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HUBBARDIASTROBUS CUNNINGHAMIOIDES GEN. ET SP. NOV., EVIDENCE FOR A LOWER CRETACEOUS DIVERSIFICATION OF CUNNINGHAMIOID CUPRESSACEAE

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Premise of research. The occurrence of six ovulate cones and six leafy branching systems, two of which show attachment of the ovulate cone, reveals a new cunninghamioid fossil conifer from the Cretaceous Apple Bay locality of Vancouver Island, Canada. This anatomically preserved plant expands our understanding of basal Cupressaceae in the fossil record.

Methodology. Specimens were studied from anatomical sections prepared by the classic cellulose acetate peel technique.

Pivotal results. Vegetative shoots have helically arranged *Cunninghamia*-like leaves with a single vascular bundle and one to three resin canals. Ovulate cones consist of numerous helically arranged bract/scale complexes with a large bract and a small ovuliferous scale with three separate tips. There are three inverted seeds/ovules attached adaxially, immediately proximal to the free scale tips.

Conclusions. This discovery reveals the presence of a new genus and species of basal Cupressaceae, *Hubbardiastrobus cunninghamioides*, in the Early Cretaceous (Valanginian; ~136 Ma) of the Northern Hemisphere. These data expand the species richness of fossil Cupressaceae and further document the Cretaceous evolutionary radiation of subfamily Cunninghamioideae.

Keywords: conifer, cunninghamioid Cupressaceae, fossil plants, Lower Cretaceous, ovulate/seed cones.

Introduction

Cupressaceae and Taxodiaceae traditionally have been regarded as distinct conifer families (sensu Pilger 1926), but a careful evaluation of morphological characters (Eckenwalder 1976) revealed that the species of both families represent a monophyletic group in which the taxodiaceous genera represent a basal grade and the cupressaceous genera form a terminal clade. Subsequent systematic analyses of nucleotide sequences and morphological characters fully support that phylogeny (Gadek et al. 2000 and references cited therein; Kusumi et al. 2000; Farjon 2005; Schulz and Stützel 2007; Rothwell et al. 2012). Based on a combination of morphological characters, nucleotide sequences, and ovulate cone development, living genera of Cupressaceae are now well resolved, and seven subfamilies can be recognized (Gadek et al. 2000). Cunninghamioideae (*Cunninghamia* R. Br. ex Rich.), Taiwanioideae (*Taiwania* Hayata), and Athrotaxoideae (*Athrotaxis* D. Don) occur in a pectinate arrangement at the base of the clade, each subfamily being represented by a single genus of one to three species (Gadek et al. 2000). The Sequoioideae

and Taxodioideae are arranged at successively higher nodes on the stem of the cupressaceous tree, and the Callitroideae and Cupressoideae (i.e., the cupressaceous clades) form sister groups (Gadek et al. 2000; Kusumi et al. 2000; Schulz and Stützel 2007).

Molecular clade dating estimates and ancestral area reconstructions suggest that Cupressaceae s.l. (Eckenwalder 1976) originated during the Triassic (Mao et al. 2012), but the rich fossil record for the family extends back only to the Early Jurassic (Escapa et al. 2008). Nevertheless, there are enough paleobotanical data for the most ancient Jurassic and Cretaceous Cupressaceae (Stockey et al. 2005b; Escapa et al. 2008; Rothwell et al. 2011, 2012; Serbet et al. 2013) to test hypotheses about the early evolution of the family with empirical evidence from the fossil record. The recent discovery of anatomically preserved leafy branches of Cupressaceae with terminal ovulate cones in the Lower Cretaceous of western Canada (Valanginian Stage; ~136 Ma) further enriches this fossil record for ancient representatives of the family and provides additional data that may prove useful in future hypothesis tests.

In this article we describe *Hubbardiastrobus cunninghamioides* gen. et sp. nov., a conifer that displays a novel combination of characters but that also shares a large number of vegetative and ovulate cone characters with living and extinct species of *Cunninghamia* R. Brown, as well as with several

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other extinct genera of the Cupressaceae (sensu Farjon 2005; Stockey et al. 2005b; Eckenwalder 2009), such as *Cunninghamiostrobus* Stopes et Fujii (1910; Cretaceous-Oligocene), the Cretaceous taxa *Mikasaostrobus* Saiki et Kimura (1993) and *Parataiwania* Nishida, Ohsawa et Nishida (1992), and the Jurassic *Hughmillerites* Rothwell, Stockey, Mapes et Hilton (2011). These data suggest that the initial phylogenetic radiations of Cupressaceae centered on a relatively small and homogeneous set of *Cunninghamia*-like species that underwent rapid diversification in the Northern Hemisphere throughout the Cretaceous.

