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PLANT-ARTHROPOD INTERACTIONS IN *ACANTHOSTROBUS EDENENSIS* (CUPRESSACEAE), A NEW CONIFER FROM THE UPPER CRETACEOUS OF VANCOUVER ISLAND, BRITISH COLUMBIA

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Premise of research. A new, morphologically distinct, anatomically preserved conifer assignable to the basal Cupressaceae, which was subject to arthropod infestation during life, has been discovered within a marine carbonate concretion from the Coniacian (Late Cretaceous) Eden Main locality of Vancouver Island, British Columbia.

Methods. Specimens were studied from anatomical sections prepared using the classic cellulose acetate peel technique.

Pivotal results. This plant, described as *Acanthostrobus edenensis* gen. et sp. nov., has helically arranged needle leaves and terminal seed cones composed of numerous helically arranged bract/scale complexes dominated by the bract. Both vegetative leaves and bracts display exceptionally long, narrow tips that may have been involved in predator deterrence. The seed cone has diminutive ovuliferous scales with free distal margins; bract/scale complexes bear two to four small, secondarily inverted ovules. Cone tissues contain arthropod feeding galleries surrounded by necrotic tissue and closing tissue (wound periderm) that proliferated throughout the specimen.

Conclusions. The new plant is clearly attributable to basal Cupressaceae (Cunninghamioideae, Taiwanioideae, and Athrotaxoideae). While it shares features with extinct Jurassic and Cretaceous Cupressaceae, it exhibits a novel combination of characters that distinguishes it from previously described genera. This discovery expands our understanding of basal cupressaceous diversity and provides insight into conifer-animal interactions during the Cretaceous.

Keywords: Athrotaxoideae, Caridae, coneworm, Cunninghamioideae, *Dioryctria*, hypersensitive response, Taiwanioideae, weevil.

Introduction

The Cupressaceae is one of seven widely recognized families of crown group conifers thought to have evolved from within a plexus of extinct transition conifers (Escapa et al. 2010; Rothwell et al. 2011; Leslie et al. 2012) assignable to the Paleozoic Voltziales sensu Rothwell et al. (2005). At present, relationships between and within these stem and crown groups remain incompletely understood (Miller 1977, 1982, 1999; Stockey 1981; Takaso and Tomlinson 1989a, 1989b; Tomlinson et al. 1993; Hernandez-Castillo et al. 2001, 2009a, 2009b; Rothwell et al. 2005, 2011; Escapa et al. 2010; Serbet et al. 2010). Investigation of family-level systematic relationships among living crown group conifers using maximum like-

lihood analysis of cpDNA (Rai et al. 2008) indicates that Cupressaceae forms a clade with Taxaceae + Cephalotaxaceae, the basal member of which is *Sciadopitys* Siebold et Zucc. (Sciadopityaceae). This clade, in turn, is sister to Araucariaceae + Podocarpaceae. As a superclade, these families are informally termed the cupressophytes (Rai et al. 2008) and have been recognized as sister to Pinaceae in numerous molecular studies (Chaw et al. 1997; Bowe et al. 2000; Quinn et al. 2002; Rai et al. 2008; Leslie et al. 2012). Until comprehensive analyses that include both living and extinct conifers are conducted, however, questions will remain about whether that topology actually represents the overall pattern of phylogeny for conifers or merely relationships among living species (Rothwell and Nixon 2006).

The fossil record of Cupressaceae is long and extensive (Stockey et al. 2005; Escapa et al. 2008), but origins of the group remain uncertain due to a paucity of anatomically preserved Mesozoic species for which whole-plant concepts have been developed (Stockey et al. 2005; Rothwell et al. 2009). At

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present, the most ancient species attributable to Cupressaceae are represented either by anatomically preserved seed cones for which the vegetative portions of the plants are unknown (e.g., *Hughmillerites juddii* [Seward et Bancroft] Rothwell, Stockey, Mapes et Hilton 2011) or by compressed specimens, which tend to display fewer systematically informative characters than permineralized seed cones, even when reconstructed from several vegetative and fertile organs (e.g., *Elatides williamsonii* Harris, *Sewardiodendron laxum* (Phillips) Harris, *Austrohamia minuta* Escapa Cuneo et Axsmith; Harris 1979; Escapa et al. 2008). Rothwell et al. (2011) have proposed a transformational series of seed cone morphologies suggesting Cupressaceae s.l. evolved from voltziacean Voltziales during the Triassic or Early Jurassic. This is concordant with the earliest evidence for Cupressaceae in Early Jurassic deposits of Argentina (Escapa et al. 2008).

Miller (1977) suggested that the extant basal members of Cupressaceae are relicts of long lines of specialization. Among permineralized basal Cupressaceae for which whole-plant concepts have been developed, the earliest is Late Cretaceous in age, and that plant (i.e., *Cunninghamia taylorii* Serbet, Bomfleur et Rothwell) is clearly a species of *Cunninghamia* R. Brown (Serbet et al. 2013). Some species of *Elatides* Heer are highly comparable to living *Cunninghamia* as well: lignified fertile and vegetative remains from Mongolia, described as *Elatides zhoui* Shi, Leslie, Herendeen, Ichinnorov, Takahashi, Knopf et Crane (2014), demonstrate that cunninghamioid morphology is highly conserved (Shi et al. 2014). The cunninghamioids appear to form a clade sister to other basal and crown Cupressaceae (Shi et al. 2014).

Ohana and Kimura (1995) hypothesized that the Cretaceous was a period of diversification for noncrown cupressaceous conifers, as most fossils attributable to the basal Cupressaceae are known from that period (Stockey et al. 2005; Escapa et al. 2008; Rothwell et al. 2011; Atkinson et al. 2014a, 2014b; Shi et al. 2014). In this article, we describe a new genus of Cupressaceae that further expands the known diversity of noncunninghamioid basal Cupressaceae. The new genus is erected on the basis of an anatomically preserved leafy stem with attached seed cone from the Upper Cretaceous of Vancouver Island, British Columbia. As is characteristic for basal cupressaceous conifers (Farjon and Ortiz Garcia 2003; Farjon 2005), *Acanthostrobus edenensis* gen. et sp. nov. has helically arranged needle leaves and bract/scale complexes with a diminutive ovuliferous scale, the complexes being dominated by the bract (Eames 1913). The specimen has two to four inverted ovules on the adaxial surface of each bract/scale complex (two on near-apical complexes) and displays extremely long and narrow leaf and bract tips that may have aided in predator deterrence and/or seed cone dispersal. Arthropod feeding galleries occur in the cone axis and several bracts and are surrounded by secondary closing tissue, which proliferated aberrantly throughout the cone. In addition to expanding known diversity of basal Cupressaceae, this cone provides insight into defensive strategies employed by conifers during the Late Cretaceous.

Material and Methods

A single seed cone and subtending leafy branch are preserved within a marine calcium carbonate concretion from

the Eden Main locality on Vancouver Island. The Eden Main locality comprises five sedimentary exposures of the Dunsuir Member of the Comox Formation (Haggart et al. 2003; Karafit 2008). The specimen described here comes from the principal exposure at Eden Main, a small quarry in which 10 m of muddy to silty, conglomeritic sandstone and greywacke breccia crop out (Schweitzer et al. 2003; Karafit 2008; A. A. Klymiuk, personal observation, 2009; D. Meckert, personal communication, 2011). Plant fossils at Eden Main are either permineralized by calcium carbonate directly within host sediments, as described by Jud et al. (2010), or anatomically preserved within semisideritic CaCO₃ concretions (Karafit 2008; Karafit and Stockey 2008) like the specimen described here.

Stratigraphy

The lowermost Comox Formation represents a shallow marine depositional setting with significant alluvial contributions (Mustard 1994). Traditionally, the Comox Formation was thought to be Santonian in age (Muller and Jeletzky 1970; Bickford and Kenyon 1988; Kenyon et al. 1992), but deposits in the Gulf and San Juan Islands have been dated to the Turonian (Haggart 1994; Haggart et al. 2005). Although Haggart (1994) and Haggart et al. (2005) argue that Turonian sediments in the Gulf and San Juan Islands ought to be considered Sidney Island Formation, Johnstone et al. (2006) recognize similar lithology and sedimentology between these and the Vancouver Island sites. As such, the Comox Formation is understood to be diachronous in nature, encompassing the Turonian to early Campanian (Mustard 1994; Johnstone et al. 2006; Karafit 2008; Karafit and Stockey 2008). The Comox Formation beds from which this specimen was obtained are exposed along the Eden Main logging road (Schweitzer et al. 2003; Karafit 2008), which is 35 km northwest of the city of Comox (lat. 49°49'52.04"N, long. 125°25'10.41"W). Beds at the quarry contain fossils of the collignonceratid ammonite *Prionocycloceras* (Haggart et al. 2003; Karafit 2008; Karafit and Stockey 2008), a genus associated with sediments of Coniacian age (e.g., Young 1959, 1963; Ward and Signor 1983; Matsumoto 1984; Zaborski 1990; Santamaria and Ricardo 1993).

