Stockeystrobus gen. nov. (Cupressaceae), and the evolutionary diversification of sequoioid conifer seed cones
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Abstract: An anatomically preserved seed cone from Late Cretaceous (Santonian-Coniacian) sediments of the Yezo Group on the Japanese Island of Hokkaido documents additional diversity among sequoioid conifers, and reveals previously unknown mechanisms for pollination and post-pollination seed enclosure in the conifer family Cupressaceae. The cylindrical seed cone of Stockeystrobus interdigitata gen. et sp. nov. consists of a central axis bearing helically arranged bract-scale complexes. Individual complexes are tightly packed and peltate in form, with completely fused bracts and scales. Peltate heads of adjacent complexes are attached to each other by elongated interdigitating epidermal trichomes. Each complex bears 6 – 8 inverted seeds on the adaxial surface of the inside of the peltate bract/scale complex head. Seeds occur in a single row, are roughly disk shaped, with broad wings in the major plane of symmetry. The nucellus is attached to the seed integument at the chalaza and free distally, with a convoluted apex. This cone reveals greater diversity of sequoioid reproductive biology than is represented among living species, and demonstrates that completely enclosed cones with well protected seeds were produced by Late Cretaceous fossil conifers of the Cupressaceae.

Key Words: conifer, Cupressaceae, pollination biology, Sequoioideae, seed cone
Introduction

The origin, evolution, and paleontological history of cupressaceous conifers have been augmented substantially in the past few years by the discovery of new genera and species among fossils of the Jurassic, Cretaceous, and Paleogene. Species of particularly informative systematic significance are represented by reproductive organs (e.g., Florin 1938-45; Clement-Westerhof and van Konijenberg-van Cittert 1991; Hernandez-Castillo et al. 2001; Hernandez-Castillo et al. 2005; Escapa et al. 2008; Rothwell et al. 2011; Bosma et al. 2012; Leslie et al. 2012). These include the most ancient representatives of the family Cupressaceae (Escapa et al. 2008) and specimens that display apparently pleisomorphic seed cone morphologies within the family (Spencer et al. 2015). Anatomically preserved fossil seed cones serve as important intermediates for a transformational series from Voltziaceae to Cupressaceae (Rothwell et al. 2011). The largest number of such fossils either are assignable to, or have a great similarity to seed cones of the subfamily Cunninghamiaioideae (e.g., Rothwell et al. 2011; Atkinson et al. 2014a, 2014b).

Fossil seed cones that conform to the cupressaceous subfamily Sequoioideae also are commonly preserved in sediments that range from the Upper Cretaceous through the Neogene (Ohsawa 1994; Stockey et al. 2005; Table 1), revealing that the clade previously was more diverse and widespread in the Northern Hemisphere (Farjon, 2005; Stockey et al. 2005). There is even evidence for the presence of the subfamily in the paleontological record of the Southern Hemisphere (i.e., Australia; Peters and Christophel; (1978; Table 1). By contrast to the rich fossil record, the subfamily Sequoioideae is currently represented by only three monotypic genera (i.e., *Sequoia sempervirens* [D. Don] Endl., *Sequoiadendron giganteum* [Lindl.] J. Buchholz, and *Metasequoia glyptostroboides* Hu and W.C. Cheng), each with an extremely limited and apparently relictual geographical distribution (Farjon, 2005). Therefore, specimens
of extinct species play an important role in revealing the patterns of sequoioid evolution and phylogeny by documenting varying ranges of structural diversity within the subfamily through time, by establishing patterns of species richness through time, and by highlighting a wider range of morphology and reproductive biology than are represented by living species.

Carbonate marine concretions from several Late Cretaceous deposits on the northern Japanese island of Hokkaido are one of the most valuable sources of fossils for characterizing diverse assemblages of anatomically preserved, Upper Cretaceous plant remains. Since their original discovery (Reiss 1907) and initial description by Stopes and Fujii (1910), specimens from Hokkaido concretions have contributed important information for characterizing the internal anatomy of late Mesozoic plants. These impressive permineralized assemblages from Hokkaido were reviewed and summarized by Nishida (1991), but numerous additional plants have been described subsequently.

The Hokkaido permineralized plant fossils include several species of seed cones assignable to the Pinaceae, Cupressaceae, and Sciadopityaceae, which provide valuable information for interpreting structural variation and evolution among conifers (Ohsawa 1994). While the largest number of such seed cones is assignable to the cunninghamioid Cupressaceae, there are several species of permineralized seed cones from Hokkaido and elsewhere that represent the subfamily Sequoioideae (Table 1). In the current paper we describe a previously unknown type of permineralized sequoioid seed cone from the Upper Cretaceous of Hokkaido, and interpret several aspects of its relationships and reproductive biology. Interestingly, this species shows a convoluted apex of the nucellus that reveals a specialized mode of pollination which is similar to that which has been documented for some living and extinct species of Araucariaceae and Podocarpaceae, but previously has not been found within the family Cupressaceae. This new Cretaceous sequoioid seed cone Rothwell and Ohana
conifer also has a distinctive mechanism for post-pollination sealing of the cone that may be a novel specialization for species that are intermediate between the essentially open seed cones of cunninghamioid Cupressaceae and the “juniper berries” that characterize some of the most highly derived seed cones of cupressoid Cupressaceae (Lemoine-Sebastian 1969; Farjon 2005).

