



PINACEOUS EVOLUTION ILLUMINATED BY ADDITIONAL DIVERSITY OF EARLY CRETACEOUS SEED CONES

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Abstract: An anatomically preserved fossil conifer seed cone has been discovered near Ono, California, providing additional evidence for the diversification of Pinaceae during the Aptian Stage of the Early Cretaceous. The specimen was measured and photographed, and then serial anatomical thin sections were prepared by the cellulose acetate peel technique. Selected peels were mounted on microscope slides, viewed, and photographed with transmitted light microscopy. Structure of the seed cone is similar to that of living and extinct representatives of the Pinaceae in the occurrence of helically arranged and imbricating foliate bract/scale complexes consisting of a small bract that subtends an ovuliferous scale bearing two inverted winged seeds on the adaxial surface. However, details of bract/scale complex vasculature, a wing that is obviously lateral to the seed body, and distinctive histological features reveal that this cone represents a new genus of extinct Pinaceae. This new genus of fossil conifers, represented by a seed cone of unique structure, further enriches the known diversity of Early Cretaceous Pinaceae. When added to the existing record of fossil seed cones, the new genus and species, *Onostrobis elongatus* ROTHWELL et STOCKEY, highlights knowledge that among early-diverging lineages of Pinaceae there has been considerable Cretaceous and Paleogene evolution that is reflected by variations among subtle characters that are recognizable only from anatomically preserved specimens.

Key words: anatomy, conifer, cotyledonary embryo, Pinaceae, seed cone

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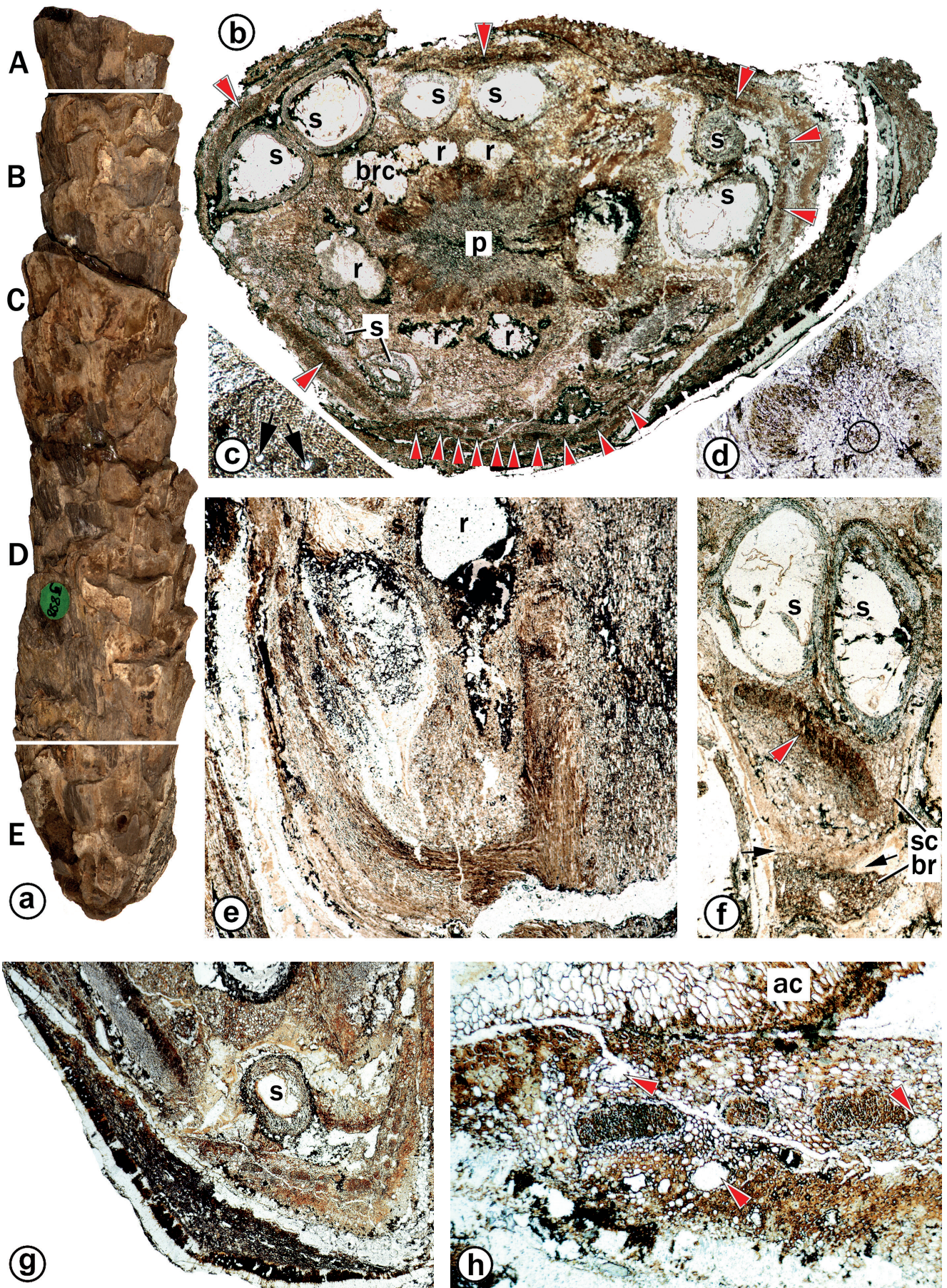
Introduction