Specimen Preparation

The original saw cut through the cone-bearing concretion exposed the specimen in slightly oblique longitudinal section. The most complete part of the cone (UAPC-ALTA P16604 G top) was sectioned in longitudinal section and then reoriented and sectioned transversely. Serial sections were produced by the cellulose acetate peel technique (Joy et al. 1956) and mounted on glass slides using xylene-soluble Eukitt (O. Kindler, Freiburg, Germany) mounting medium. Images were captured with a Leica DC 500 digital scanning camera (Leica Microsystems, Wetzlar, Germany) mounted on a Leica MZ16 dissecting microscope and on a Leica DM5000 B compound microscope. All images were processed with Adobe Photoshop. Specimens and slides are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results

Systematics

Order—Coniferales

Family—Cupressaceae Bartling

Genus—*Acanthostrobus* Klymiuk, Stockey
et Rothwell, gen. nov.

Generic diagnosis. Cupressaceous leafy branches with helically arranged needle leaves with attenuated leaf tips and terminal seed cones. Seed cone cylindrical, with numerous helically arranged bract/scale complexes. Bracts prominent, with inflated base and extremely elongated, acuminate tip; single scale tip separating from bract near apex. Two to four inverted ovules attached to adaxial surface of bract/scale complex immediately proximal to single scale tip. Seed wings lateral, formed of integumentary tissue. Single vascular trace entering bract/scale complex, apparently unbranched at level of ovule attachment; one resin canal branching from cauline system to enter bract/scale complex; single row of several at level of ovule attachment and more distally. One resin canal in attenuated bract tip.

Etymology. *Acanthostrobus* (Greek *akantha* = spine [Anglicized to *acantho*] + *strobos* = cone) is named for the distinctive cone, characterized by extremely elongated and acuminate bract tips.

Type species. *Acanthostrobus edenensis* Klymiuk, Stockey, et Rothwell, sp. nov.; figs 1–5.

Specific diagnosis. Needle leaves hypostomatic, with single terete trace and one prominent resin canal adaxial to trace; leaves rhomboidal in transverse section, at least 8 mm long, 1.5–2 mm wide by 1 mm high, imbricate, with long, attenuate apices. Seed cone, at least 25 mm long and ca. 10 mm in diameter, cylindrical, borne terminally. Cone axis ca. 2 mm in diameter, pith 330–350 μm in diameter, composed of thick-walled isodiametric parenchyma. Vascular cylinder largely continuous; primary xylem endarch. Secondary xylem tracheids 10–20 μm wide, 300–325 μm long. Cortex ca. 1.5 mm wide, with ca. 11–13 resin canals, parenchymatous with sclerenchyma fibers near vascular cylinder and at periphery. Bract/scale complexes vascularized by single vascular strand associated with one abaxial resin canal. Bract inflated near axis, winged, parenchymatous with sclerotic hypodermis, at least 10 mm long, rhomboidal in transverse section; developing as many as nine resin canals near cone margin; inflated portion ca. 6.5 mm wide, ca. 2 mm high, with long acuminate tip. Free tip of ovuliferous scale ca. 2 mm long, up to 3.5 mm wide; separation from bract beginning laterally.

Etymology. The specific epithet *edenensis* refers to the Eden Main collecting locality.

Holotype hic designatus. Specimen consisting of unprepared remains, cellulose acetate peels and microscope slides from leafy shoot and apical cone in concretion designated UAPC-ALTA P16604 G top, G xs, and F bot.

Stratigraphy. Dunsmuir Member, Comox Formation.

Age. Coniacian, 86.3–89.8 Ma.

Description

General features. *Acanthostrobus edenensis* is represented by a single cylindrical seed cone measuring 25 mm long by 8–9 mm wide (fig. 1A), subtended by a short segment of vegetative shoot-bearing needlelike leaves (figs. 1A, 1B, 1D, 2). Apices of both vegetative leaves and cone bracts are conspicuously long and narrow (figs. 1A, 2A). The cone is composed of helically arranged bract/scale complexes (fig. 1A, 1D) borne perpendicular to the cone axis (figs. 1A, 3A). The ovuliferous scale of the bract/scale complex is highly fused to the dominant bract but is free at the distal margin (figs. 1A, 3D, 4A). Two to four immature ovules are preserved on the adaxial surface of each ovuliferous scale throughout most of the cone (figs. 1A, arrowheads, 3B), but those bract/scale complexes at the apex of the cone are probably infertile (fig. 1A).

Subtending vegetative zone. A vegetative zone with helically arranged needlelike leaves subtends the cone (figs. 1A, 1C, 1D, 2A). The vegetative stem is histologically comparable to the cone axis (figs. 1A, 2A). It has a pith (fig. 2A) surrounded by a stele, consisting of tiny endarch collateral bundles with secondary xylem, and cortex (figs. 1C, 2A). The secondary xylem is ca. 240 μm thick, consisting of 6–8 rows of radially aligned tracheids (fig. 1C) and inconspicuous uniseriate wood rays, and is surrounded by a zone of less completely preserved phloem up to 110 μm thick (fig. 1C). The woody cylinder is relatively continuous but shows prominent multiseriate pith rays (fig. 1C). Tracheids of the vascular cylinder are 10–18 μm wide and 300–325 μm long. Most exhibit scalariform thickenings or bordered pits (fig. 4D). The cortex contains prominent resin canals and is composed of randomly arranged parenchyma cells with distinct walls, some of which display dark internal contents (figs. 1B, 1C, 2A).

Vegetative leaves are imbricate, with very long and narrow apices that are slightly incurved (figs. 1A, 2A) and at least 8 mm long (figs. 1A, 2A). Leaves diverge from the stem at 45°–60° and then gently bend distally (figs. 1A, 2A). In transverse section, leaves are rhomboidal to diamond shaped (figs. 1B, 2B), 1.7 mm wide by 0.91 mm high. The adaxial surface of the leaf is slightly concave, with the exception of a medial ridge (figs. 1B, 2B, 2D). Each leaf has a terete vascular strand (fig. 2B, 2D, arrows) and a single resin canal (figs. 1B, 1D, 2B, 2D). Mesophyll consists of relatively closely spaced parenchyma cells, many of which have prominent dark walls and/or internal contents (figs. 1D, 2). A sclerotic hypodermis one or two cells thick (fig. 2D) is present only on the abaxial surface (fig. 2B). Sunken stomata occur on the abaxial surface (fig. 2C, arrowheads).

Cone axis. The cone axis is similar to that of the subtending stem (figs. 1A–1C, 2A). The stele encloses a narrow pith composed of dark-walled parenchyma cells lacking contents (fig. 1B, 1C). No resin canals are associated with the pith and vascular tissues, but several are present within the cortex (figs. 1A–1C, 2A). The cortex is ca. 1.4 mm wide and is composed predominantly of thin-walled parenchyma tissue (figs. 1B, 1C, 2A), although inconspicuous scattered sclereids occur in proximity to the vascular cylinder. There is also a narrow sclerotic hypodermis, 140–170 μm wide, which is discernible in the basal vegetative region of the cone.



Fig. 1 *Acanthostrobus edenensis* gen. et sp. nov. Holotype UAPC-ALTA P16604. A, Radial section through ovulate cone and subtending leafy shoot showing extremely elongated tips on both bracts (b) and subtending leaves (l). Note positions of ovules (arrows), arthropod galleries (g), and necrotic tissue (n). G top #2 × 6. Scale bar = 5 mm. B, Transverse section through vegetative shoot immediately proximal to cone showing histology of stem cortex with resin canals (r) and helically arranged leaves in cross section. G x.s. #42 × 18. Scale bar = 2 mm. C, Enlargement of stem in B showing cauline bundles surrounding pith (p), one diverging leaf trace (arrow), and cortex with resin canals (r). G x.s. #42 × 30. Scale bar = 1 mm. D, Longitudinal section through vegetative shoot and base of cone showing attached leaves and bract/ovuliferous scale complexes. Lines at right identify regions of leafy stem and cone base. F Bot #3 × 25. Scale bar = 1 mm.