**Occurrence, materials and methods**

The anatomically preserved seed cone that forms the basis for this study was collected from the Upper Cretaceous Yezo Group by Mr. Hiroshi Takahashi in a streambed near Tappu, Obiracho, Rumoi-gun on the Japanese Island of Hokkaido. Based upon the most recent stratigraphic work for this area, sediments from which the fossil was collected are most likely part of the Hoborogawa Formation (Yezo Group), which is considered to be Coniacian – Santonian in age (Takashima et al. 2004). The cone was labeled “inflorescence?” among specimens of the Kimura collection of anatomically preserved plants from marine nodules that are housed in the Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan. The specimen was prepared many years ago by the junior author. It is represented by 30 microscope slides of mounted cellulose acetate peel sections prepared from a single seed cone, as well as three unprepared segments of the cone. All of these cone segments and microscope slides, as well as eight additional segments of the concretion (that do not contain parts of the cone), are identified as National Museum of Nature and Science specimen number NSM PP-9373.

The cone was exposed in oblique section by the original saw cut. The segments were glued back together, leaving a space of the appropriate thickness to accommodate the saw kerf (see Fig. 3C), and then recut into six segments (shown in Fig. 1A) to expose the specimen in cross section. A small number of anatomical sections (i.e., peel preparations) were prepared from

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several of the exposed surfaces to document cone features in cross section. Microscope slides were made from those peels. Two 25 x 75 mm slides were made of peels from the apical-most segment (at the top of Fig. 1A; i.e., slides C1-1 and C1-2) and two 25 x 77 mm slides were made of peels from the adjoining face of the next segment (i.e., slides C2-1 and C2-2). These revealed tangential sections near the apex of two bract/scale complexes that are attached near the apex of the cone axis (i.e., Figs. 3A, 5A). Seventeen 50 x 75 mm slides were made of peels showing cone cross sections from surfaces of other segments (i.e., slides a-1, 1-1, 1-2, 1-77, 2, 2-1, 2-2, 3, 3-2, 4, 4-2, 5, 5-1, 5-2, 6, 6-1, and 6-2). The exact surfaces from which the peels were made are not known because those surfaces are no longer exposed. The cone segments were then glued back together, leaving the appropriate thickness to accommodate material lost in the saw cuts, and the specimen was re-cut to expose the cone in slightly oblique radial view (see Fig. 1A). Four 50 x 75 mm slides were made from peels (two from each side of the longitudinal saw cut (i.e., slides L1-1, L1-2, L2-1, L2-2). The cone was also ground from the outside to expose the bract-scale complexes in tangential views (e.g., Fig. 3C), and five 25 x 75 mm slides were made from those peels (i.e., slides T1 – T5).

Peels were made using the cellulose acetate peel technique (Joy et al. 1956). Images were captured with transmitted light at Oregon State University by a Better Light digital scanning back (Better Light, Placerville, California) focused through a Leitz Aristophot large-format camera using either Summar macro lenses or a Zeiss Model L compound microscope, and processed using Adobe Photoshop (Adobe, San Jose, California, USA). Line diagrams of bract/scale complex vascular tissue were prepared by tracing xylem bundles from photographs of the relevant levels.

**Systematic Paleobotany**

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Order Coniferales *sensu* Eckenwalder

Family Cupressaceae Gray

Subfamily Sequoioideae Saxton

Genus *Stockeystrobus* Rothwell & Ohana gen. nov.

*Generic diagnosis:* Cylindrical sequoioid seed cone with large number of helically arranged peltate bract/scale complexes. Adjacent peltate heads closely spaced, connected by interdigitating epidermal trichomes. Vascularization of complexes diverging as single radial bundle; dividing laterally to produce adaxial row of terete bundles, and vertically to produce single abaxial bundle; abaxial bundle dividing distally to form concentric ring within peltate head. Inverted seeds borne in single row on inside of adaxial surface of peltate head; seeds with nucellus free from integument distal to chalaza; nucellar apex convoluted.

*Etymology:* The generic name *Stockeystrobus* (*Stockey* + *strobus* [= cone]) is proposed in honor of Dr. Ruth A. Stockey, Oregon State University, Professor Emerita from the University of Alberta, for her recognition of the global occurrence of anatomically preserved plant remains in Jurassic-Neogene marine deposits worldwide, her tireless development of the paleobotanical history of Canada, and her transformational contributions to the understanding of conifer structure, phylogeny and evolution through time.

*Type species:* *Stockeystrobus interdigitata* Rothwell & Ohana sp. nov., (Figs. 1-5).

*Specific diagnosis:* Cone >4.7 cm long, ~2.7 cm in diameter; woody axis with complete cylinder of secondary xylem, scattered sclereids in parenchymatous pith; cortical resin canals absent. Complex ground tissue parenchymatous, with numerous resin rodlets, abaxially positioned resin canals in peltate head; abaxial hypodermis of closely spaced parenchyma and sclerotic bundles. Conspicuous epidermal cells elongating at lateral margins of bract/scale head.
to form interdigitating trichomes. Seeds six – eight per bract/scale complex, disc-shaped with broad wing surrounding body.


*Type locality*: Stream bed near Tappu, Obira-cho, Rumoi-gun on the Japanese Island of Hokkaido, Japan.

*Stratigraphy and age*: Hoborogawa Formation, Upper Yezo Group; Late Cretaceous (Conacian – Santonian; Takashima et al. 2004).

*Etymology*: The specific epithet *interdigitata* refers to the inter-fingering epidermal trichomes that connect adjacent bract/scale complex heads, and that provide complete post-pollination enclosure of the seeds.