Through the characterization of fossils to document the history of life, paleontology provides the best direct evidence for the overall pattern and tempo of plant evolution (Coiro 2023). For conifers, evidence that extends from the Pennsylvanian to the Present (Hernandez-Castillo et al. 2009), reveals that species of Pinaceae evolved no later than the Late Jurassic (Rothwell et al. 2012), and suggests that all pinaceous genera with living species appeared no later than the Eocene (Klymiuk and Stockey 2012, Leslie et al. 2012). Although our knowledge of the overall pattern of pinaceous evolution is constrained by preservational imperfections and by the disarticulated nature of most paleontological evidence, fossilized seed cones that show internal anatomy provide a large percentage of systematically informative morphological characters for conifers and often serve as a reliable proxy for whole plant phylogenies (e.g., Miller 1976, Smith and Stockey 2001, Gernandt et al. 2018). Therefore, the continuing characterization of additional species of extinct conifer seed cones measurably enhances this valuable resource for evaluating conifer phylogeny (Gernandt et al. 2016).

In the current study we characterize and name an additional new genus and species of extinct Early Cretaceous pinaceous conifers based on an anatomically preserved seed cone with a novel combination of systematically informative characters and an unusual overall shape. This cone provides further evidence for explosive evolutionary diversification of Pinaceae during the Early Cretaceous, and for evaluating the generic distribution of pinaceous species toward the end of the Mesozoic.

Material and methods

The specimen consists of a somewhat abraded, anatomically preserved seed cone that was found among other recently redeposited plant and animal fossils in a stream bed located in the southwest corner of Section 12, T30N, R7W of the Ono quadrangle, a short distance from the town of Ono, California (see Stockey and Smith 2000 for details). Because the surrounding deposits are from the same source as rocks of the streambed the cone is almost certainly derived from near the base of the Upper Chickabally Member of the Budden Canyon Formation (Stockey and Smith 2000), which



Text-fig. 1. *Onostrobos elongatus* gen. et sp. nov. Holotype specimen CASG 3888. a: External view of abraded, incomplete cone showing bases of diverging bract/scale complexes. Five segments of specimen lettered A–E. CASG 3,888 x1.2. b: Cross section of cone with parenchymatous pith (p), woody stele, parenchymatous cortex, and helically arranged bract/scale complexes, each with a pair of adaxial, basally attached, winged seeds (s). Ovuliferous scale (OS) traces that consist of a wide xylem bundle

is considered to represent the Bedoulian Stage of Aptian Age (121–113 Ma), Early Cretaceous (Murphy et al. 1969, Dailey 1973; see USGS National Geologic Map Database, Geolex – Significant Publications 2024 [https://ngmdb.usgs.gov/Geolex/UnitRefs/BuddenCanyonRefs_4836.html] for summary).

As discovered, the fossil was broken into three fragments, the end members of which were cut in cross section to produce a total of five cone segments lettered A–E (Text-fig. 1a). Each cut surface was serial sectioned using the cellulose acetate peel technique (Joy et al. 1956) producing cross sections of the cone (Text-fig. 1b). Segment B was then reoriented and peeled to expose the cone in longitudinal sections (Text-fig. 1e, f). Microscope slides were prepared using the xylene soluble mounting medium Eukitt (O. Kindler GmbH & Co, Freiberg, Germany), and images were captured using a Better Light digital scanning back (Better Light Inc., Placerville, California, USA) mounted on a Leitz Aristophot large format camera, and focused through either Summar lenses or a Zeiss WL compound microscope. Images were processed and Text-figures constructed using Adobe Photoshop CS3 (Adobe, San Jose, California). Cone segments, peels, and microscope slide preparations are housed at the Geology Collection of California Academy of Sciences, San Francisco, CA as CASG specimen 3,888.

The new generic and species names are registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP).

Systematic palaeobotany

Order Coniferales GOROZHANKIN, 1904

Family Pinaceae *Pinaceae* SPRENG. ex F.RUDOLPHI, 1830 nom. cons.

Genus *Onostrobus* ROTHWELL et STOCKEY gen. nov.

Type. *Onostrobus elongatus* ROTHWELL et STOCKEY sp. nov.

Plant Fossil Names Registry Number. PFN003375 for new genus.

Etymology. *Ono* + *strobis* (= cone), is proposed to reflect the collecting locality of the holotype specimen.

Generic diagnosis. Pinaceous conifers with cylindrical seed cones having small parenchymatous bracts

and larger ovuliferous scales that remain attached to cone axis at seed dispersal. Ovuliferous scale and bract separating from each other near cone axis, beginning at margins. Bract and ovuliferous scale vasculature originating from axis stele separately, ovuliferous scale trace diverging as three bundles forming an inverted U-shaped configuration. Two inverted winged seeds adaxially attached near base of ovuliferous scale; interseminal ridge absent. Wing attached toward base of seed body and laterally.