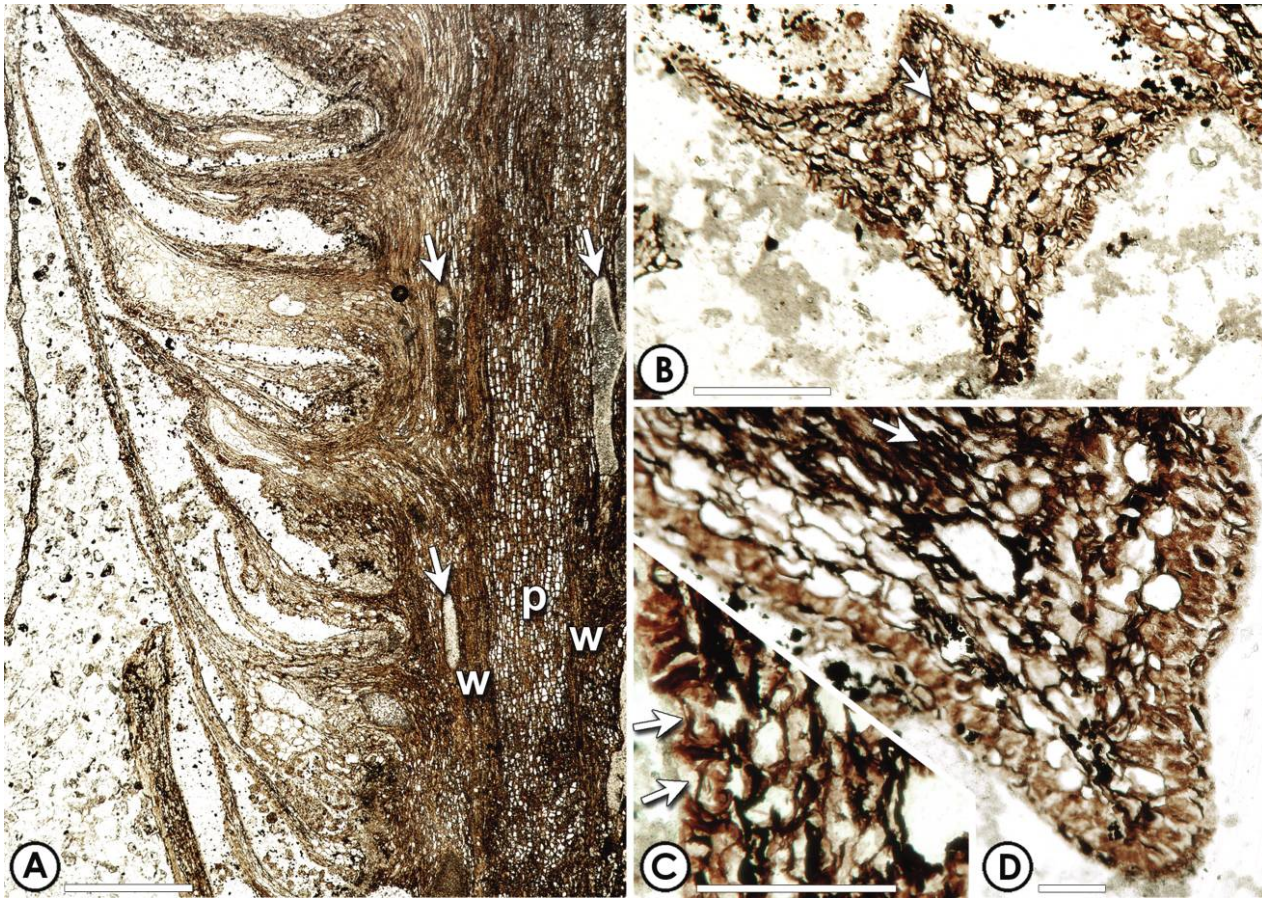


Fig. 2 *Acanthostrobus edenensis* gen. et sp. nov. Holotype UAPC-ALTA P16604. A, Longitudinal section through vegetative shoot showing morphology and histology of stem and diverging leaves. Note parenchymatous pith (p) surrounded by cylinder of wood (w) and cortex with resin canal system (arrows). G top #7 × 9. Scale bar = 2 mm. B, Transverse section of diamond-shaped leaf showing single resin canal abaxial to terete leaf trace (arrow). Note parenchymatous mesophyll and prominent epidermis. G x.s. #42 × 75. Scale bar = 0.25 mm. C, Cross section at margin of leaf showing mesophyll and epidermis with two stomata (arrows). G x.s. #41 × 280. Scale bar = 0.1 mm. D, Leaf in cross section showing histology of parenchymatous mesophyll, sclerotic abaxial hypodermis, single resin canal, and terete vascular bundle (arrow). G x.s. #43 × 92. Scale bar = 0.1 mm.

Bract/scale complex. Bract/scale complexes are dominated by the bract, which is inflated and winged (figs. 1A, 1D at top, 3A–3D) and extends from the cone axis for ca. 4 mm before bending abruptly toward the cone apex (figs. 1A, 2A), diminishing in diameter rapidly (figs. 1A at right, 3E) and continuing for an additional 7 mm or more as a terete tip (figs. 1A, 3E). The inflated portion of the bract, with which the diminutive ovuliferous scale is largely contiguous (fig. 3A), is broadly rhomboidal (figs. 1D, 3B). Bracts are up to 6.5 mm wide by 2.3 mm high, as seen in cross sections of the midregion (figs. 1D at top, 3B). The abaxial surface and lateral margins of the inflated portion of the bract are densely sclerotic (fig. 3A, 3B at right, 3C–3E). Mesophyll is composed of closely spaced parenchyma cells with prominent walls (fig. 3A–3D). In some areas of the cone, the mesophyll cells generally lack contents (e.g., fig. 3A, 3B), but in other areas, most mesophyll cells of the bract/scale complexes have amber or black contents (figs. 1D at top; 3A–3D). The distal, apically oriented portion of the

bract is long and narrow and resembles the distal portion of the needle leaf (figs. 1A, 3E).

Vascular tissue to the bract/scale complex diverges from the axial cylinder as a triangular to ovoid collateral bundle (fig. 4A, 4B), 60–70 μm wide. It extends distally through the inflated portion of the bract (e.g., fig. 4C) and does not divide horizontally. At the level of ovule attachment, the vascular bundle consists of a loose aggregation of tracheids, but at more distal levels, vascular tissue has not been identified. The manner in which the putative vascular trace to the ovuliferous scale and/or ovules diverges from that of the bract is unknown. The vascular trace of the bract/scale complex is accompanied by a single abaxial resin canal, ca. 90 μm in diameter (fig. 4A at bottom center), which branches from the axial resin canal system (fig. 1A at bottom center). At the base of the bract/scale complex, the resin canal gives rise to two additional canals laterally (fig. 4C). These lateral resin canals are of smaller diameter, 40–45 μm , and continue to successively divide within the