**Description**

The specimen is cylindrical, at least 4.7 cm long and 2.7 cm in diameter, with parallel sides and a rounded apex (Fig. 1A). The cone base is not present, so the original length of the specimen is longer than the preserved segment. More than 40 helically arranged, peltate bract/scale complexes (Figs. 1A, 1B) diverge from the woody axis, each producing a single row of six to eight seeds that fill the interior of the cone (Figs. 1A, 1C, 5C). Tangential views of the cone reveal that each complex head is laterally elongated and either is adjacent to and/or closely spaced with respect to the heads of adjacent complexes (Fig. 3C). This includes the apical-most complexes, which are fertile and appear to be well formed (Figs. 1A, at top; Fig. 5A).

The pith of the cone axis is parenchymatous with small clusters of scattered sclereids (Fig. Cretaceous sequoioid seed cone Rothwell and Ohana
Many pith parenchyma cells have dark contents, but some display clear lumens (Figs. 2A, 2B). Primary xylem is difficult to identify (e.g., Fig. 2B). Vascular tissue surrounding the pith consists of a continuous cylinder of secondary xylem made up of radially aligned tracheids, 24 - 49 µm in diameter, that are rectangular to oval in cross section. Regular radial rows of secondary tracheids extend from near the pith to the periphery of the zone on some radii (Fig. 2A). On other radii (Fig. 2A, upper right; 2B) the evenness of the rows is disrupted about eight to twelve cells from the pith, and there is an abrupt change in the size of the tracheids in each row (Fig. 2B), suggesting the presence of an incomplete possibly traumatic growth ring. However, tracheids throughout the wood are inconsistently preserved as the result of what appears to be destructive calcite recrystallization (Figs. 2A, 2B), irregularities in the tracheid rows undoubtedly having been amplified by taphonomy. Secondary tracheids display wall thickening patterns that range from scalariform (Fig. 2D) to uniseriate, circular bordered pits (Fig. 2D, at blue arrowhead).

Tissues to the periphery of the woody cylinder are incompletely preserved, so that vascular cambium, secondary phloem cannot be distinguished from cells of the primary cortex (Fig. 2A). There is no evidence of resin canals in the cone axis. A continuous zone of periderm made up of several rows of radially aligned cells is present near the margin of the cone axis (Fig. 2A, at p). Bract/scale complexes diverge from the axis at about 90° (Figs 1A and 1B, at red arrowheads) as a slender woody stalk (Figs. 1A, 1B, 2C). Stalks extend for approx. 5 mm before broadening into a head that measures ca. 15 mm wide, 10 mm high, and 2 mm thick, and that lies closely adjacent to the heads of adjacent complexes (Figs. 1A and 1B, at black arrowheads). Internally, the stalk is dominated by a radial woody trace (Figs. 1B, 2C, 4A) that is surrounded by a narrow zone of incompletely preserved ground tissue like that of the cone axis (Fig. 2C),
including a narrow zone of periderm near the surface of the axis (Fig. 2C, at p).

Vascular tissue to each bract/scale complex diverges from the axis as a radial rod (Figs. 1A and 1B at t, 2C; 4A) that divides at the base of the peltate head to produce a line of adaxial collateral bundles (Figs 1C-E, 4B, 4C) and a single abaxial collateral bundle (Figs 1C and 1D, at black arrowheads, 4B). In cross sections of the cone (Fig. 1C) the vascular tissue forms a T-shaped configuration at this level (Fig. 4B). Bundles are represented by radial rows of tracheids (Fig. 3B). The abaxial bundles diverge from the lateral margins of central trace to produce the row of bundles in the complex head (Figs. 1D, 1E; 4B). In the most distal sections the adaxial row (Fig. 4D) forms an irregular line (Figs. 3A, at green arrowheads; 4D, 5A) in which the bundles are roughly inverted in orientation (i.e., with the position of the phloem toward the adaxial surface; directions of green arrowheads in Fig. 3A). The abaxial bundle divides at a more distal level (Fig. 4C) to produce a concentric ring of collateral bundles (Figs. 3A, 4C, 4D) in which the positions of phloem are oriented toward the periphery of the ring (Fig. 3A, in directions of red arrowheads).

Ground tissue of the complex head is often incompletely preserved (Figs 3A-D, 3F), but when well preserved it consists of closely spaced parenchyma cells. There are a large number of resin rodlets in the peltate heads (Fig. 3G), which are quite prominent in those complexes where parenchyma is absent or incompletely preserved (Fig. 3F). Toward the abaxial surface of the peltate head the parenchyma cells are somewhat smaller than elsewhere, and form a hypodermis in which there is a row sclerenchyma bundles (Figs. 3F, 3G at arrow). No resin canals have been identified in the complex stalks, but there are resin canals toward the abaxial side of in the peltate complex heads (e.g., Figs. 1E and 3G, at r). Proximal to the peltate head, the epidermis is made up of small cells and is inconspicuous (Figs. 3F, at bottom; 3G, at right). By contrast, cells of the

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adaxial epidermis become larger and much more prominent near the head (Figs. 3E, at upper left; 3F, at top; 3H, at left). Such epidermal cells have an inflated appearance (e.g., Figs. 3E, 3F, 3H). All epidermal cells become much more elongated at the lateral margins of the peltate head (Fig. 3I), and interdigitate (Figs. 3C-3E, 3H). So tightly interlocking are the trichomes of adjacent complexes (Figs. 3E, 3H) that the interior of the cone must have been almost completely sealed prior to seed dispersal. Interlocking trichomes are unicellular, have a wall at the base, intermittently contain dark contents (Figs. 3E, 3H, 3I), and range up to 500 µm long.