Onostrobus elongatus ROTHWELL et STOCKEY sp. nov.

Text-figs 1–3

Holotype. (hic designatus) Paleobotanical specimen CASG 3,888 housed in the Geology Collections, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA.

Repository. Geology Collections, California Academy of Sciences, San Francisco, California, USA.

Plant Fossil Names Registry Number. PFN003376 for new species.

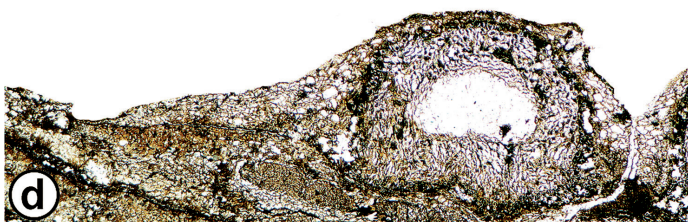
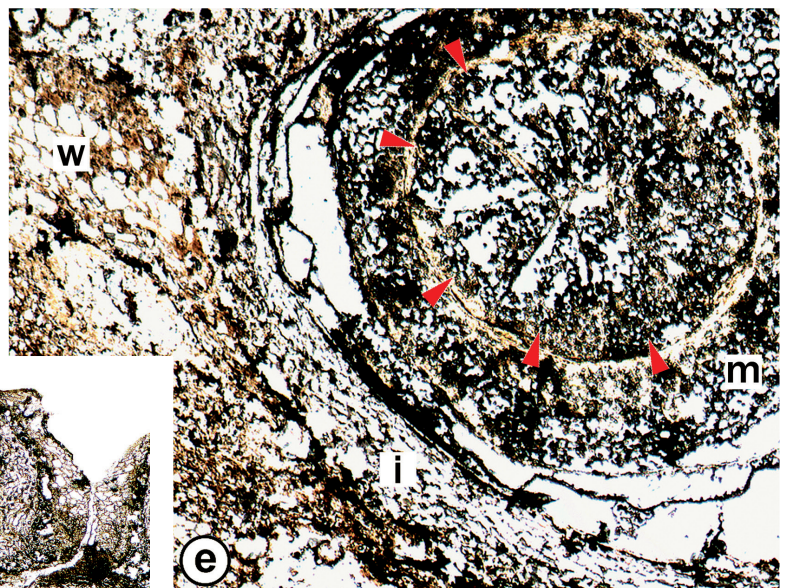
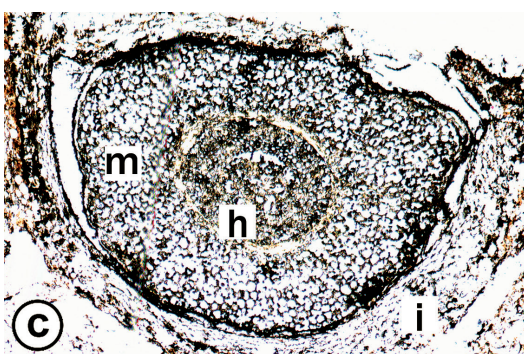
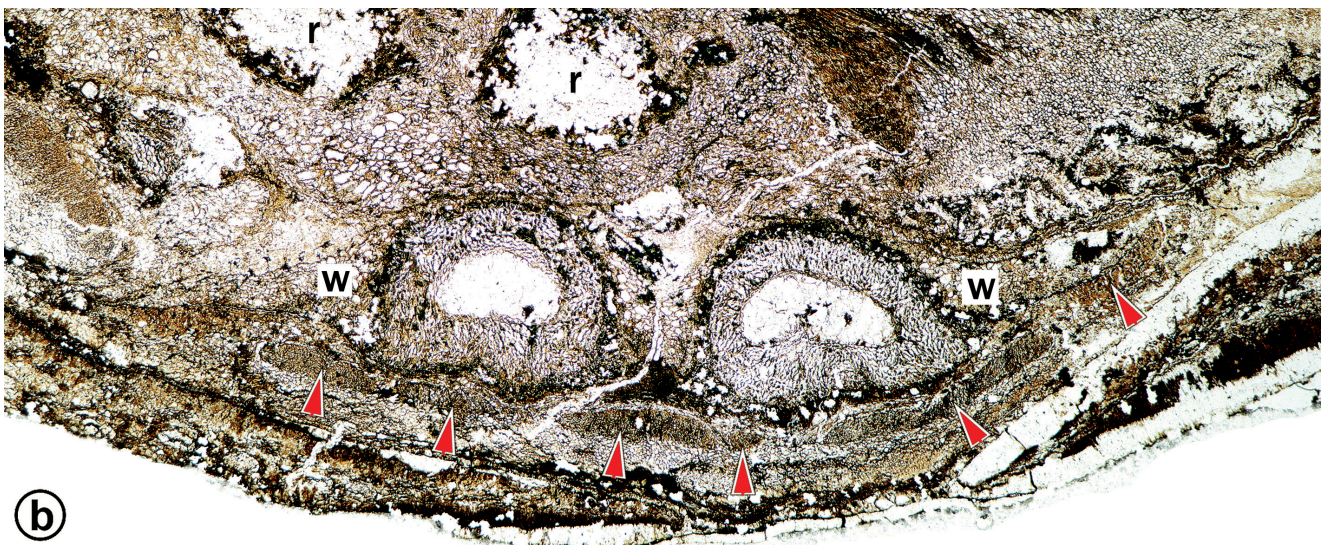
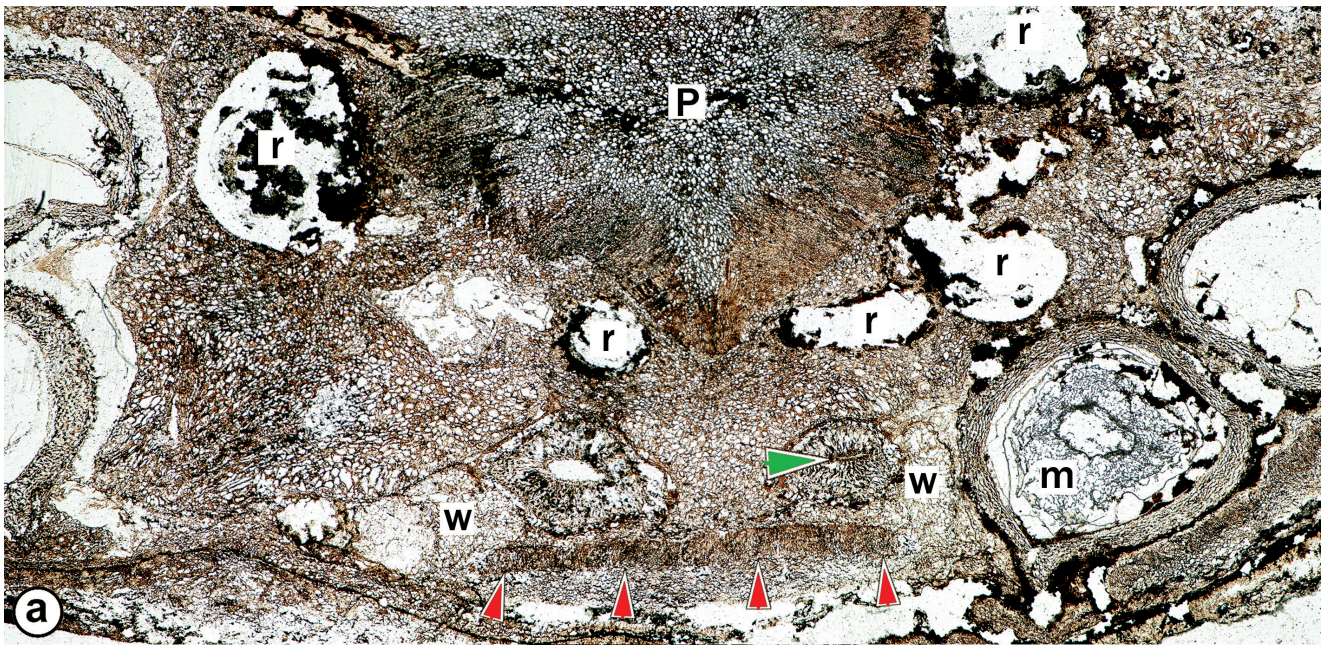
Etymology. The specific epithet *elongatus* refers to the overall shape of the cone.