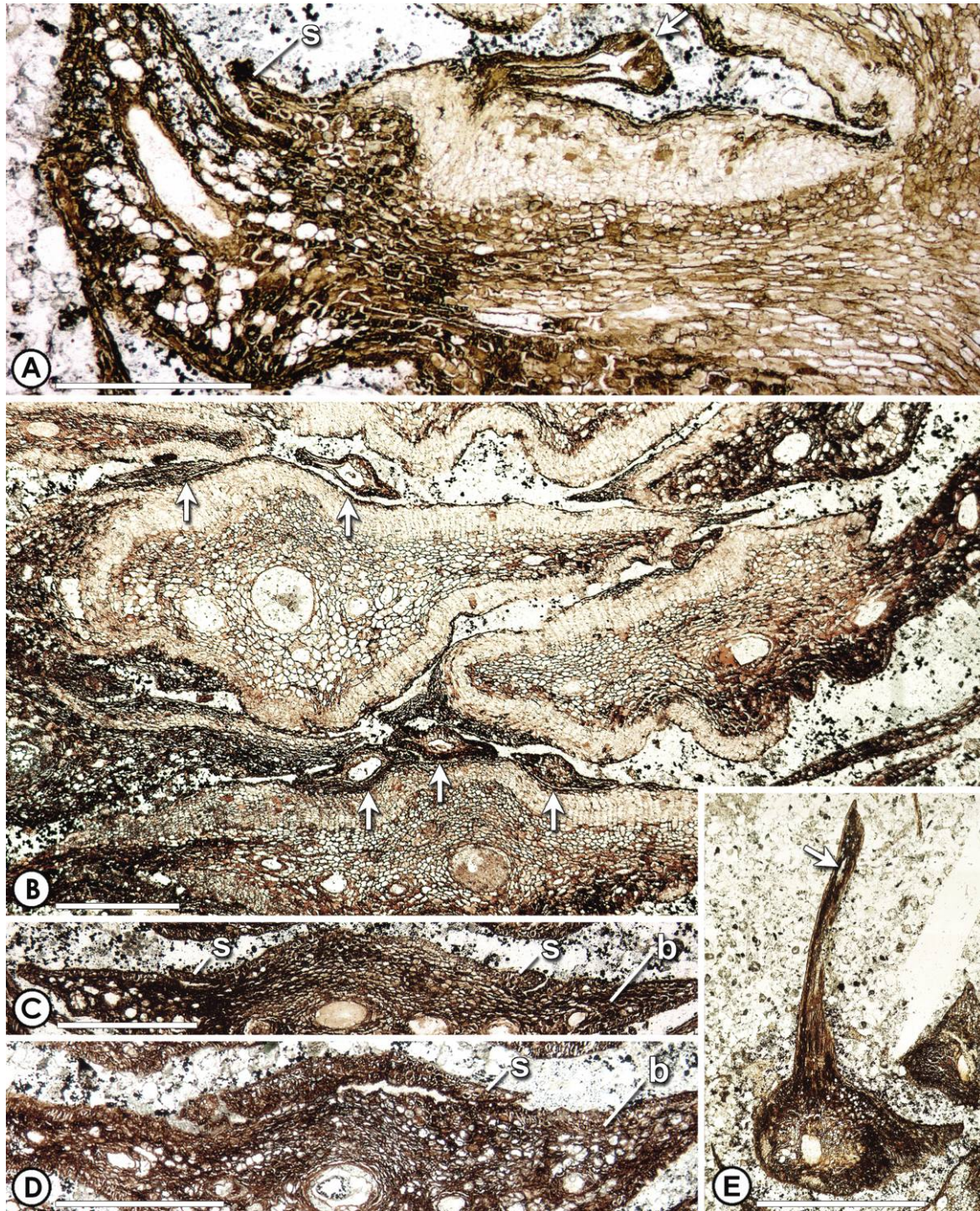


Fig. 3 Cone of *Acanthostrobus edenensis* gen. et sp. nov. Holotype UAPC-ALTA P16604. *A*, Longitudinal section through bract/scale complex showing large bract with diverging free tip of ovuliferous scale (s) and one inverted ovule. Note parenchymatous and sclerenchymatous mesophyll and radially aligned cells of secondary closing tissue and/or wound response tissue on adaxial side of bract/scale complex below ovule and also on abaxial side of distally adjacent complex (above). Arrow indicates position of ovule micropyle. G top #4 × 67. Scale bar = 0.5 mm. *B*, Tangential section of cone showing bract/scale complexes in cross section near level of seed attachment. Complex near top has two immature seeds in positions of attachment (arrows) above and complex with two immature seeds in growth positions, resin canals, and histological features, including extensive development of secondary tissues immediately below epidermis. Bract/scale complex near bottom has three immature seeds and comparable histological features. F bot #51 × 22. Scale bar = 1 mm. *C*, Cross section of bract/scale complex at level where scale tip is beginning to separate from bract (b) at lateral margins (s). G top #179 × 25. Scale bar = 1 mm. *D*, Cross section of bract/scale complex slightly more distal than *C* showing free tip of separated ovuliferous scale (s) above bract (b). G top #202 × 28. Scale bar = 1 mm. *E*, Tangential section of cone in longitudinal section showing inflated horizontal region of bract with single resin canal and upturned terete apical region with single resin canal (arrow). F bot #171 × 14. Scale bar = 2 mm.

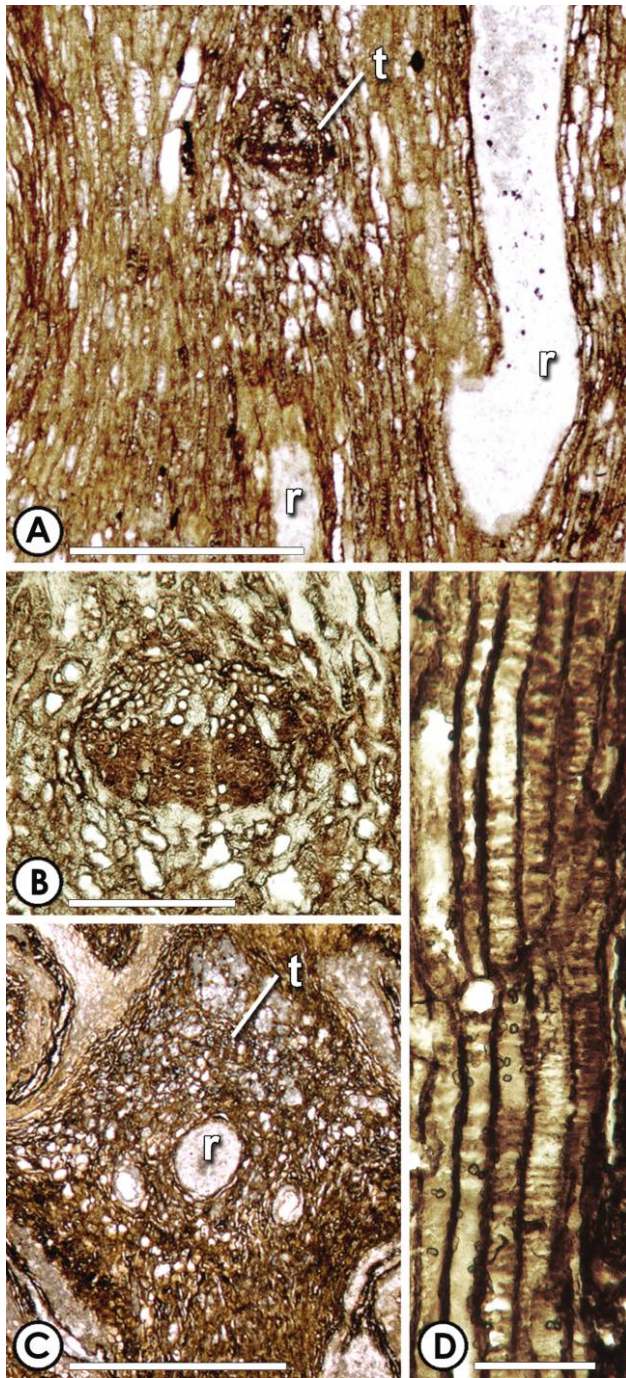


Fig. 4 Cone of *Acanthostrobus edenensis* gen. et sp. nov. Holotype UAPC-ALTA P16604. **A**, Longitudinal section of cone axis showing trace (t) to bract/scale complex at level of divergence immediately distal to resin canal (r) that diverged from axial resin canal (e.g., at right). G top 52 × 65. Scale bar = 0.5 mm. **B**, Enlargement of trace to bract/scale complex near level in **A** showing collateral bundle with xylem above and phloem below. G top 69 × 115. Scale bar = 0.2 mm. **C**, Tangential section of cone showing diamond shaped bract/scale complex just distal to level of divergence, with single trace (t) adaxial to three resin canals (r). G top 93 × 30. Scale bar = 1 mm. **D**, Radial section of xylem in cone axis showing tracheid wall thickenings. G top 2 × 340. Scale bar = 50 μ m.

inflated portion of the bract, producing a row of up to nine resin canals (figs. 1B at top, 3B–3D).

The ovuliferous scale separates from the adaxial surface of the bract distal to the positions of ovule attachment (fig. 3A), forming a single free tip that is 1.8–1.9 mm long and up to 3.4 mm wide (fig. 3A, 3D). Separation begins at the sides of the scale tip (fig. 4C, s) and proceeds toward the center in more distal sections. The free tip of the ovuliferous scale is sclerotic (fig. 3C, 3D) and is not dissected or lobed as in some other basal taxodioid Cupressaceae.

Ovules. The ovuliferous scale bears two to four inverted ovules adaxially (figs. 1A, arrowheads, 3B, arrowheads). Three ovules are most common, but at least one complex with four has been identified. Complexes with two ovules occur toward the cone apex (fig. 3B, arrows near top). Complexes with three ovules bear the central ovule directly adaxial to the central resin canal (fig. 3B at bottom), but there is no ovule in that position directly adaxial in complexes with two or four ovules (fig. 3B at top).

Ovules are flattened and winged (figs. 3B, 5B), measuring up to 1 mm long and 170 μ m high. At the widest point, where the integument forms two lateral winglike flanges (figs. 3B, 5B), the largest ovules are 1.3 mm wide. All attached ovules are immature and generally lack histological differentiation of the integumentary layers (figs. 3B, 5A, 5B), although sclerotesta is present near the micropyle of some specimens (figs. 3A, arrow, 5A). This indicates that integumentary differentiation is basipetal, as is characteristic for gymnosperms. The nucellus typically consists of a solid mass of shrunken tissue attached to the integument at the chalaza and free distally (fig. 3A). There is no hollow at the base of the nucellus, and megagametophyte tissue has not been observed in any of the ovules (figs. 3A, 5B, 5C), revealing that the ovules may have been preserved at a stage prior to megasporogenesis. Near the apex of the cone, an immature and/or aborted bract/scale complex bears a tiny erect ovule (fig. 5C), suggesting that seeds of this species are secondarily inverted.