The interior of the cone is tightly packed with inverted seeds that are elongated in longitudinal sections and cut in the minor plane of seed symmetry (Figs. 1A, 1B, 5C, 5E). Individual seeds are attached in a single row to the adaxial surface on the inside of the peltate bract/scale complex head (Fig. 5A), and oriented with the micropyle directed back toward the cone axis (Fig. 5C). In cross sections the seeds appear to be flattened because of the occurrence of a broad wing that surrounds the roughly cylindrical seed body (Figs. 5B, 5D), and that gives the seeds a round/oval outline in longitudinal sections of the major plane of symmetry (Fig. 5D, at bottom). Seeds measure ca. 5.5 mm long, 5.5 mm wide in the major plane of symmetry, and 1.0 mm thick in the minor plane of symmetry.

The integument consists of an outer epidermis (Fig. 5F, at arrows) a zone of sclereids two to three cell layers thick, and an inner zone of thinner walled cells that are incompletely preserved (Figs. 5C-5G). A prominent cuticle is preserved at the inner margin of the integument (Figs. 5E-5G). At the chalaza, the sclerotic zone of the integument is concave in longitudinal sections (Figs. 5C, 5E), and in areas of seed attachment each seed appears to be elevated on a mound of bract/scale complex tissue (Fig. 5A). No vascular tissue has been identified extending toward or entering the base of the seeds.
The nucellus is attached to the integument only at the base of the seed (Fig. 5E). It is free distally, which is emphasized by a prominent nucellar cuticle and an inner integumentary cuticle (Figs. 5E, 5F). There are two or three layers of nucellar cells that surround a central area that either is empty (Fig. 5F) or that contains a granular material (Fig. 5E). The latter may represent the remnants of cellular megagametophyte tissue that otherwise is not preserved. Alternatively, the ovules may have been preserved at the free nuclear stage of megagametophyte development. At the apex of the seed the nucellus consists of incompletely preserved cells, and has a distinctly undulating outer margin of (Fig. 5G). Whether the central area represents a pollen chamber or a cellular nucellar apex could not be determined from the available specimens. However, there is no evidence of pollen within the apical region of the nucellus or elsewhere within the cone or seeds.

**Discussion**

Compact seed cones with large numbers of helically arranged bract/scale complexes are produced by conifers of the Voltziaceae, Cheirolepidiaceae, Pinaceae, Araucariaceae, Sciadopityaceae, Cupressaceae, and Podocarpaceae (i.e., *Saxegothaea*), but many taxa have only one or two seeds per bract/scale complex (i.e., species of Cheirolepidiaceae, Pinaceae, and *Saxegothaea*; Sporne 1965; Rothwell et al. 2005; Escapa et al. 2012; Leslie et al. 2012), whereas *Stockeystrobus* has six to eight. Voltziacean seed cones typically are long narrow structures with a lax arrangement of bract/scale complexes, distinctive evidence of vegetative scales, one to three seeds per fertile short shoot or ovuliferous scale complex, and are much more ancient than the new cone described here (e.g., Florin 1948-51; Mapes and Rothwell 1984; Clement-Westerhof 1988; Hernandez-Castillo et al. 2001; Rothwell et al. 2005; Looy, 2007; Leslie 2011). Compact cones with larger numbers of seeds, like *Stockeystrobus*, are found in the families

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Sciadopityaceae and Cupressaceae (e.g., Hirmer, 1936; Sporne, 1965). Among such species, only cones of Cupressaceae subfamily Sequoioideae and a few Cretaceous cupressaceous conifers of uncertain affinities (e.g., *Cunninghamamites lignitum* [Sternberg] Kvaček) consist of cones with numerous helically-arranged complexes which bear several inverted seeds that are adaxially attached to the underside of a peltate head (Hirmer, 1936; Schulz and Stützel 2007).

*Cunninghamamites* originally was thought to be closely related to the cunninghamamoid Cupressaceae (e.g., *Cunninghamamites* K.B. Presl ex Sternberg) on the basis of similar vegetative features. However, the occurrence of specimens with a solitary pollen cone attached to a leafy shoot (i.e., *Cunninghamamites oxycedrus* Presl ex. Sternberg), and with seed cones composed of helically arranged, peltate bract/scale complexes attached to leafy shoots (e.g., *Cunninghamamites lignitum*, *C. squamosus* Heer; Table 1; Kvaček 1999; Bosma et al. 2012) suggest that those species could have closer affinities to the cupressaceous subfamily Sequoioideae (Table 1).

*Krassilovia mongolica* Herrera, Shi, Leslie, Knopf, Ichinnorov, Takahashi, Crane et Herendeen (Herrera et al. 2015) is an Early Cretaceous (Aptian-Albian) fossil conifer with seed cone characters that are somewhat reminiscent of *Stockeystrobus* and other genera of the Sequoioideae. As also is common among cupressaceous seed cones, those of *K. mongolica* are ovoid with helically arranged bract/scale complexes (Farjon 2005). In agreement with species of Sequoioideae, the ovuiferous scale of *K. mongolica* is roughly peltate with a row of five inverted and winged seeds attached adaxially to the underside of the peltate head (Herrera et al. 2015). However, *K. mongolica* has a narrow bract that separates from the complex and displays a free tip like that of *Cryptomeria japonica* (Hirmer 1936; Takaso and Tomlinson 1989) rather than the completely fused bract and scale of sequoioid cupressaceous seed cones (Table 1).

