundle at left has just divided to produce smaller bundle at arrowhead. B bot no. 54,  $\times 12$ . C, Transverse section showing leaf trace bundle configuration at stem margin. Note the eight bundles arranged in linear fashion, with largest two at margins. B bot no. 72,  $\times 10$ .

of leaf traces (fig. 3B). Additional divisions of the peripheral bundles form a row of up to eight crescent-shaped bundles at the outer margin of the cortex (figs. 1C, 3C). The bundles at the ends of the row are larger than those toward the center (fig. 3B, 3C).

The cortex is quite broad, accounting for more than one-half the radius of the fossil stem at some levels (fig. 1C), and in no sections is the outer margin preserved, with the possible exception of one area near the base (fig. 4E). The ground tissue is composed of both brachysclereids and parenchyma cells (figs. 1C, 4C), as in the pith. In addition, elongate, distally forking, secretory canals lined with thick-walled epithelial cells are present in the cortex (fig. 1B, at arrowheads; figs. 1C, 4A, 4C, 4F).

Rings and plates of radially aligned cells that appear similar to narrow cork cambial zones occur throughout the ground tissues (figs. 1C, 3C, 4C, 4D). In most areas, these cambia are bifacial and have thick-walled phellem-like cells to one side and thin-walled phelloderm-like cells to the other (figs. 1C, 4C, 4D). Others are unifacial and have only thin-walled phelloderm-like cells to one side (fig. 3C). Differential growth rings also occur partway through the wood but are not con-

tinuous around the stem, as would be expected for seasonal growth rings (figs. 1C, 2A). Some can be seen ending abruptly, as in figure 2A.

Roots are preserved in the cortex. They are diarch and typically consist of a small stele surrounded by a thin zone of parenchyma and an outer dark, epidermal layer (fig. 4D, at bottom). Roots are typically 308–423  $\mu\text{m}$  in diameter. They either diverge from the stem stele (not figured) or originate in association with zones of anomalous cell division (fig. 4D). The roots follow a winding course through the cortex and are typically observed in oblique section.