Arthropod galleries and wound response. Several areas of the cone axis and bract/scale complexes contain arthropod galleries. Galleries containing spheroidal to ellipsoidal coprolites measuring 40–120 μ m in diameter are round to cylindrical in cross section and 280–610 μ m wide (figs. 1A, 5D, 5G). Galleries in the axis (fig. 1A, g) and bract/scale complexes (fig. 5D, 5F) are surrounded by darkened, atypical ground tissue and sequestered from the remainder of the cone by narrow zones of radially aligned, thin-walled, secondary parenchyma cells that form a closing tissue (fig. 5D, 5F, 5G). The largest of these enclosed zones (fig. 1A, g) is vertically elongated, ca. 0.7 mm in diameter. Darkened cells interior to the closing tissue are of smaller diameter than typical cortical cells (fig. 5G at center). We interpret these cells as necrotic tissue. Coprolite-filled galleries extend at least partially through the necrotic zone (fig. 5G). Finally, there is an ellipsoidal gallery within a bract/scale complex, midway between the base and the level of seed attachment (fig. 5D, 5F). This latter gallery measures ca. 0.2 mm × 0.5 mm in section view and contains an irregularly shaped, dark-colored substance that shows no plant cell wall structure (fig. 5F); it is surrounded by two or more layers of more or less radially aligned, thin-walled cells of secondary origin.

Secondary ground tissue occurs throughout the cone as light-colored thin plates comprising 2–15 rows of radially aligned parenchyma cells (fig. 5). This tissue developed in multiple sites: within the cortex of the cone axis (fig. 5D), between

the cone axis and bases of ovuliferous scales (fig. 5C, 5E), adjacent to the epidermis on both the abaxial and adaxial surfaces of the bracts (fig. 5A, 5B, 5D), and within the ground tissues of the bract/scale complexes (fig. 5D, 5E, 5G). This ex-

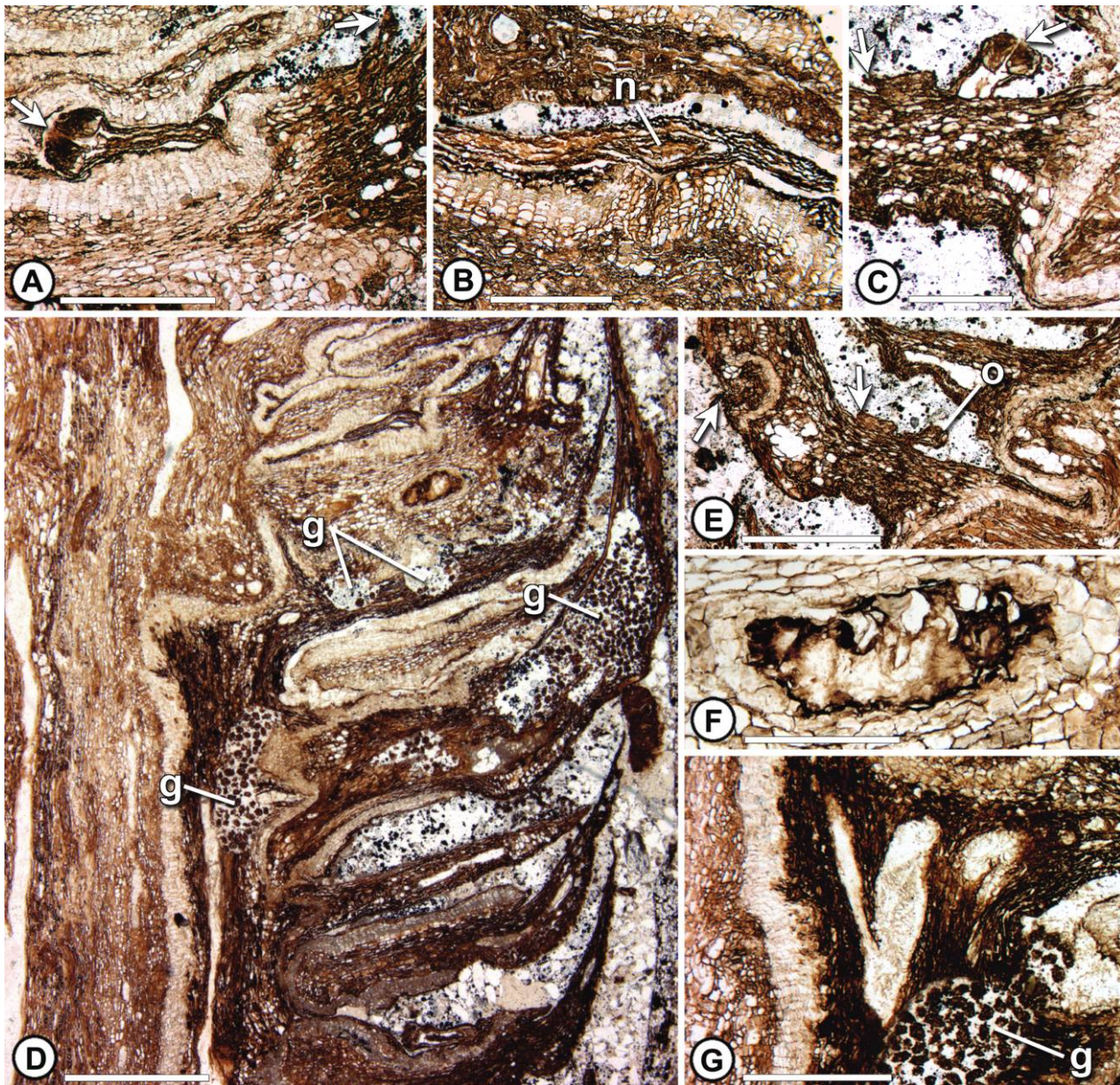


Fig. 5 Evidence of plant-animal interactions in *Acanthostrobus edenensis* gen. et sp. nov. Holotype UAPC-ALTA P16604. *A*, Longitudinal section through ovuliferous scale bearing inverted ovule proximal to free tip (arrow). Note micropylar opening (arrowhead) of inverted ovule oriented toward cone axis and sclerotesta differentiated at apex. G top #8 × 48. Scale bar = 2 mm. *B*, Transverse section through ovule in growth position showing expansion of integument to form lateral wings and solid nucellus (n) adjacent to zone of closing tissue made of radially aligned secondary parenchyma. G top #142 × 76. Scale bar = 0.25 mm. *C*, Longitudinal section through bract/scale complex near cone apex showing erect, putatively aborted ovule primordium proximal to free tip (left arrow) of ovuliferous scale. Right arrow identifies micropyle of ovule with sclerotesta differentiated distally. Note radially aligned cells forming closing tissue that separates bract/scale complex from tissue of cone axis (at right). G top #18 × 64. Scale bar = 0.25 mm. *D*, Longitudinal section through cone axis and ovuliferous scale complexes showing wound response (radially aligned cells) to arthropod dwelling galleries (g) with internal coprolites. G top #23 × 22. Scale bar = 1 mm. *E*, Longitudinal section through putatively aborted bract/scale complex showing developing ovule primordium (o) proximal to free scale tip (right arrow). Note isolated zone of wound parenchyma (left arrow). G top #10 × 22. Scale bar = 1 mm. *F*, Longitudinal section of bract ground tissue showing resin-filled gallery lacking coprolites. G top #18 × 120. Scale bar = 0.2 mm. *G*, Longitudinal section through outer cortex of cone axis showing gallery segregated from cone axis by closing tissue. G top #31 × 46. Scale bar = 0.5 mm.

tensive proliferation may have occurred in response to excavation of galleries. Such tissue is also present immediately below the positions of ovule attachment (figs. 4A, 5A, 5B) and resembles closing tissue commonly produced in the regions of seed abscission in other cupressaceous cones (e.g., *Hughmillerites juddii* [Seward and Bancroft] Rothwell, Stockey, Mapes et Hilton). Unlike closing tissue in other taxodioids, in *A. edenensis*, the radially aligned secondary ground tissue is continuous with the extensive thin plates of secondary ground tissue described earlier (figs. 4A–4C, 5A–5G).

Discussion

The conifer described here as *Acanthostrobus edenensis* gen. et sp. nov. exhibits a plexus of morphological and anatomical characters shared only with other basal members of Cupressaceae (Farjon 2005; Escapa et al. 2008; Rothwell et al. 2011; Atkinson et al. 2014a, 2014b). The plant has helically arranged needlelike leaves, and the terminal seed cone consists of a large number of helically arranged bract/scale complexes. Each bract/scale complex is dominated by an inflated bract, with the ovuliferous scale small and inconspicuous (fig. 6). Two to four flattened, inverted seeds with a narrow wing are attached to the adaxial surface of the bract/scale complex immediately proximal to the separation of a single short scale tip (fig. 6). The new cone, however, differs from all living basal Cupressaceae in the combination of anatomical characters it exhibits (table 1 and its distinctive bract morphology).

Among extant Cupressaceae, the ovuliferous scale is inconspicuous in basal members of the family (Escapa et al. 2008). In *Taiwania* Hayata and *Athrotaxis selaginoides* D. Don, the scale is entirely fused to the bract (Eames 1913; Liu and Su 1983), appearing as only a small bulge in the latter (Eames 1913; Jagel 2001). In *Athrotaxis cupressoides* D. Don, the ovuliferous scale is larger than the bract and separates from it near the tip, while in *Athrotaxis laxifolia* Hook., the ovuliferous scale, although large, appears as mostly a bulge on the adaxial surface of the bract (Eames 1913) and not as an entirely separate structure. The single short, free scale tip of *Acanthostrobus* resembles that of *Cunninghamia* (Lambert) Hooker (Farjon 2005; Rothwell et al. 2011; Serbet et al. 2013).