*Krassilovia* has five extremely distinctive spines at the margin of the peltate scale head that
are reminiscent of those on the ovuliferous scale of *Cryptomeria japonica* and many Permian and Triassic species of Voltziaceae (Clement-Westerhof, 1988; Rothwell et al. 2005), but that interlock with adjacent scales in a unique fashion not known from any other fossil or living conifer (Herrera et al. 2015). Moreover, seed cones of *Krassilovia* disaggregate at maturity to shed individual bract/scale complexes (Herrera et al. 2015), as do some species of some taxodiaceous Cupressaceae (e.g., *Taxodium disticum* [L.] Rich.). If vegetative leafy shoots commonly associated with fossils of *Krassilovia* and assignable to *Podozamites* Braun represent the same plant as *K. mongolica*, then that species may be transitional between Voltziaceae and stem group Cupressaceae (Andrew Leslie, pers. comm., January 2016), but *K. mongolica* does not have the appropriate combination of characters to be assigned to the Sequoioideae.

*Stockeystrobus* shares with most other genera of Cupressaceae, subfamily Sequoioideae a helical arrangement of bract/scale complexes, inverted seeds, and seeds that are attached in a single row (Table 1; Farjon 2005; Stockey et al. 2005). While cylindrical seed cones, like that of *S. interdigitata* are not characteristic of other species within the subfamily, (Table 1; Farjon 2005) some species occasionally produce cones that approach a cylindrical shape (e.g., see *Sequoiadendron giganteum*; https://www.google.com/#q=Sequoiadendron+giganteum).

*Stockeystrobus* also has a unique vascular architecture of the bract/scale complex. As is common for species of Cupressaceae, the bract/scale complex vasculature of *S. interdigitata* diverges from the cone stele as a single bundle (Fig. 2C; Lemoine-Sebastian 1968, 1969) that divides distally (Table 1; Lemoine-Sebastian 1968, 1969; Ohsawa 1994; Rothwell et al. 2011; Atkinson et al., 2014a, 2014b). As interpreted by Lemoine-Sebastian, the adaxial bundles would represent the ovuliferous scale, while the abaxial bundle represents the bract trace (Lemoine-Sebastian 1968, 1969). Only in *Stockeystrobus* does the bract/scale complex vascular bundle...
first divide to produce a row of adaxial “ovuliferous scale trace” bundles and a single abaxial “bract trace” bundle (Figs. 1C-1E), with the abaxial bundle dividing more distally to produce a concentric ring of bundles toward the bract/scale apex (Fig. 3A, 4).

An additional distinctive feature of the bract/scale vasculature of Stockeystrobus is the orientation of the collateral bundles near the bract/scale apex. The adaxial row consists of cauline bundles with the position of the phloem oriented toward the adaxial surface (orientation of green arrow heads in Fig. 3A), whereas the abaxial bundles form a concentric ring with the position of the phloem oriented toward the outside of the ring (orientation of red arrowheads in Fig. 3A). This distal bract/scale complex vascular tissue configuration is not known elsewhere among seed cones of the Cupressaceae (Lemoine-Sebastian 1968, 1969; Ohsawa 1994).

The highly convoluted, invaginated, or “stipitate” (Eames 1913) apical region of the nucellus of S. interdigitata (Fig. 5G) is a particularly distinctive character of Stockeystrobus. Among living and extinct conifers such a convoluted nucellus occurs most commonly in the Araucariaceae (Stockey 1975, 1978). In Araucariaceae this character is associated with a specialized mode of pollination wherein the nucellus extends out of the micropyle of the ovule; pollen lands on the cone scale or extended nucellar apex, and then the nucellus is withdrawn back into the integument as pollen tubes grow toward the megagametophyte (Eames 1913). As illustrated by Eames (1913) for Agathus australis, withdrawal of the nucellar apex back through the micropyle into the seed cavity results in a convoluted surface of the nucellus in post-pollination stages of development (Plate I, Fig. 4 of Eames 1913; Owens et al. 1995). A similar pollination mechanism appears to characterize Saxegothaea conspicua Lindley (Tison, 1908; Chamberlain, 1935), but it is unclear whether the post-pollination nucellus displays a highly convoluted apical region. Although the structure of the pollen chamber has been characterized
for several species of both living and extinct Cupressaceae e.g., Takaso and Owens 1996; Owens et al. 1998; Tomlinson 2012; Spencer et al. 2015), *Stockeystrobus digitata* is the first species of the family in which this character has been found. This feature could be interpreted as either a strong indication that a specialized pollination mechanism like those of Araucariaceae and *Saxegothaea* (Tison, 1908; Owens et al. 1998) also was characteristic of some Cretaceous species of the subfamily Sequoioideae, or that it is plesiomorphic among the (Sciadopityaceae + Cupressaceae) + (Araucariaceae + Podocarpaceae) clade (Leslie et al., 2012) as a whole.

Perhaps the most novel feature of *Stockeystrobus interdigitata* is the closely spaced and elongated epidermal trichomes that occur along adjacent surfaces bract/scale complexes (Figs. 3C, 3D, 4B-D), and that tightly interlock (Fig. 3G) to seal the interior of the cone. Such trichomes are unicellular and represent elongations of the ordinary epidermal cells found elsewhere on the bract/scale complexes. Whereas closely adjacent (e.g., in living species of Sequoioideae prior to seed dispersal) and even laterally fused bract/scale complexes (e.g., in species of *Juniperus*) are common in the family Cupressaceae (Farjon 2005), *Stockeystrobus* is the only genus in which the closely adjacent complexes are connected by tightly interlocking epidermal trichomes to seal the interior of the cone and presumably to protect the developing seeds from predation.