#### *Galleries, Associated Wound Reaction Tissue, and Coprolites*

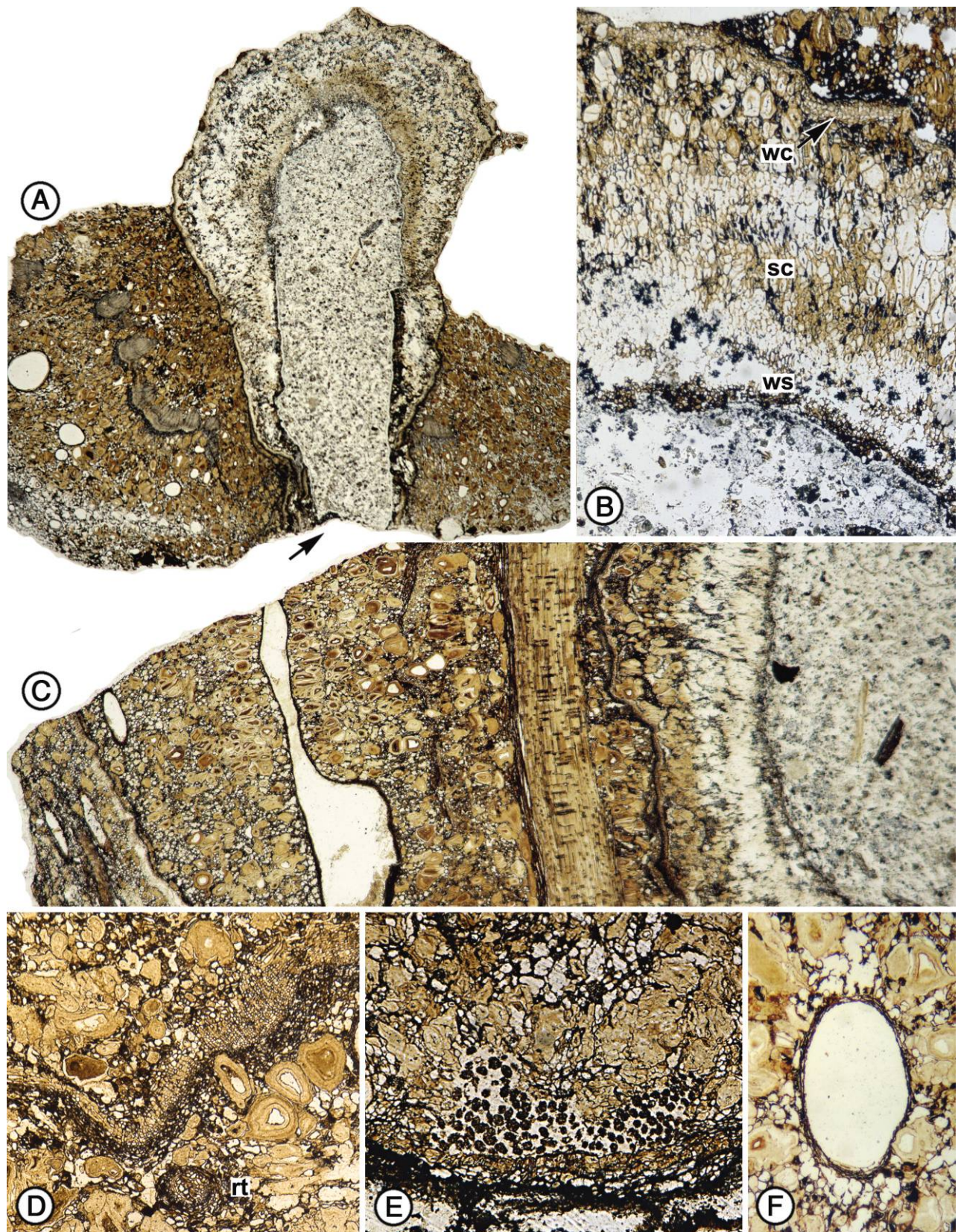
A 3-mm-diameter, sediment-filled hole occurs on the side of the stem near the upper surface (fig. 1A, 1D, at arrows). This hole extends through the cortex and into the pith, where almost all of the primary pith tissue is absent from the upper half of the fossil (figs. 1D, 4A). The resulting gallery is filled with sediment and lined with wound reaction tissue up to 4.3 mm thick (fig. 4A) that consists of three distinct layers: wound cambium and tiered parenchyma (fig. 4B, at arrow) approximately 182  $\mu\text{m}$  thick, a zone of medium to large brachysclereids with variable preservation (fig. 4A–4C), and a thin layer of small, isodiametric, thick-walled, possibly suberized cells along the wound surface (fig. 4B).

Small, irregular galleries 0.2–1.6 mm across and lacking wound reaction tissue occur in the cortex near the base of the stem (fig. 4E). Evenly spaced coprolites fill the galleries. These coprolites are spherical to ovoid in cross section and range in size from 45 to 100  $\mu\text{m}$  across (fig. 4E). Surfaces of the coprolite are smooth to slightly bumpy. Contents are densely compact with no recognizable remains.

#### Discussion

The stem *Saxicaulis meckertii* represents an unbranched bennettitalean plant on the basis of the presence of a large pith, narrow woody cylinder, broad cortex, the direct leaf traces, and dense wood. The presence of well-developed wood in *S. meckertii* indicates that the stem was not a young seedling. The overall shape, lack of branching, and absence of persistent leaf bases and ramentum are reminiscent of the tuberous, subterranean form of living cycads observed in *Zamia*, *Bowenia*, and a few species of *Macrozamia* Miquel, *Cycas*, *Microcycas* (Miq.) A. DC., and *Encephalartos* Lehmann (Chamberlain 1919; Chen et al. 2004; D. W. Stevenson, personal communication, 2010). Also consistent with short stature is the presence of short, wide sieve cells with oblique end walls in the phloem of *S. meckertii*, whose presence suggests low risk of transport disruption due to cell collapse (Ryberg et al. 2007). Consequently, this fossil tentatively marks the first documentation of a bennettitalean with a subterranean stem. It is also possible, however, that the stem was low growing but subaerially exposed and that any persistent leaf bases have been worn off by weathering processes. Anatomical evidence for a contractile stem, a feature common to some subterranean cycads (Stevenson 1980), is lacking. The





**Fig. 4** *Saxicaulis meckertii* Jud, Rothwell et Stockey sp. nov. Holotype (P14,371 UAPC-ALTA) showing evidence of plant-animal interactions, wound response biology, and details of the secretory canals. A, Transverse section of stem near apex (from top piece shown in fig. 1D) showing



tangential leaf trace bundle configuration, C-shape of individual bundles, and novel growth form warrant the establishment of the new genus *Saxicaulis* and reveal that the structural diversity among Cretaceous Bennettitales was greater than recognized previously.