Type locality. Streambed located in the southwest corner of Section 12, T30N, R7W of the Ono Quadrangle, a short distance from the town of Ono California, USA.

Stratigraphy and age. Upper Chickabally Member, Budden Canyon Formation, Early Cretaceous; Aptian Age; Bedoulian Stage.

Specific diagnosis. Cone more than 16.1 cm long and 2.1 cm wide, with thin, foliate cone scales. Axis with parenchymatous pith and secondary xylem cylinder lacking resin canals; axis stele dissected by divergence of xylem to bract/scale complexes. Bract/scale complex vasculature of three traces forming inverted U-shape in scale base, opening out into single plane to become straight; dividing into several strands in scale base. Bract with at least one accompanying resin canal; bract trace of few loosely arranged tracheids. Large, apparently lysigenous canals in cone axis; two canals abaxial to vasculature of each bract/scale complex. Scales with prominent abaxial and adaxial bands of hypodermal sclerenchyma; resin canals abaxial, adaxial and between vascular bundles in ovuliferous scale. Embryos with ca. 8–9 cotyledons.

(single arrowhead) basally and row of several xylem bundles (multiple arrowheads) more distally. Note pairs of large resin canals (r) associated with each diverging OS trace, some of which branch CASG 3,888 B top No. 27 x6. c: Cross section of OS trace with small holes in wood that resemble resin canals (arrows) among radial rows of incompletely preserved tracheids. CASG 3,888 B side No 71 x36. d: Tangential section showing inverted trilobed, U-shaped OS trace and scattered tracheids of bract trace (within circle) just peripheral to divergence from cone stele. CASG 3,888 B side No. 69 x13. e: Radial section of cone showing diverging xylem to bract/scale complex. CASG 3,888 B side No. 42 x10. f: Tangential section of cone showing ovuliferous scale (sc) with two inverted seeds (s) separating from fleshy bract (b) immediately distal to divergence from cone axis. Bract has one resin canal and no vascular bundle at this level. Note bract and ovuliferous scale separate from margins, inward (arrows) CASG 3,888 B side No. 17 x17. g: Cross section at cone periphery showing ovuliferous scales distal to separation from axis. CASG 3,888 B top No. 24 x7. h: Anatomy of ovuliferous scale in cross section showing segmented bract xylem surrounded by parenchyma, with several layers of sclerenchyma cells toward periphery of both abaxial and adaxial surfaces. Note positions of small resin canals (arrowheads) with incompletely preserved cells of epithelial lining. See also parenchymatous cortex of axis (ac). CASG 3,888 B top No. 22 x31.



Text-fig. 2. *Onostrobus elongatus* gen. et sp. nov. Holotype specimen CASG 3888. a: Cross section of cone showing features of axis and peripheral ovuliferous scale bases. Seeds show bilateral micropylar canal that appears slit-like near apex of seeds (green arrow). Note also continuous band of scale xylem at this level CASG 3,888 B top No. 3712. b: Somewhat more distal level of cone than in (a). Note segmented xylem of scale trace at this level. CASG 3,888 B top No. 32 x16. c: Cross section of seed showing

Description. The holotype is an incomplete ovuliferous cone that is cylindrical and the preserved segment has an extended length/width ratio for a pinaceous seed cone (i.e., ca. 7.7:1; Text-fig. 1a). Despite missing both base and apex, and having been abraded and weathered after fossilization, the specimen measures 16.1 cm long and 2.1 cm in diameter. It preserves the bases of helically arranged bract/scale complexes at the surface (Text-fig. 1a, b), but more apical regions of the scales are missing. Therefore, the presence or absence of a scale apophysis or umbo is unknown.

In cross sections the cone has a parenchymatous pith of cells 20–56 μm in diameter (mean = 37.9 μm , $n = 50$), with prominent walls. The pith is surrounded by a zone of dense wood made up of radial rows of tracheids up to 35 cells wide (Text-figs 1b, 2a). Tracheids are shrunken away from each other, and range 20–30 μm in diameter. Ray cells are not preserved, but there are radially elongated spaces that separate some rows of tracheids that represent the positions where rays originally were located (Text-fig. 2a). Such spaces are 10–20 μm wide suggesting that the rays were uniseriate and constructed of parenchyma cells of about the same diameter. The woody cylinder is interrupted by the divergence of vascular tissue to bract/scale complexes (Text-fig. 1b). No resin canals are present in the pith or wood of the cone axis (Text-figs 1b, 2a).

The cone axis has a conspicuous system of axial canals in the cortex (Text-figs 1b, e, 2a, b), and two are associated with the divergence of each bract/scale complex (Text-fig. 2a, b). Such canal pairs are consistently located abaxial to the diverging ovuliferous scale vascular bundle in the cortex of the cone axis (Text-figs 1b, 2a). They are large and conspicuous near the stele (680–1,000 μm) but decrease in size rapidly toward the periphery of the axis (Text-fig. 2a). A few canals in each cross section are in the process of branching (Text-fig. 1b, at brc, Text-fig. 2a, at brc). Branching canals are dilated to nearly twice the diameter of other resin canals (i.e., up to 1.4 mm; Text-figs 1b, 2a). An epithelial lining appears to be absent from these canals (Text-fig. 3g), and they often display some black contents (Text-figs 1b, 2b).

Although no resin canals have been found in the stele of the cone axis, there are possible examples in the secondary xylem of diverging ovuliferous scale traces (e.g., Text-fig. 1c). Most sections show no evidence of such structures (e.g., Text-fig. 3a, c), but in a few sections there are round structures 31–42 μm in diameter that possibly could be resin canals. Such structures sometimes occur in a row that is close to the interior of the secondary xylem (Text-fig. 3g), and typically have a gray, non-cellular rim, but a few show remnants of what may have been an epithelial lining (Text-fig. 3g, at arrow).

Each bract/scale complex consists of an ovuliferous scale with two adaxially positioned and inverted seeds near