Acanthostrobus, however, has two to four ovules per bract/scale complex and thus compares more closely to *Athrotaxis* (which bears three to six seeds) than to living and extinct species of *Cunninghamia* (typically three seeds per complex; Serbet et al. 2013) or *Taiwania* (two seeds per complex or, less commonly, one; Farjon 2005). In *Athrotaxis*, as in *Acanthostrobus*, the terminal scales of the cone lack ovules (Jagel 2001). *Sciadopitys* (Sciadopityaceae) is also characterized by the presence of multiple seeds per bract/scale complex, but the ovuliferous scale and bract are similar in size and exhibit less fusion than in cupressaceous cones (Farjon 2005).

Vascularization of the *Acanthostrobus* bract/scale complex is similar at its origin to that of *Cunninghamia* (Radais 1894; Aase 1915; Nishida and Higa 1985), occurring as a single unit with a slight abaxial curvature. The origins (if any) of an ovuliferous scale trace in *Acanthostrobus* have not been demonstrated. By contrast, vascular traces in *Athrotaxis* cones are, at their origins from the cone axis, distinctly C-shaped

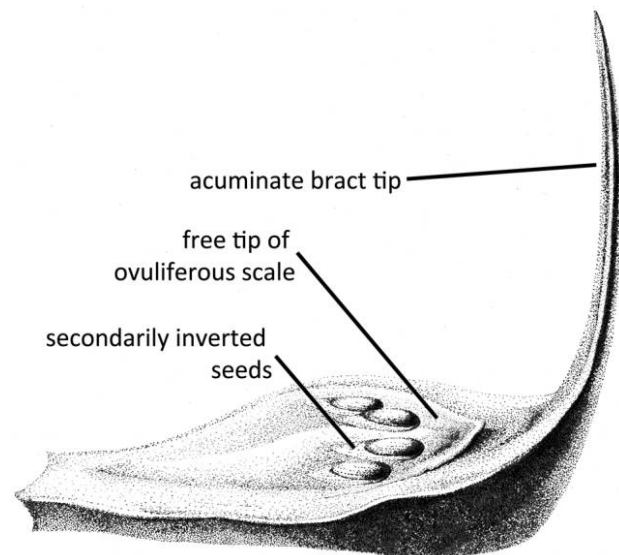


Fig. 6 Reconstruction of bract/scale complex of *Acanthostrobus edenensis* showing condition with four ovules.

(with abaxial curvature) in *A. laxifolia* and *A. selaginoides* and completely cylindrical in *A. cupressoides* (Eames 1913).

Externally, the *Acanthostrobus* seed cone shows distinctly acuminate bract tips that are very elongate (fig. 6). Among living basal Cupressaceae, seed cones of *A. selaginoides* do have pronounced bract tips, but they are not as dramatically elongate as in *Acanthostrobus*. Moreover, the seed cones of this species are roughly ovoid in shape, not cylindrical as in *Acanthostrobus*. Finally, leaves of *A. selaginoides* are less rhomboidal in transverse section than those of *Acanthostrobus*, with a more pronounced vascular strand and prominent scattered adaxial fibers in the mesophyll (Farjon 2005, pl. 27, fig. 3).

Comparisons with Jurassic Cupressaceae

The new cone is easily distinguished from all of the oldest (Jurassic) cupressaceous conifers that have been described previously (Escapa et al. 2008; Rothwell et al. 2011; Zhang et al. 2012). Like extant *Taiwania*, *Austrohamia minuta* Escapa, Cuneo et Axsmith and *Austrohamia acanthobracteata* Zhang, D’Rozario, Wang et Yao have only one or two seeds per ovuliferous scale (more consistently two in *A. acanthobracteata*), which appears to have been entirely fused to the bract (Escapa et al. 2008; Zhang et al. 2012). *Hughmillerites juddii* exhibits three free scale tips, one of which is associated with each of the seeds (Rothwell et al. 2011), whereas in the new cone, the scale tip is entire at its distal margin. Additionally, the ovuliferous scale of *Hughmillerites* forms a distinct interseminal ridge between each of the seeds (Rothwell et al. 2011), a feature not present in *Acanthostrobus*. Finally, *A. edenensis* differs from *H. juddii* in terms of the architecture of the resin canal system within the bract/scale complex. Although both species have a single resin canal at the origin of the complex, in *A. edenensis*, the resin canal divides into multiple lateral canals, whereas in *Hughmillerites*, the initial resin canal does not subdivide, and additional resin canals adaxial to the vascular tissue

Table 1

Comparison of Fossil and Extant Basal Cupressaceae

	Ovuliferous cone											Leaves			
	Age	Shape	Fusion of scale with bract	Vascular trace: first division vertical	Seeds	Intersegmental ridge(s)	Scale distal to seed; entire or lobed	Continuous with axial system	Branching in bract/scale complex	Resin canal system			Stomatal position	Leaf tip shape	
										No. at origin	No. at divergence from cone axis	Position with respect to vascular trace at level of seed body			
<i>Acanthostrobus edensis</i> ^a	Late Cretaceous	Cylindrical	Free at tip	No	(2)3-4	Absent	Entire	Yes	Present	1	3	Abaxial	Rhomboidal	Hypostomatic	?Pointed, ?falcate
<i>Athrotaxis selaginoides</i>	Extant	Ovoid	Free at tip	No	3-6	Absent	Absent	?	Present	1	3	Adaxial	Rhomboidal	Hypostomatic	Pointed, falcate
<i>Austrohamia acanthobractea</i> ^a	Middle Jurassic	Ovoid	Fused	?	1-2	?Absent	Absent	?	?	?	?	?	Dorsiventrally flattened	?	Rounded, ?falcate
<i>Austrohamia minuta</i> ^a	Early Jurassic	Ellipsoid	Fused	?	1-2	Absent	Absent	?	?	?	?	?	Dorsiventrally flattened	?	Rounded, falcate
<i>Cunninghamia lanceolata</i>	Extant	Ovoid	Fused	No	3	Absent	Slightly lobed	Yes	Present	1	1	Abaxial	Dorsiventrally flattened	Hypostomatic	Pointed, nonfalcate
<i>Cunninghamia taylorii</i> ^a	Late Cretaceous	Ovoid	Fused	No	3	Absent	Slightly lobed	Yes	Present	1	?1	Abaxial	Dorsiventrally flattened	Hypostomatic	Pointed, (non)falcate
<i>Cunninghamiostrobus goederitzi</i> ^a	Oligocene	Ovoid	Fused	No	4	Absent	Lobed	Yes	Present	3	3	Adaxial	?	?	?
<i>Cunninghamiostrobus hubei</i> ^a	Early Cretaceous	Ovoid	Free at tip	No	3	Present	Lobed	Yes	Present	3	3	Adaxial	Dorsiventrally flattened	?Amphistomatic	?
<i>Cunninghamiostrobus yubariensis</i> ^a	Late Cretaceous	Cylindrical	Free at tip	No	3	Present	Absent	Yes	Present	3	3	Adaxial	?	?	?
<i>Elatides bommeri</i> ^a	Middle Jurassic	Ovoid	Free at tip	?	3	Absent	Entire	?Yes	Absent	?1	?1	?	Rhomboidal	Epistomatic	Rounded, falcate
<i>Elatides harrisi</i> ^a	Early Cretaceous	Ovoid	Free at tip	?	3	?Absent	Entire	?Yes	?Absent	?1	?1	?	Rhomboidal	Epistomatic	Rounded, falcate
<i>Elatides williamsonii</i> ^a	Early Cretaceous	Ovoid	Free at tip	?	5	?Absent	Lobed	?	?	?	?	?	Rhomboidal	Hypostomatic	Rounded, falcate
<i>Elatides zhouti</i> ^a	Early Cretaceous	Ovoid	Free at tip	?	4-6	?Absent	Entire or lobed	?	?	?	?	?	Dorsiventrally flattened	Epistomatic	Rounded, falcate
<i>Hubbardiostrobus cunninghamioides</i> ^a	Early Cretaceous	Cylindrical	Free at tip	No	3	Absent	Lobed	No	Absent	0	1	Abaxial	Rhomboidal	?	Pointed, falcate
<i>Hughmillerites iuddii</i> ^a	Late Jurassic	Ovoid	Free at tip	Yes	3	Present	Lobed	Yes	Absent	1	1	Adaxial	?Rhomboidal	?	Pointed
<i>Mikasaostrobus hokkaidoensis</i> ^a	Late Cretaceous	Ellipsoid	Free at tip	Yes	4-5	Absent	Entire	Yes	Present	1	3	Abaxial	Rhomboidal	Hypostomatic	Pointed, falcate
<i>Parataicania nihongi</i> ^a	Late Cretaceous	Ellipsoid	Free at tip	Yes	5	Absent	Entire	Yes	Present	1	1	Abaxial	?	?	?
<i>Sciadopitys verticillata</i>	Extant	Ovoid	Free	No	5-9	Absent	Lobed	Yes	Present	2	3	Adaxial	Rhomboidal	Amphistomatic	Pointed, nonfalcate
<i>Sewardiodendron laxum</i> ^a	Middle Jurassic	Ellipsoid	Free at tip	No	3	Absent	Lobed	?	?	?	?	?	Dorsiventrally flattened	Hypostomatic	Pointed, nonfalcate
<i>Taiwania cryptomerioides</i>	Extant	Ovoid	Fused	Yes	2	Absent	Absent	Yes	Present	1	1	Abaxial	Dorsiventrally flattened	Amphistomatic	Pointed, falcate

Sources. Stopes and Fujii 1910; Eames 1913; Ogura 1930; Harris 1953; Miller 1975; Liu and Su 1983; Zhou 1987; Miller and Crabtree 1989; Nishida et al. 1992; Saiki and Kimura 1993; Ohsawa 1994; Yao et al. 1998; Farjon 2005; Escapa et al. 2008; Rothwell et al. 2011; Zhang et al. 2012; Serbet et al. 2013; Atkinson et al. 2014a, 2014b; Shi et al. 2014.