Some of the features that characterize *S. meckertii* are shared with cycads and other bennettitaleans. Trunks of both Cycadales and most Bennettitales are pachycaulous and characterized by a high ratio of ground tissue to vascular tissue (e.g., Wieland 1906, 1916; Stevenson 1990). In cycads, this tissue results from growth by a primary thickening meristem (Stevenson 1990). In overall habit, plants in both orders are usually sparsely branched. However, exceptions occur in both groups: in the bennettitaleans *Wielandiella* Nathorst (1909), *Williamsoniella* Thomas (1916), *Bucklandia pustulosa* Harris (1969), and *Ischnophyton* Delevoryas et Hope (1976) and in the cycad *Nilssoniocladus* Kimura et Sekido (1975). Plants in both orders typically retain an armor of persistent leaf bases, except for some much-branched bennettitaleans and subterranean forms of Cycadales (Chamberlain 1919). Similarities in these features as well as in leaf morphology (Dower et al. 2004) have historically led some to suspect a close relationship between Cycadales and Bennettitales (Wieland 1906; Chamberlain 1935). Despite strong support from reproductive morphology that Cycadales and Bennettitales are separate lineages, the similarities between Bennettitales and Cycadales have continued to interest botanists and paleobotanists (Norstog and Nichols 1997; Crepet and Stevenson 2009), and there remains a need for additional morphological studies to clarify the limits of bennettitalean diversity.

In addition to differences between Cycadales and Bennettitales in reproductive organs and stomatal patterns (Rothwell et al. 2009), we have noted differences in vegetative features. Trunks of the two groups can be distinguished on the basis of features of the wood, leaf traces, and, when present, leaf bases and cone traces (table 1). Although there are some exceptions (e.g., *Bowenia serrulata*: Gregus 1968; *Lysoxylon*: Gould 1971), cycads are characterized typically by “loose” wood having abundant multiseriate parenchymatous vascular rays, some bearing leaf traces or mucilage canals, whereas bennettitalean stems display more dense wood with fewer and more narrow vascular rays (Bancroft 1912; Wieland 1916; Taylor et al. 2009). Polyxyly occurs in several extinct and extant genera of cycads (Hermesen et al. 2006) but not for any unequivocal bennettitaleans (Nishida et al. 1991). Cycads often have vascular bundles in the pith associated with mucilage canals or comprising cone domes (Stevenson 1990), features also absent in any unequivocal bennettitaleans (Wieland 1906). Distinctive girdling leaf traces that originate simultaneously from multiple cauline bundles to supply a

single leaf occur in cycads (Langdon 1920), whereas the leaf traces of bennettitaleans originate from a single cauline bundle and extend directly into the frond base (Wieland 1906; Scott 1909; Yamada et al. 2009). Leaf bases of cycads have vascular bundles arranged in an open inverted-omega configuration or some variation thereof (Hermesen et al. 2006), while those of bennettitaleans are variously arranged in simple or complex closed arrangements (Wieland 1906; Scott 1909; Yamada et al. 2009). Finally, when present, the vascular supply of axillary cones in Bennettitales is distinct from the vascular supply of terminal cones in cycads (Stevenson 1988, 1990; Rothwell et al. 2009).

Since the latter half of the twentieth century, species of Bennettitales have been assigned to one of only two families, Cycadeoidaceae Buckland (1828) or Williamsoniaceae Caruthers (1870; Delevoryas 1962). Familial relationships are traditionally based on features of the cones (reviewed in Rothwell and Stockey 2002; Stockey and Rothwell 2003) and, with less precision, geologic occurrence and overall habit. In order to compare *S. meckertii* with these two families, vegetative features of the trunks are discussed below.