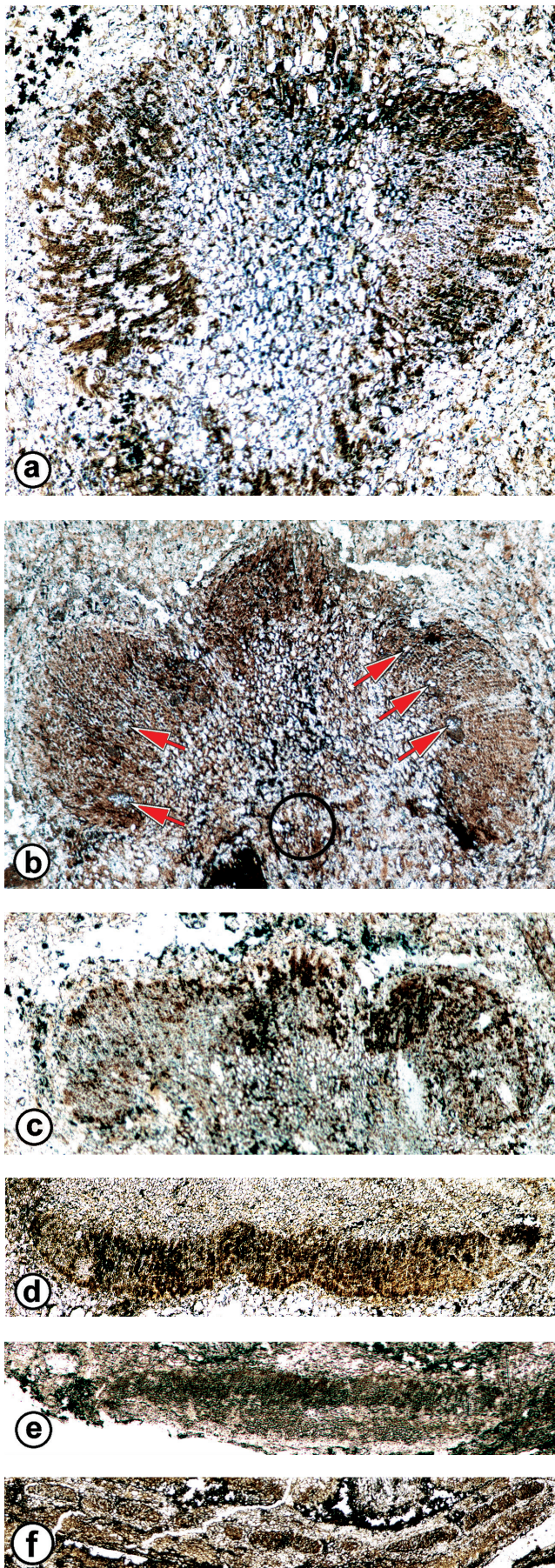
the base. The ovuliferous scale is subtended by a short fleshy bract in which one lateral resin canal is preserved (Text-fig. 1f), but there is no vascular tissue distal to divergence of the bract. Ovuliferous scales are parenchymatous at the level of seed attachment (Text-fig. 1f), but have several layers of both abaxial and adaxial hypodermal sclerenchyma at more distal levels (Text-figs 1b, 2a). As seen in radial sections, the ovuliferous scale xylem separates from the stele at about a 90° angle and then bends gently distally before entering the base of the scale (Text-fig. 1e). In tangential views from the periphery of the stele to the periphery of the cone axis, the scale xylem first appears as bulges (Text-fig. 3a), then separates as three closely adjacent bundles that form an inverted U-shape (Text-fig. 3b). In successively more tangential sections, the scale xylem opens out into a linear, three-lobed configuration (Text-fig. 3c). In transverse sections the scale xylem shows a similar three-lobed configuration within the axis cortex (Text-fig. 3d), and then appears as a straight band of xylem at the margin of the axis (Text-fig. 3e). Shortly after separating from the axis, at the level where seeds are attached, the scale xylem separates into several wide bundles (Text-fig. 3f).

Immediately distal to divergence from the cone axis the ovuliferous scales have several layers of both abaxial and adaxial hypodermal sclerenchyma and interspersed parenchyma (Text-fig. 1h) that gives those with incompletely preserved histology the appearance of having a dark peripheral zone (Text-fig. 1b, g, 2a, b). The ground tissue consists of parenchyma cells between and surrounding the vascular bundles (Text-fig. 1h). There are also a number of small resin canals with an incompletely preserved epithelial lining abaxial to, adaxial to, and between the vascular bundles (Text-fig. 1h, at arrowheads). Tissue preservation deteriorates in quality at more distal levels of the free bracts (Text-fig. 1b, g at lower left), where neither vascular tissue nor resin canals can be identified.

Before separating from the cone stele, vasculature of the bract/scale complex appears as lateral bulges of tracheids in longitudinal sections (Text-fig. 3a). The ovuliferous scale xylem separates from the stele of the cone axis as three adjacent xylem strands that form an inverted U-shaped bundle (Text-fig. 3b, Tab. 1). Toward the periphery of the cone axis cortex, the three bundles fuse to form a U-shaped bundle that opens out into a more linear three-lobed bundle (Text-figs 2a, 3c, d), and then becomes an unlobed linear bundle in cross sections (Text-figs 2a, 3e, f). Distal to the level where the ovuliferous scale separates from the cone axis the bundle divides into 8–10 strands (Text-figs 2a, b at arrowheads, 3f). More distally in the free ovuliferous scales, incomplete preservation precludes identification of vascular tissue (Text-figs 1b, 2a, b).