Note. Items shown in parentheses indicate rare or occasional cases; a question mark denotes missing, inferred, or ambiguous data.

^a The species is extinct.

originate de novo (Rothwell et al. 2011; Atkinson et al. 2014b). *Acanthostrobus* also differs from the Jurassic compression-impression taxa *Sewardiodendron laxum* and *Elatides williamsonii* Harris. The ovuliferous scale of *Sewardiodendron* is dissected into free tips, each of which is associated with one of typically six seeds (Yao et al. 1998), and although *E. williamsonii* is similar to *A. edenensis* in having a single free ovuliferous scale tip with an entire (or undissected) distal margin, it differs in bearing up to five seeds per scale (Harris 1943). Features of the vascular and resin canal systems cannot be determined for either *S. laxum* or *E. williamsonii*.

Comparisons with Cretaceous Cupressaceae

The combination of characters exhibited by *Acanthostrobus* also distinguishes the new taxon from previously described basal taxodioid conifers from Cretaceous sediments. Compression-impression specimens from Liaoning (China), described as *Elatides harrisii* Zhou, produce a single large resin canal (Zhou 1987), a feature that agrees with the anatomically preserved *Elatides bommeri* Heer from the Wealden Supergroup of Belgium (Harris 1953). Like the Jurassic *E. williamsonii*, these two Cretaceous species of *Elatides* have a free ovuliferous scale tip with an entire margin, and the bracts have an acuminate tip (Harris 1953; Zhou 1987). In these features, *Acanthostrobus* is in agreement with *E. bommeri* and *E. harrisii* but differs with respect to the number of ovules per bract/scale complex, as the aforementioned *Elatides* species bear three ovules per scale (Harris 1953; Zhou 1987). A third species assigned to *Elatides*, *E. zhoui* (Shi et al. 2014), does bear four to six ovules per scale but does not exhibit acuminate bract tips like those of *Acanthostrobus* or *E. harrisii*. Moreover, some ovuliferous scales of *E. zhoui* are distally lobed (in association with ovules), while others remain entire; this character thus appears to be plastic in this species. By contrast, all ovuliferous scales in *A. edenensis* are entire.

Among anatomically preserved Cretaceous Cupressaceae, *Parataiwania nihongi* Nishida, Ohsawa et Nishida from the Late Cretaceous Yezo Group of Hokkaido also has a single free ovuliferous scale tip (Nishida et al. 1992). However, the ovuliferous scale typically bears five seeds, and *Parataiwania* has a discontinuous resin canal system, with lateral abaxial resin canals initiated de novo (Nishida et al. 1992). Furthermore, in *Parataiwania*, the vascular tissue of the bract/scale complex is not inverted (sensu Eames 1913, having xylem adaxial to phloem), as opposed to the condition seen in most basal members of Cupressaceae, including *A. edenensis*, *Cunninghamia* spp., and all three species attributed to *Cunninghamiostrobus* Stopes and Fujii (Ogura 1930; Miller 1975; Miller and Crabtree 1989; Saiki and Kimura 1993; Serbet et al. 2013).

Species attributed to *Cunninghamiostrobus* may not comprise a natural assemblage (Ohsawa 1994), and, excepting that they bear three seeds per ovuliferous scale, cones in this genus have few similarities to extant *Cunninghamia* (Miller 1975). Among characters specific to the ovuliferous cone, the only potential synapomorphy uniting the three species of *Cunninghamiostrobus* is the presence of three resin canals at the origin of the bract/scale complex from the cone axis (table 1). *Cunninghamiostrobus yubariensis* was originally described

by Stopes and Fujii (1910), and the concept of that species was later expanded by Ogura (1930) and Ohana and Kimura (1995) on the basis of specimens collected from the Santonian-Turonian Upper Yezo Group. Unlike the other species attributed to *Cunninghamiostrobus*, and unlike extant *Cunninghamia*, *C. yubariensis* has an ovuliferous scale that is entirely fused to the bract. The bract/scale complex, when viewed in some sections through the chalazal region of the ovules, also appears to exhibit a small interseminal ridge. Ohana and Kimura (1995) describe the seeds as being inserted within adaxial swellings of the scale. In this respect, *C. yubariensis* resembles *Austrohamia* and *Taiwania*, as presented in the transformational series hypothesized by Rothwell et al. (2011). *Cunninghamiostrobus hueberi* Miller and *Cunninghamiostrobus goedertii* Miller and Crabtree from the Lower Cretaceous of California and Oligocene of Washington, respectively, exhibit the free scale tips more typical of basal Cupressaceae (Miller 1975; Miller and Crabtree 1989). Each of the free scale tips is dissected, with an individual lobe associated with each ovule; *C. hueberi* bears three ovules separated by interseminal ridges. *Cunninghamiostrobus goedertii* may bear four seeds per scale (Miller and Crabtree 1989; Rothwell et al. 2011), but with this exception (i.e., some bract/scale complexes of *A. edenensis* bear four ovules), *Acanthostrobus* does not resemble species included in *Cunninghamiostrobus*.

Acanthostrobus likewise does not resemble *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey (2014a), which phylogenetic analyses place within the cunninghamioid clade (Shi et al. 2014). The ovuliferous scale of *H. cunninghamioides* is lobed, and unlike other basal Cupressaceae, the resin canals of the bract/scale complex arise de novo and not from the axial resin canal system (Atkinson et al. 2014a).

Among anatomically preserved basal cupressaceous conifers described to date, *A. edenensis* bears the greatest similarity to *Mikasaastrobus hokkaidoensis* Saiki and Kimura, described from the Upper Cretaceous Yezo Group. In both species, the ovuliferous scale may bear four ovules and is not dissected or lobed (Saiki and Kimura 1993). Additionally, leaves subtending and/or associated with both *M. hokkaidoensis* and *A. edenensis* are hypostomatic with sunken guard cells (Saiki and Kimura 1993). The architecture of the resin canal system of *Mikasaastrobus* is a configuration shared with extant *Athrotaxis*, the three species of *Cunninghamiostrobus*, and *A. edenensis*. In all of these conifers, there are three resin canals present at the base of the bract/scale complex. However, only in *Mikasaastrobus* and *Acanthostrobus* are the three resin canals derived from the axial system as a single initial canal.

Acanthostrobus does differ from *Mikasaastrobus* in the morphology of the bract/scale complex, which in *Mikasaastrobus* is distally spatulate (Saiki and Kimura 1993), whereas the bracts of the *A. edenensis* have a distinctly acuminate apex. Cones of the two genera also differ in terms of the architecture of the vascular system, which in *Mikasaastrobus* is similar to *Parataiwania* in that the vascular strand is not inverted (Saiki and Kimura 1993). Furthermore, *Mikasaastrobus* is also more similar to *Parataiwania*, *Taiwania*, and the Jurassic *H. juddii* in that the basal branching of the vascular trace is horizontal, not vertical as it is in most basal cupressaceous taxa including a Cretaceous species of *Hughmillerites* (e.g., Rothwell et al. 2011; Atkinson et al. 2014b).

The novel combination of characters exhibited by the seed cone of *A. edenensis* (i.e., single free bract tip, two to four seeds, architecture of the vascular and resin canal systems, dramatically attenuated leaf and bract tips; table 1) clearly distinguishes this new genus from all previously described genera and species of basal Cupressaceae (Escapa et al. 2008; Rothwell et al. 2011; Atkinson et al. 2014a; Shi et al. 2014).