The Cycadeoidaceae is represented by *Cycadeoidea* Buckland (1828) and *Monanthesia* Wieland ex Delevoryas (1959), which have similar but distinctive morphologies. These plants are pachycaulous, with stems that range from globose to subarborescent columnar forms several meters high. Stems are covered in numerous multicellular scales that form a ramentum surrounding persistent leaf bases and frequently attached cones borne in the axils of leaves (Taylor et al. 2009). Internally, stems of Cycadeoidaceae display secondary phloem that is generally thick in relation to the xylem (Wieland 1906; Ryberg et al. 2007). The pattern of leaf trace divergence also appears highly conserved in Cycadeoidaceae; where a single bundle diverges from the stele and on a direct path through the cortex, the bundle becomes C-shaped and highly dissected until the trace forms an elliptical pattern in transverse section with a depression on the adaxial side in the leaf base (Wieland 1906; Scott 1909; Yamada et al. 2009). *Saxicaulis meckertii* lacks persistent leaf bases or a protective ramentum, has a narrow zone of secondary phloem, and has a highly distinct pattern of leaf trace divergence, where the initial bundle divides in the inner cortex and the resulting bundles continue to divide through the cortex, producing a tangentially oriented row of up to eight bundles in cross section. Each bundle displays a unique crescent shape, opening abaxially. These features warrant the exclusion of *Saxicaulis* from the Cycadeoidaceae.

Stems assigned to the Williamsoniaceae are primarily compression fossils or casts. The few species of williamsoniaceous stems that display anatomy that can be compared with that of *S. meckertii* are assigned to the genus *Bucklandia*

wound entrance/exit hole (at arrow), gallery, wound reaction tissue, stele, and cortex. A top no. 29,  $\times 5$ . B, Close-up of wound reaction tissue showing, from top to bottom, ground tissue in upper right, wound cambium (*wc*) at arrow, wide zone of sclereids (*sc*), thick-walled or suberized layer of wound surface tissue (*ws*), and sediment. A side B no. 4,  $\times 20$ . C, Near-radial longitudinal section of stem showing, from right to left, sediment in gallery, wound reaction tissue, wound cambium, remainder of pith, vascular tissue, and cortex containing zones of traumatic cellular proliferation, secretory canals, and leaf trace bundle at lower left. A side A no. 20,  $\times 10$ . D, Zone of traumatic cellular proliferation in cortex with associated adventitious diarch root (*rt*). A top no. 72,  $\times 27$ . E, Close-up of gallery filled with coprolites and lacking wound reaction tissue. B bot no. 61,  $\times 7$ . F, Close-up of secretory canal in cortex showing epithelial lining. A top no. 74,  $\times 25$ .

Table 1

## Trunk Anatomy of Cycadales and Bennettitales

Stem characters	Cycadales	Bennettitales	Sources
Pith:			
Cone domes	Present in some genera	Absent	Artabe et al. 2004; Hermsen et al. 2006; Rothwell et al. 2009
Medullary bundles	Present in some genera	Absent	Artabe et al. 2004; Hermsen et al. 2006
Wood:			
Ray width	1 to many cells	1–2 (3–4) cells	Norstog and Nichols 1997; Rothwell et al. 2009; Taylor et al. 2009
Polyxyly	Present in some genera	Absent	Stevenson 1990; Nishida et al. 1991; Hermsen et al. 2006
Leaf traces:			
Divergence from stele	Multiple sites around the stele	Single site	Scott 1909; Langdon 1920
Course through cortex	Girdling	Direct	Taylor et al. 2009
Arrangement in leaf base	Inverted omega	Closed <sup>a</sup>	Wieland 1906; Scott 1909; Yamada et al. 2009

Note. Only those general anatomical characteristics of cycadophyte stems that can be used to distinguish between cycads and bennettitaleans are included.

<sup>a</sup> While all previously reported leaf bases and rachides display the “closed” configuration made up of five or more bundles, it is not clear whether *Saxicaulis meckertii* shared this character, given the unique arrangement of leaf trace bundles in the cortex.

Presl (Sternberg 1825), which consists of columnar to arborescent cycadophytic trunks covered in persistent leaf bases (with the exception of the compression fossil *Bucklandia pustulosa* Harris [1969], which displays leaf scars, but they are not tightly packed or imbricate, as in other species of *Bucklandia*; however, the stem was found in connection with the bennettitalean cone *Williamsonia leckenbyi* [Harris 1969]). Note that the type, *Bucklandia anomola* (Stokes and Webb) Presl, and many other species of *Bucklandia* are not anatomically preserved (Sternberg 1825; Seward 1917; Sharma 1967; Harris 1969).