The bract separates from the ovuliferous scale immediately after the bract/scale complex becomes free from the cone axis. The bract trace divides from the cone

integument (i), cellular megagametophyte (m), and hypocotyl (h) of embryo. CASG 3,888 E top No. 3 x20. d: Cross section of winged seed attached to adaxial surface of cone scale in (b) with other tissues removed to emphasize wing tissue. CASG 3,888 B top No. 32 x16. e: Cross section of seed showing integument (i), cellular megagametophyte (m), and embryo at level of cotyledons (at arrowheads). CASG 3,888 E top No. 3 x23.



Text-fig. 3. *Onostrobus elongaus* gen. et sp. nov. Holotype specimen CASG 3888. a–c: Tangential views. d–f: Cross sections of diverging bract/scale complex vasculature. a: Configuration of vasculature at divergence from stele of

axis stele separately from the ovuliferous scale vasculature. At the level of separation it consists of a small number of loosely arranged tracheids (within circle in Text-figs 1d, 3b). At more distal levels, the bract is constructed of closely spaced parenchyma cells and has one lateral resin canal, but shows no evidence of the bract trace (Text-fig. 1f).

Two inverted winged seeds are adaxially attached near the base each ovuliferous scale (Text-figs 1a, f, 2b, d). Seeds have a body that is ellipsoidal in shape (Text-figs 1b, f, 2b, d), ca. 6 mm long and ca. 3 mm in diameter in the midregion. The integument has a prominent zone of cells that are incompletely preserved, but appear to have thick walls (Text-figs 1b, f, 2b, d). To the inside of that zone there are one or two layers of larger thin-walled cells (Text-fig. 2d, e). The outer integumentary zone surrounds the seed body. It consists of parenchyma cells (Text-fig. 2b, d, e) that are continuous with and have a histology that is identical to that of a seed wing (Text-fig. 2b, d, e) that extends both laterally and basally (Text-fig. 2b, d).

Several seeds contain a cellular megagametophyte of closely spaced thin-walled cells (Text-fig. 2c, e). A few seeds also contain a well-preserved cotyledonary embryo (Text-fig. 2c, e). Embryos are straight. They consist of a hypocotyl that is round in cross sections, consisting of a central zone of presumed vascular tissue and a peripheral cortical zone (Text-fig. 2c). Embryos have several cotyledons apically that are triangular in cross sections (Text-fig. 2e). The exact number of cotyledons cannot be determined from the available evidence, but the seed in Text-fig. 2e has five (at arrowheads), that make up somewhat more than 180° of the circumference of the embryo, suggesting there are a total of ca. 8–9.

Discussion

As emphasized by Germandt et al. (2018) the most systematically informative pinaceous fossils consist of anatomically preserved seed cones that range in age from the Jurassic to the Paleogene. Such cones have helically arranged bracts and ovuliferous scales that are largely separate from each other, two inverted seeds attached adaxially to each ovuliferous scale, and a system of resin canals. A small number conform to two genera with living species (i.e., five species of *Pinus* and one species of *Picea*), with the remainder assigned to four genera of extinct

cone axis. CASG 3,888 B side No. 32 x32. b: Slightly more peripheral section than (a) showing three lobed, inverted U-shaped configuration of scale vasculature and small number of loosely arranged tracheids (circle) representing bract trace within cortex of cone axis. CASG 3,888 B side No. 71 x24. c: More peripheral tangential section of scale vasculature, where bundle has opened out to form three-lobed bar. CASG 3,888 B side No. 25 x22. d: Ovuliferous scale bundle forming three-lobed bar in cross section at about same level as tangential section in (c). CASG 3,888 B top No. 3 x18. e: Cross section of ovuliferous scale bundle forming solid bar at more peripheral level than (d). CASG 3,888 B top No. 27 x16. f: Ovuliferous scale bundle at periphery of cone axis, forming segmented bar. CASG 3,888 B top No. 29 x10.

Table 1. Comparative features of seed cones for living and extinct Pinaceae.

Taxon	Bract/Scale xylem at origin	Scale trace configuration	Cone length/width ratio	Large lysigenous canals abaxial to ovuliferous scale xylem in cone axis
<i>Onostrobus</i> spp.	separate bundles	3 lobed, abaxially concave	> 7.7/1.0	present
<i>Pinus</i> spp.	single bundle	cylinder	< 4.5–1.0	absent
Living non- <i>Pinus</i> Pinaceae	separate bundles	abaxially concave	< 3.0/1.0	absent
<i>Pityostrobus</i> spp.	separate bundles, usually; 8 spp. single bundle	abaxially concave occasionally as 2 bundles	< 2.5/1.0	absent
<i>Obiraostrobus</i> spp.	separate bundles	abaxially concave, may split into 2 bundles	1.6–2.1/1.0	absent
<i>Pseudoaraucaria</i> spp.	separate bundles	abaxially concave	< 3.0–1.0	absent
<i>Eathiestrobus mackenziei</i>	separate bundles	2 terete bundles	2.4–1.0	absent

species (Gernandt et al. 2018). The latter are *Eathiestrobus* ROTHWELL, G.K.MAPES, STOCKEY et J.HILTON (one species), *Obiraostrobus* TAK.OHSAWA, M.NISHIDA et H.NISHIDA (two species), *Pseudoaraucaria* FLICHE (six species), and *Pityostrobus* NATHORST emend. Dutt (1916) (Tab. 1). There are more than 30 species of *Pityostrobus*, but only 29 of the best preserved permineralized cones are considered to be well enough known for them to be included in the most comprehensive phylogenetic analyses of Pinaceae to date (Gernandt et al. 2018).