Within Cupressaceae some cones have ovuliferous scales that either develop relatively late with respect to other cone structures, or remain diminutive to maturity, or are so highly fused to the bract that the ovuliferous scale complex appears to be a single structure (e.g., Takaso and Tomlinson 1989a, 1989b, 1990, 1991, 1992; Schulz and Stützel 2007). This has led some authors to suspect that some conifer seed cones may be equivalent to simple, rather than compound shoot systems, and therefore have an independent evolutionary origin from conifers.
that have compound seed cones (e.g., Tomlinson et al. 1993). However, more recent studies that include transformational series of cone scale morphologies from Voltziaceae to Cupressaceae (Rothwell et al. 2011), and that emphasize comparative developmental morphology (Schulz and Stützel 2007) and the regulatory genetics that underlies variations in mature cone scale structure (Rothwell et al. 2011; Rudall et al. 2011; Spencer et al. 2015), reveal that all cupressaceous cones are variously modified compound shoot systems as originally hypothesized by Florin (1951, 1954) and summarized by Rothwell et al. (2011). These studies explain our inability to recognize morphologically distinct bracts and ovuliferous scales in the compound seed cones of sequoioid Cupressaceae, including *Stockeystrobus*.

Throughout the history of lignophytes there has been a progressive trend toward condensation of seed-producing structures into increasingly modified and compact fertile structures (e.g., Rothwell 1982) that represent parallel evolution (Taylor and Taylor 2009) for heightened levels of protection of developing ovules and seeds (Leslie 2011). Notable examples of those are the cupulate seed bearing organs produced by a wide variety of extinct plants referred to as seed ferns (Taylor et al. 2006; Taylor and Taylor 2009; Taylor et al. 2009; Rothwell and Stockey 2016), and the compact seed cones of Bennettitales (Wieland 1906). More specifically to the focus of the current study, ovulate fructifications of the most ancient conifers are lax aggregations of either fertile zones (e.g., *Thucydia mahoningensis* Hernandez-Castillo, Rothwell et Mapes; Hernandez-Castillo et al. 2001) or compound cones (e.g., *Emporia* [Mapes & Rothwell] Rothwell & Mapes spp.; Hernandez-Castillo et al. 2009) that become successively more compact through time (Leslie, 2011).

This trend is clearly reflected by the increasingly compact and consolidated seed cones at successively more distal levels of the cupressaceous phylogenetic tree (i.e., from Subfamily Cretaceous sequoioid seed cone Rothwell and Ohana
Cunninghamioideae to subfamily Sequoioideae to tribe Cupresseae of subfamily Cupressoideae; Farjon 2005). Among living species of conifers, seed protection is achieved either by having the complexes closely-spaced prior to seed dispersal (e.g., Sequoioideae), by the production of spine-like structures on the cones (e.g., Pinus; Coffey et al. 1999; and possibly Krasslovia; Herrera et al. 2015) or by the close spacing and fusion of adjacent complexes (e.g., Juniperus L.). Sealing of the cone by tightly interlocking epidermal trichomes of closely adjacent bract/scale complex heads, and pollination via a mechanism that produces the highly convoluted apical surface of the nucellus (e.g., Eames, 1913) as illustrated by Stockeystrobus, reveals the occurrence of a combination of reproductive specializations that previously have been unknown among living or extinct cupressaceous cones. These mechanisms not only emphasize that that the subfamily Sequoioideae was more systematically diverse in the Late Cretaceous than in the modern flora, but also reveals that the extinct sequoioid conifers were more biologically diverse as well.

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Palaeontographica 166 B: 1-15.


Table 1. Morphological/anatomical characters of living and extinct seed cones that conform to the sequoioid Cupressaceae. Characters of *Stockeystrobus interdigitata* and concordant characters of other species in bold type.