Plant-Animal Interactions

The cone of *A. edenensis* shows both structural specializations for predator deterrence and physiological response to arthropod damage. The extremely long spinelike leaf and bract tips give the seed cone a distinctly burrlike appearance, suggesting animal-mediated whole-cone dispersal for this conifer. However, burrs of living plants that attach to the fur and feathers of animal dispersers typically have barbs or hooks that aid in attachment (Armstrong 1979), whereas the leaf and bract tips of *A. edenensis* are smooth. Moreover, the cone of *A. edenensis* is attached to the vegetative shoot, and there is evidence of seed abscission within the cone as in other cupressaceous conifers (Rothwell et al. 2011). This combination of features suggests the spinelike leaf and bract tips of *A. edenensis* were more likely a specialization for predator deterrence than dispersal. Such spinelike leaf tips would probably have been of little obstacle to vertebrate herbivores (Palo and Robbins 1991; Belovsky and Schmitz 1994; Skarpe et al. 2012) but are in the size range associated with a reduction in infestation by some chewing, sucking, and ovipositing insects (Moles et al. 2013 and references therein).

Obviously, the putative spinelike defenses of *A. edenensis* were not fully effective, as cortical and bract/scale tissues of the cone bear evidence of arthropod infestation (e.g., fig. 5D). Coprolites (= frass) occur throughout the putative arthropod galleries in the cone axis and bract/scale complexes. The margins of these galleries generally exhibit precise cutting, and two tunnels, when seen in transverse section (fig. 5D, upper g), exhibit regular, circular margins. This provides an indication of the maximum size of the arthropod(s) that produced these bores, as the infesting agents must have been no greater than the diameter of the tunnels themselves. Gallery diameters and frass size are consistent with that of oribatid mites (Labandeira et al. 1997; Kellogg and Taylor 2004) and early instar larvae of lepidopteran coneworms (Fatzinger 1970; Merkel 1982; Whitehouse et al. 2011) or conatophagous weevils (Oberprieler 2014).

Oribatid mites, which comprise a diverse assemblage of 10–20 families of soil-dwelling decomposers, are ubiquitous in many paleoecosystems as early as the Devonian (Norton et al. 1988; Norton 1990; Labandeira et al. 1997; Schaefer et al. 2010). Oribatid mite galleries have previously been reported from ground tissues of another Eden Main fossil, the bennettitalean stem *Saxicaulis meckertii* Jud, Rothwell et Stockey (fig. 4E in Jud et al. 2010). The galleries in *A. edenensis* are, however, inconsistent with those of *S. meckertii*, as oribatid galleries in the latter have rough, irregular margins. Moreover, the galleries in *A. edenensis* elicited a host response, indicating that the injury must have occurred while the cone was attached and growing.

Acanthostrobus edenensis contains extensive zones of thin, light-colored plates of radially aligned cells throughout the axis and bract/scale complexes of the cones (figs. 3A, 3B, 5A–5E,

5G). These cells are similar to closing tissues in other cupressaceous seed cones (e.g., *H. juddii*; Rothwell et al. 2011), where such tissue forms in response to seed release from the ovuliferous scale. In the context of *A. edenensis*, these cells proliferate abnormally throughout the cone; we thus infer that they formed in response to injury. This interpretation is consistent with wound response in living plants: in what has been characterized as the hypersensitive response (Bleiker and Uzonovic 2004), a reactive oxidative burst sterilizes the wound site, leading to localized tissue necrosis, followed by development of suberized wound periderm that isolates the injured tissue (Biggs 1985; Franceschi et al. 2005). The radially aligned tissue in *A. edenensis* appears to isolate necrotic tissue from the cone axis (i.e., fig. 5D, 5G; cf. fig. 8(a) in Franceschi et al. 2005). The association of both necrotic tissue and wound periderm with arthropod damage is compelling evidence that the cone was attacked during development.

Despite extensive infestation, there is no evidence of seed predation, which is concordant with a range of specializations known for cone-infesting arthropods (Turgeon et al. 1994). Conatophages, insects that attack and/or inhabit the axis and bract/scale complexes, are thought to be the most ancient and least specialized of seed cone predators, followed by those that infest both the bract/scale complexes and the seeds (conatospematophages); specialization on seeds alone (spermatophagy) is thought to be more derived (Turgeon et al. 1994). Of the three conifer seed cones discovered at the Eden Main locality, which include *A. edenensis*, *H. cunninghamioides* (Atkinson et al. 2014a), and an undescribed species, none shows evidence of seed predation (G. W. Rothwell, personal observation); only *A. edenensis* shows extensive evidence of infestation. This suggests that conatophages were well established by the Coniacian stage of the Cretaceous but that more derived conatospematophages and spermatophages had yet to become established in the environment represented by the Eden Main assemblage.

The conatophage that infested this *Acanthostrobus* cone may have been a lepidopteran coneworm, which is an economically important pathogen of living conifers (Ebel et al. 1980; Barbosa and Wagner 1989), and has been studied predominantly in this context. Most are members of the genus *Dioryctria* (Pyralidae: Phycitinae), and although most *Dioryctria* research focuses on species specializing in Pinaceae, the *pygmaella* group (sensu Whitehouse et al. 2011) infests cupressaceous conifers (Merkel 1982; Whitehouse et al. 2011). Most species feed on cones only as mature larvae (Barbosa and Wagner 1989); after eggs are deposited on cone surfaces, larvae frequently make several exploratory bores (Merkel 1982; Whitehouse et al. 2011). This behavior is consistent with several features in the *A. edenensis* cone: a small zone of isolated wound periderm on one bract (fig. 5E at upper left) and a narrow resin-filled gallery (fig. 5F) could represent initial entrance attempts. In addition to a distinct larval entrance hole, cones infested with *Dioryctria* also generally have obvious frass deposits bound with silk on their surfaces (Ebel et al. 1980; Barbosa and Wagner 1989). A small amount of frass in *A. edenensis* does occur outside of the galleries themselves, between the bract/scale complexes; this could represent wash-out from the gallery during initial entrainment into the surrounding sediments or could be remnants of external frass deposits consistent with coneworm feeding.

Weevils (Coleoptera: Curculionoidea) are also plausible culprits for the damage seen in *A. edenensis*. The late Jurassic through Cretaceous evolution and diversification of weevils is clearly linked to the rise and dominance of conifers during the Mesozoic (Oberprieler et al. 2007). Weevils owe their successful exploitation of conifers to two important adaptations: mycetophagy and the practice of fungal agriculture within wood and evolution of the oviposition rostrum, which facilitates predation upon conifer reproductive structures (Anderson 1995; Oberprieler et al. 2007). Although widespread, the mycetophagous ambrosia weevils (Curculionoidea: Scolytinae) are unlikely contenders, as most construct intricate galleries in stem wood. Although the genus *Conophthorus* does infest cones, these scolytine weevils are predominantly specialists of pineaceous conifers (Barbosa and Wagner 1989). Moreover, females bore into cone bases to construct egg galleries with blind pockets and frequently girdle the cone (Barbosa and Wagner 1989). The galleries in *A. edenensis* do not exhibit egg gallery architecture or axial girdling, and although fungal body fossils have been observed in the cone (A. A. Klymiuk, personal observation), they are not attributable to ambrosia fungi associated with mycetophagous weevils.

Better contenders among the weevils are found within Caridae, an early-diverging family whose members are probably relicts of a more diverse prehistoric fauna (Oberprieler et al. 2007). Many basal weevils specialize in conifer reproductive structures: most are pollen feeding, but at least one carid genus is known to infest seed cones of cupressaceous conifers in the Southern Hemisphere (Oberprieler et al. 2007). Females of the genus *Car* use the oviposition rostrum to drill holes and deposit eggs into seed cones of *Callitris* (Oberprieler et al. 2007). Each cone is typically infested by a single larva, which feeds within the fleshy bract/scale complexes and around the subtending branch (Oberprieler 2014). In both respects, carid beetles are plausible candidates for the infestation in *A. edenensis*. This presumes that damage resulted from an early instar and was limited by the hypersensitive response; in this context, the resin-filled cavity (fig. 5F) may represent the oviposition puncture. Today, carids occur in the Southern Hemisphere,

but like cupressaceous conifers, their fossil record indicates that they were diverse in the Northern Hemisphere during the Late Cretaceous (Oberprieler et al. 2007; Legalov 2012).

Conclusion

Acanthostrobus edenensis displays a unique combination of characters that expands our understanding of Cretaceous evolution and diversification among basal Cupressaceae. The distinctively elongated bracts of *A. edenensis* also represent a novel morphology for cupressaceous conifers. The cone contains feeding galleries and damage consistent with lepidopteran coneworms or carid weevils. Coprolites could be attributed to either and are also similar in dimensions to those of oribatid mites (which, as soil-based detritivores, are not thought to have elicited the host response). Thus, the identity of the arthropod invader remains ambiguous. Because this cone was subject to infestation during development, structural and anatomical features of the host response have been preserved. Necrotic tissues surrounded by wound periderm indicate that this Late Cretaceous conifer employed wound responses comparable to the hypersensitive response of living conifers.

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