Onostrobus elongatus represents an additional, previously unknown, extinct pinaceous conifer that has a compact seed cone with helically arranged bract/scale complexes consisting of small parenchymatous bracts subtending larger ovuliferous scales that each bear two adaxially attached, inverted, winged seeds. The holotype specimen is incomplete, but the preserved segment is cylindrical and has a particularly high length (ca. 16.1 cm long): width (2.1 cm) ratio (i.e., 7.7:1) for pinaceous seed cones (Tab. 1). The cone has bracts and ovuliferous scales that separate from each other at about the level of divergence from the cone axis, and the separation progresses from the margin toward the center of the complex. The bract is short and fleshy with one resin canal, and xylem that terminates in the axis cortex. Pith and cortex of the cone axis are parenchymatous, the stele is woody, and there is a system of cortical canals that are conspicuously dilated at levels of branching. Two inverted seeds are adaxially attached near the base of each ovuliferous scale, and there is no interseminal ridge of scale tissue between the seeds. Small resin canals with an epithelial lining occur throughout the parenchymatous tissue distal to the attachment of seeds to the ovuliferous scales. Therefore, *O. elongatus* provides additional systematically informative evidence for the Early Cretaceous diversity of extinct Pinaceae.

Configuration of the bract/ovuliferous scale xylem at the level of divergence from the axis stele in tangential view is one of the most distinctive characters of *Onostrobus elongatus*. Whereas, in *Pinus* the xylem diverges as a cylinder from which the bract trace separates distally (e.g., Miller 1974), in all other pinaceous genera bract and scale xylem diverge separately (Miller 1976, Gernandt et al. 2018). In many living and extinct pinaceous species (e.g., *Pseudoaraucaria* spp., *Pityostrobus lynnnii* (E.W.BERRY) C.N.MILL.), the scale

xylem typically diverges as a single, inverted U-shaped bundle, while in others it separates as two bundles that may or may not fuse at more distal levels (e.g., *Pityostrobus andraei* SEWARD; Alvin 1953). *Onostrobus elongatus* is the only species of Pinaceae that is known to have ovuliferous scale xylem that separates as three bundles (Tab. 1). An additional novel feature of *O. elongatus* is the occurrence of large, apparently lysigenous canals that occur abaxial to the ovuliferous scale xylem in the cone axis (Tab. 1).

Results of the Gernandt et al. (2018) phylogenetic analyses conform to and support the two traditionally recognized major groups of Pinaceae, a pinoid clade and an abietoid grade or clade, and place *Eathiestrobus* at or near the base of the pinoid clade (Gernandt et al. 2018). *Pseudoaraucaria* spp. and *Obiraostrobus* spp. are nested within the abietoids (i.e., Gernandt et al. 2018: fig. 3), and *Pseudoaraucaria* spp. forms a polyphyletic assemblage within the abietoid grade (Gernandt et al. 2018). In those results *Obiraostrobus* spp. forms a small clade that is the sister group to *Pseudoaraucaria gibbosa* (COEM.) ALVIN, all of which are nested among species of *Pityostrobus* within the abietoid grade (Gernandt et al. 2018). In the reduced consensus tree of living+fossil taxa (Gernandt et al. 2018), species of *Pityostrobus* are distributed across the Pinaceae tree as a polyphyletic assemblage of several grades, clades, and individual species (see fig. 3 of Gernandt et al. 2018). Those results are concordant with the broad understanding that the genus *Pityostrobus* is a highly unnatural complex of species with disparate combinations of intergrading characters.

Up to the present, studies of living and extinct Pinaceae have not produced the understanding needed to segregate *Pityostrobus* species into taxonomically meaningful categories (e.g., Smith and Stockey 2001, Gernandt et al. 2018). In an additional attempt to address this issue, we added *Onostrobus elongatus* to the morphological matrix of Gernandt et al. (2018). That analysis employed the methodology of Gernandt et al. (2018) but the results did not reflect improved resolution over previous works (e.g., Smith and Stockey 2001, 2002, Smith et al. 2016, Gernandt et al. 2018). Although addition of *O. elongatus* to the known taxon set does not meaningfully improve phylogenetic resolution of Pinaceae, it does further increase diversity that reflects explosive evolution of the family during the Early Cretaceous.

As a result of the increasing rapidity with which fossilized pinaceous seed cones are being discovered and characterized, and the failure of currently available evidence to allow for resolution of pinaceous phylogeny (see literature cited of Gernandt et al. 2018), we strongly suspect that we are still at an early stage of discovery with respect to extinct species of the family. If so, we can expect that future studies will reveal a much larger number of extinct pinaceous species from the late Mesozoic and Paleogene, and remain optimistic that continuing discoveries and characterizations of fossil seed cones will ultimately facilitate improved phylogenetic resolution of this major seed plant clade.

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