<table>
<thead>
<tr>
<th>Character Species</th>
<th>Geol. Age/range</th>
<th>Shape</th>
<th>Length (mm)</th>
<th>Max. diam. (mm)</th>
<th>Complex arrang.</th>
<th>No. of complexes</th>
<th>Axial resin canals</th>
<th>Complex form</th>
<th>Interdigitate tricomes</th>
<th>V. T. in peltate head</th>
<th>Seeds per scale</th>
<th>Rows of seeds</th>
<th>Seed orient.</th>
<th>Seed wing</th>
<th>Convoluted nucellar apex</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Stockeystrobus interdigitata</em></td>
<td>Late Cretaceous (Coniacian-Santonian)</td>
<td>cylindrical</td>
<td>&gt;42</td>
<td>24</td>
<td>helical</td>
<td>&gt;40</td>
<td>-</td>
<td>peltate</td>
<td>+</td>
<td>adaxial row + abaxial ring</td>
<td>6-8</td>
<td>1</td>
<td>inverted</td>
<td>wide</td>
<td>+</td>
</tr>
<tr>
<td>1. <em>Archicupressus nihonii</em></td>
<td>Late Cretaceous (Coniacian-Santonian)</td>
<td>ellipsoidal</td>
<td>38</td>
<td>17</td>
<td>helical</td>
<td>12+</td>
<td>+</td>
<td>peltate with apical spine</td>
<td>-</td>
<td>reniform ring</td>
<td>1</td>
<td>1</td>
<td>erect</td>
<td>narrow or absent</td>
<td>-</td>
</tr>
<tr>
<td>2. <em>Aurosequoia wintonensis</em></td>
<td>Late Cretaceous</td>
<td>ellipsoidal</td>
<td>9-16</td>
<td>6-11</td>
<td>helical</td>
<td>29-49</td>
<td>-</td>
<td>peltate</td>
<td>-</td>
<td>2 bundles</td>
<td>4-7</td>
<td>1</td>
<td>inverted</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>4. <em>Cunninghamites squamosus</em></td>
<td>Late Cretaceous</td>
<td>ovoid</td>
<td>45-63</td>
<td>30-42</td>
<td>helical</td>
<td>&gt;34 (≤52)</td>
<td>?</td>
<td>peltate with apical spine</td>
<td>-</td>
<td>?</td>
<td>2 (or more)</td>
<td>1</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>5. <em>Drunellera kurmanniae</em></td>
<td>Late Cretaceous (Campanian)</td>
<td>ellipsoidal</td>
<td>20-30</td>
<td>17-23</td>
<td>helical</td>
<td>≤27</td>
<td>+</td>
<td>peltate</td>
<td>-</td>
<td>flattened oval ring</td>
<td>≤13</td>
<td>2</td>
<td>inverted</td>
<td>wide</td>
<td>?</td>
</tr>
<tr>
<td>7. <em>Metasequoia milleri</em></td>
<td>Eocene</td>
<td>subglobe-cylindrical</td>
<td>~25</td>
<td>~17</td>
<td>decussate</td>
<td>≤30</td>
<td>+</td>
<td>peltate with distal groove</td>
<td>-</td>
<td>flattened oval ring</td>
<td>4+</td>
<td>1</td>
<td>inverted</td>
<td>wide</td>
<td>-</td>
</tr>
<tr>
<td>12. <em>Yezosequoia shimanukii</em></td>
<td>Late Cretaceous (Coniacian-Santonian)</td>
<td>ellipsoidal</td>
<td>22-25</td>
<td>25-29</td>
<td>helical</td>
<td>≤35</td>
<td>+</td>
<td>peltate with apical spine</td>
<td>-</td>
<td>flattened oval ring</td>
<td>4</td>
<td>1</td>
<td>inverted</td>
<td>narrow</td>
<td>?</td>
</tr>
<tr>
<td>13. <em>Yushirostrobus nakajimae</em></td>
<td>Late Cretaceous (Coniacian-Santonian)</td>
<td>ellipsoidal</td>
<td>45</td>
<td>26</td>
<td>helical</td>
<td>25+</td>
<td>+</td>
<td>peltate with distal groove</td>
<td>-</td>
<td>oval ring + intern. bundles</td>
<td>3-4</td>
<td>1</td>
<td>erect</td>
<td>narrow</td>
<td>?</td>
</tr>
<tr>
<td>14. <em>Metasequoia glyptostroboides</em></td>
<td>recent</td>
<td>ellipsoidal</td>
<td>15-30</td>
<td>15-18</td>
<td>decussate</td>
<td>18-25</td>
<td>+</td>
<td>peltate with distal groove</td>
<td>-</td>
<td>reniform ring</td>
<td>6-8</td>
<td>1</td>
<td>inverted</td>
<td>narrow-wide</td>
<td>-</td>
</tr>
<tr>
<td>15. <em>Sequoia sempervirens</em></td>
<td>recent</td>
<td>ellipsoidal</td>
<td>15-30</td>
<td>13-18</td>
<td>helical</td>
<td>18-25</td>
<td>+</td>
<td>peltate with distal groove</td>
<td>-</td>
<td>reniform ring</td>
<td>6-8</td>
<td>1</td>
<td>inverted</td>
<td>narrow</td>
<td>-</td>
</tr>
<tr>
<td>16. <em>Sequoiadendron giganteum</em></td>
<td>recent</td>
<td>ellipsoidal</td>
<td>30-95</td>
<td>25-65</td>
<td>helical</td>
<td>28-45</td>
<td>+</td>
<td>peltate with distal groove</td>
<td>-</td>
<td>flattened oval ring</td>
<td>8-10</td>
<td>2</td>
<td>inverted</td>
<td>wide</td>
<td>-</td>
</tr>
</tbody>
</table>

**Figure captions**

**Fig. 1.** *Stockeystrobus interdigitata* gen. et sp. nov. Holotype, National Museum of Nature and Science specimen number NSM PP-9373. A, Slightly oblique longitudinal section of cone, near-radial at apex and radial at base, showing cylindrical shape, peltate (red arrowhead) bract-scale complexes with heads (h) that are connected by interlocking trichomes (black arrowheads), radial complex traces (t) diverging from axis (a) and numerous inverted seeds. Five horizontal white lines across cone represent cross sections (e.g., Fig. 1B) made before cone was reassembled, leaving spaces to compensate for thickness of cone removed. Slide L1-1 x3. B, Cross section of cone showing axis (a), diverging complex traces (t), one attached peltate bract-scale complex (red arrowhead), and numerous inverted seeds in growth position on the inner surface of peltate complex heads (h). Black arrowheads identify positions of interlocking trichomes that attach adjacent heads. Slide 4 x4.4. C, Cross section of cone showing bract/scale trace (t) at level where trace begins to divide to produce adaxial bundle (black arrowhead) and several abaxial bundles. Slide 1-77 x11. D, Cross section of cone showing complex head at slightly more adaxial level than Fig. 1C, where adaxial bundle (arrowhead) and several adaxial bundles already have separated. Note several seeds in position of attachment, and resin canal (r) in ground tissue. Slide 1-2 x8. E, Cross section of cone showing complex head at slightly more adaxial level than Fig. 1D, where adaxial bundles form single row, and there is one adaxial bundle (at arrowhead). Note histology, resin canal (r), and periderm on adaxial surface of head. Slide 2-1 x9.