It is possible that some species of *Bucklandia*, possibly including the type, actually represent cycads and/or some other group and not bennettitaleans (Nishida et al. 1991). The only anatomically preserved stems that are also associated with cones of Williamsoniaceae are *Bucklandia indica* Seward (1917), used in the classic reconstruction of *Williamsonia sewardiana* Sahnii (1932), and *Bucklandia sahnii* Bose (1953). *Bucklandia indica* and *B. sahnii* share with the present specimen leaf traces that extend directly into the frond base without girdling the stem, narrow secondary phloem relative to secondary xylem, dense wood, and circular bordered pits. However, both *B. indica* and *B. sahnii* differ from *S. meckertii* in having an arborescent growth form, growth rings, a narrow cortex covered in persistent leaf bases, and in the pattern of leaf trace divergence. In these species, a single bundle diverges from the stele, becomes C-shaped opening adaxially, and then divides into 5–11 bundles, resulting in a typical closed bennettitalean arrangement of the leaf trace bundles visible in the persistent leaf bases. Secretory canals are absent from the pith of *S. meckertii* and present in the pith of *B. indica* (Seward 1917; Saiki and Yoshida 1999) but were not reported in *B. sahnii* (Bose 1953). Other anatomically preserved stems assigned to the morphogenus *Bucklandia* are not associated with cones. These include *Bucklandia buzzardensis* (Stopes) Seward, *Bucklandia squamata* (Carruthers) Seward, *Bucklandia yatesii* (Carruthers) Seward, *Bucklandia*

*morrisii* (Carruthers) Seward (1917), *Bucklandia guptai* Sharma (1967), *Bucklandia choshiensis* Nishida (1969), *Bucklandia dichotoma* Sharma (1969), *Bucklandia tsuruokae* Nishida et al. (1983), and *Bucklandia kerae* Saiki et al. (1999). None of these stems display any more similarity with *S. meckertii* than can be found with *B. indica* or *B. sahnii*, and they display a wide range of variation with respect to polyxyly, growth rings, wood histology, medullary bundles, and number and arrangement of leaf trace bundles associated with each leaf base. Several may be cycads rather than bennettitaleans (Watson and Sincock 1992; for a more detailed discussion of this problem, see Nishida et al. 1991). A detailed revision of the genus including new preparations of old material would be helpful for confirming the taxonomic identities and systematic affinities of these *Bucklandia* species. No features of the stem clearly warrant inclusion of *S. meckertii* in Williamsoniaceae.

*Saxicaulis meckertii* is not assigned to either family of Bennettitales as they are currently defined. It therefore will remain an “orphaned genus” until the relationships within Bennettitales are better understood or reproductive material is recovered. Nevertheless, *S. meckertii* represents an important addition to our understanding of bennettitalean diversity at a time when relationships of Bennettitales to other seed-plant clades is being revisited (Crepet 2000; Friis et al. 2007; Rothwell et al. 2009; Crepet and Stevenson 2009).

## Fire Ecology

On the basis of abundant fusainized plants and growth rings in conifer wood, the Eden Main flora is interpreted to have occurred in a warm, seasonally wet/dry landscape prone to forest fires (Karafit 2007). *Zamia pumila* L., a living cycad with a subterranean stem, occurs in fire climax forests of Florida (Négron-Ortiz and Gorchov 2000). When leaves are burned, the stem is presumably protected underground (Stevenson 1980; Négron-Ortiz and Gorchov 2000), and increased growth



follows the fire event for several years (Norstog and Nichols 1997). *Saxicaulis meckertii* may have been similarly adapted to the frequent forest fires inferred for the Eden Main flora.

#### *Plant-Animal Interactions*

Evidence of animal interactions with bennettitalean plants is rare but diverse (see review in Labandeira et al. 2007; for foliar damage types, see also Ash 1996; Labandeira 2002; Pott et al. 2008). Galleries and borer tunnels filled with frass or coprolites and lacking wound reaction tissue have been observed in cones of several species of *Cycadeoidea* (Reymanowna 1960; Delevoryas 1968; Crepet 1972, 1974) and in reproductive structures of two species of *Williamsonia* (Bose 1968; Stockey and Rothwell 2003). Insect damage has also been observed in two bennettitalean trunks. Tunnels filled with coprolites were found in the ramentum, vascular tissues, and cortex of *Cycadeoidea* sp., with evidence of wound reaction (Reymanowna 1960); galleries filled with coprolites and lacking wound reaction tissue were observed in the cortex of *B. kerae* and were first interpreted as evidence of oribatid mites (Saiki and Yoshida 1999) but may instead represent some early instar larva (Labandeira et al. 2007).

Bennettitalean foliage has also yielded evidence of plant-insect interactions. *Anomozamites* Schimper leaves from the Middle Jurassic of Yorkshire display galls (Harris 1942; Labandeira 2002), feeding traces have been observed on pinnae from the Upper Triassic of North America (Ash 1996), and fossil egg chorions and ovipositional damage have been found on foliage from the Upper Triassic of Austria (Pott et al. 2008). The egg chorions may represent beetles, dragonflies, sawflies, or other allied basal Hymenoptera, while the ovipositional damage was most likely caused by either dragonflies or damselflies (Pott et al. 2008). Feeding traces observed in pinnae were bordered by dark reaction tissue, and the damage has been attributed broadly to “grazing insects” (Ash 1996).

Although fossil evidence of insect damage on Bennettitales is limited, the few examples are remarkably diverse, including evidence of cone boring, anthophily (pollination), pollenivory, wood borings, cortex borings, leaf oviposition, leaf grazing, and leaf galling (Reymanowna 1960; Bose 1968; Delevoryas 1968; Crepet 1972, 1974; Ash 1996; Saiki and Yoshida 1999; Labandeira 2002; Stockey and Rothwell 2003; Labandeira et al. 2007; Pott et al. 2008). In the present specimen, living ground tissue was clearly preferentially consumed, and the vascular tissue was avoided as the herbivore passed from the stem margin to the pith. Undamaged ground tissue is composed of abundant large sclereids and smaller parenchyma cells. The absence of coprolites associated with this gallery is unfortunate, because coprolites can be used to identify herbivores (Labandeira et al. 1997). The presence of fungal hyphae in the wood and oribatid mite coprolites in

the cortex suggest that the plant was dead for some time before preservation; it is possible that coprolites of the herbivore that created the gallery were consumed by microbial or fungal activity before preservation (C. C. Labandeira, personal communication, 2010).

Modern cycads may serve as analogs for inferring which groups of borer insects feed on tough, resinous ground tissues such as are inferred for *S. meckertii*. Larvae of about seven species of beetles (Coleoptera), four of which are weevils (Curculionidae), and one species of moth (Lepidoptera) are known to feed on ground tissues of living cycads (Whitelock 2002; Marler and Muniappan 2006). Termites have also been known to feed on damaged or dying cycad stems (Whitelock 2002). Candidate beetle taxa can be extended beyond those that feed on modern cycads to include archostomatan beetles of the families Cupedidae and Obrienidae (extinct weevil-like beetles), Anobiidae (woodworm beetles), and Buprestoidae (jewel beetles) on the basis of size, clade age, and borer lifestyle (Labandeira et al. 1997; C. C. Labandeira, personal communication, 2009). Although they have not been associated conclusively with bennettitalean damage, archostomatan obrieniid beetles and belid weevils (Curculionidae) have been noted to co-occur with bennettitaleans in Mesozoic deposits (Arnoldi 1977; Zherikhin and Gratshev 1993; Gratshev and Zherikhin 2003; Klavins et al. 2003). Although the taxonomic identity of the borer that fed on *S. meckertii* remains in question, this fossil provides evidence of a new form of bennettitalean plant-animal interaction represented by a borer arthropod that targets living pith tissue.

Coprolites found in permineralized plant tissues can be attributed to oribatid mites on the basis of size, shape, texture, contents, and context sensu Labandeira et al. (1997). Oribatid mite fecal pellets can be found throughout the plant fossil record but have been recognized only twice previously in Cretaceous plant fossils (Labandeira et al. 1997; Stockey and Rothwell 2004). The coprolites in the present fossil conform to those produced by oribatid mites. These coprolites help fill the gap in evidence for oribatid mites as plant detritivores in Cretaceous ecosystems and provide the first reported definitive evidence that oribatid mites fed on bennettitalean plants.

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