**Fig. 2.** *Stockeystrobus interdigitata* gen. et sp. nov. Holotype, National Museum of Nature and Science specimen number NSM PP-9373. A, Cross section of cone axis showing pith, cylinder
of wood, and primary cortex both inside and outside of radially aligned periderm cells. Red arrowhead identifies sclereids in pith. Slide A1 x35. B, Enlargement of pith and wood of cone axis, showing parenchyma with and without dark internal contents, and rows of radially aligned secondary tracheids. Gaps between rows of tracheids represent uniseriate rays. Slide A1 x80. C, Oblique cross section of complex stalk enlarged from Fig. 2B, showing radial structure with abundant wood, primary cortex, and periderm (p). Slide 4 x28. D, Radial section of wood showing tracheids with scalariform thickenings and uniseriate bordered pits (blue arrowhead). Slide 1-2 x380.

Fig. 3. Stockeystrobus interdigitata gen. et sp. nov. Holotype, National Museum of Nature and Science specimen number NSM PP-9373. A. Tangential section of cone showing peltate head of complex in cross section, and distal to seed attachment. Note row of vascular bundles toward adaxial surface (green arrowheads) and ring of vascular bundles (red arrowheads) toward abaxial surface. Ground tissues incompletely preserved. Arrowheads point in direction that xylem maturation occurred and secondary xylem tracheids were added. Slide C2-1 x37. B, Enlargement of vascular bundle at lower right of Fig. 1A, showing rows of secondary tracheids that reveal bundle orientation, and spaces between tracheid rows that represent uniseriate rays. Slide C2-1 x140. C, Tangential section of cone showing adjacent complex heads (h) with incompletely preserved ground tissues and dense interlocking trichomes on adjoining surfaces. Horizontal white line represents position of saw cut. Slide T5 x9. D, Enlargement of trichomes interconnecting adjacent complex heads (h) in Fig. 3D. Slide T5 x16. E, Interdigitating trichomes at lateral margins of adjoining peltate bract/scale complex heads. Note how epidermal cells in adjacent regions (upper left) increase in size to form the elongated trichomes. Slide L1-1
x75.  F, Cross section of complex at level between position of seed attachment and level where adjacent complexes are connected by interlocking trichomes. Adaxial epidermis consists of papillate cells. Note abaxial hypodermis of tightly-packed parenchyma and fibers, adjacent resin canals (r), and internal zone of less completely preserved tissue that shows prominent resin rodlets. Slide 3-2 x40.  G, Longitudinal section of well-preserved complex head with distal surface at right. Note longitudinal rows of ground parenchyma with resin rodlets, hypodermis of tightly packed parenchyma and fibers, and resin canal (r). Slide 5-2 x32.  H, Cross section of cone showing interlocking epidermal trichomes that connect adjacent bract/scale complex heads (h). Slide 1-2 x28.  I, Interdigitating trichomes and adjacent mesophyll cells at margin of peltate bract/scale complex head, showing that each trichome consists of single enlarged epidermal cell. Slide 1-77 x130.

**Fig. 4.** Line diagram tracings of vascular system in holotype of *Stockeystrobus interdigitata* gen. et sp. nov. All from cross sections of cone, x5. National Museum of Nature and Science specimen number NSM PP-9373. Bract/scale margin drawn in zig-zag pattern where lined with interdigitating trichomes; xylem bundles represented in black. A, Proximal level of stalk at level where xylem forms a rod with abundant secondary xylem. Slide 3. B, Roughly T-shaped bundle dividing at base of peltate head, producing row of abaxial bundles and single adaxial bundle. Slide 5-2. C, Slightly more distal section than in Fig. 4B, showing row of abaxial bundles, and adaxial bundles dividing to form ring. Slide 2-1. D, Distalmost section of peltate head, showing abaxial row and adaxial ring of xylem bundles. Slide C2-1.

**Fig. 5.** *Stockeystrobus interdigitata* gen. et sp. nov. Holotype, National Museum of Nature and
Science specimen number NSM PP-9373. A, Tangential section of two peltate bract/scale complex heads (h) from apex of cone, showing adaxially attached seeds (s) on head toward bottom of figure. Note adaxial row of bundles in each head. Adaxial surfaces of adjacent heads oriented toward each other, because heads arise from opposite sides of cone axis apex. Slide C2-1 x9. B, Seeds in various planes of section, several of which show wide wings at each side of nearly round seed cavity. Slide L1-1 x9. C, Cross section of cone showing inverted seeds in longitudinal view and in position of attachment to underside of adaxial surface of complex head. Note adaxial row of vascular bundles in complex head (arrowheads), separation of seeds from complex head by periderm (p) that also surrounds cone axis (a). Slide 2-2 x14. D, Seeds in various planes of section, showing wide wings (w) surrounding seed body (b) in cross section (upper right) and in major plane of longitudinal section (bottom). Note periderm (p) of cone axis (at right) extends out onto adaxial surface of bract-scale complex (at bottom) to level of seed attachment (Fig. 4C near left). Slide L1-1 x 9. E, Longitudinal section of seed in position of growth with micropyle at right. Note nucellus (n) attached to integument (i) only at chalaza, and chalazal chamber (at left). Slide 2-1 x30. F, Oblique cross section of seed cavity at mid-level showing integument with external epidermis (arrow) zone of sclereids, and inner zone in longitudinally oriented cells bounded by internal cuticle (i). Note nucellus (n) consists of two to three cell layers surrounding central hollow and bounded by external cuticle. Slide 4 x70. G, Oblique longitudinal section near seed apex showing convoluted nucellar apex (na) within integument (i). Slide 4 x50.