Material and Methods

Hubbardiastrobus cunninghamioides is represented by six leafy vegetative shoots and six ovulate cones that are preserved by cellular permineralization in calcium carbonate concretions derived from a carbonate-cemented graywacke matrix at the Apple Bay locality on northern Vancouver Island, British Columbia, Canada (Stockey et al 2005a). The locality is situated on the beach along Quatsino Sound (lat. 50°36'21"N, long. 127°39'25"W; UTM 9U WG 951068) on the northern end of Vancouver Island. Sediments were previously regarded as Lower Cretaceous (Barremian) Longarm Formation equivalents (Jeletzky 1976; Haggart and Tipper 1994), which correspond to Jeletzky's Barremian variegated clastic unit (Sweet 2000). More recently, carbon isotope analysis has narrowed the age to ~136 Ma (D. R. Gröcke, personal communication), which is now in the Valanginian Stage of the Early Cretaceous (Walker et al. 2012).

Specimens were sectioned by the well-known cellulose acetate peel technique (Joy et al. 1956). Slides were mounted in Eukitt (O. Kindler, Freiburg, Germany) xylene-soluble mounting medium. Images were captured using a PowerPhase digital scanning camera (Phase One, Copenhagen) and processed using Adobe Photoshop 7.0 (Adobe, San Jose, CA). Peels and microscope slides of the specimens are currently housed in the Oregon State University paleobotanical collections under numbers OSU P15, P16, P23, P25. The permanent repository for most of this material is the Museum of Natural and Cultural History, Condon Museum, University of Oregon, Eugene (nos. F-55435–F-55438). One specimen is housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA P13,099 C bot).

Results

Systematics

Order—Coniferales

Family—Cupressaceae Bartlett

Subfamily—Cunninghamioideae Silba

Genus—*Hubbardiastrobus* Atkinson, Rothwell et Stockey gen. nov.

Generic diagnosis. Conifer with alternate branching and helically arranged, decurrent needle leaves; leaf tips incurved.

Ovulate cones terminal; cylindrical; bract/scale complexes helically arranged. Three ovules/seeds per bract/scale complex; inverted at maturity; interseminal ridges absent. Ovuliferous scale diverging from bract distal to ovules as three separate tips. Bract/scale trace diverging from cone axis stele as oval bundle; initial divisions horizontal. Ground tissue of stems and cones parenchymatous with scattered sclereids in pith and cortex. Leaves with scattered fibers in mesophyll; hypodermis sclerotic. Resin canals in stem cortex; diverging with leaves as single central resin canal abaxial to leaf trace. Adaxial mesophyll of leaves a uniseriate palisade; abaxial spongy mesophyll of several cell layers. Leaf trace located within horizontally elongated zone of small cells with dark contents.

Type. *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey sp. nov.

Etymology. The genus *Hubbardiastrobus* is proposed in honor of Sharon Hubbard, Parksville, Vancouver Island, for her assistance with fossil plant collecting and her generous donation of numerous plant specimens for study and *strobos* for cone.

Species. *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey sp. nov. (figs. 1–5).

Specific diagnosis. Ultimate branches 2.5 mm in diameter; pith 160–300 μ m in diameter. Leaves 4–7 mm long, decurrent, diverging at 75°–85°, bending upward distally; ~2.5 mm wide, 1.4 mm thick at level of divergence, narrowing and becoming roughly diamond shaped distally. One to three resin canals at leaf base; central resin canal continuous from stem cortex, lateral resin canals arising de novo. Ovulate cones 13–15 mm long, 4 mm in maximum diameter; consisting of numerous (>40) closely spaced, helically arranged bract/scale complexes. Bracts diverging at angles of 60°–90°, bending apically; 2–3 mm long and 2.5–4.0 mm wide. One resin canal entering complex from cone axis, additional resin canals arising de novo, numbering up to ~9 in single row. Most ovules (~95%) immature or abortive, 150–240 μ m long, 120–200 μ m wide, 60–110 μ m thick; with bilateral symmetry and narrow lateral wings. Mature seeds (~5%) up to 710 μ m long, 625 μ m wide, 390 μ m thick, with integument of thin-walled endotesta, multiseriate sclerotesta, and outer zone of thin-walled sarcotesta. Nucellus separate from integument to near base; megaspore membrane conspicuous.

Holotype hic designatus. Ovulate cone borne terminally on leafy shoot, represented by peels and slides of specimen P23A bot and B top in Oregon State University Paleobotanical Collections; permanently housed as specimen number F-55435 in the Museum of Science and Culture, University of Oregon, Eugene (figs. 1A, 1B, 1E, 1F, 2F, 2G, 5A).

Paratypes. Ovulate cones and attached leaves represented by peels and slides of specimen P15B top (figs. 1D, 2A–2E, 3A, 4F, 4G; specimen no. F-55436) and P16A bot (figs. 3B, 4A–4C, 4E, 4I, 5B–5D; specimen no. F-55437; UAPC-ALTA P13099 C bot). Vegetative shoots (fig. 1C; specimen no. F-55438).

Type locality. Apple Bay, northern Vancouver Island (lat. 50°36'21"N, long. 127°39'25"W; UTM 9U WG 951068).

Stratigraphic position and age. Longarm Formation equivalent, Valanginian Stage, Early Cretaceous.

Etymology. The specific epithet *cunninghamioides* reflects

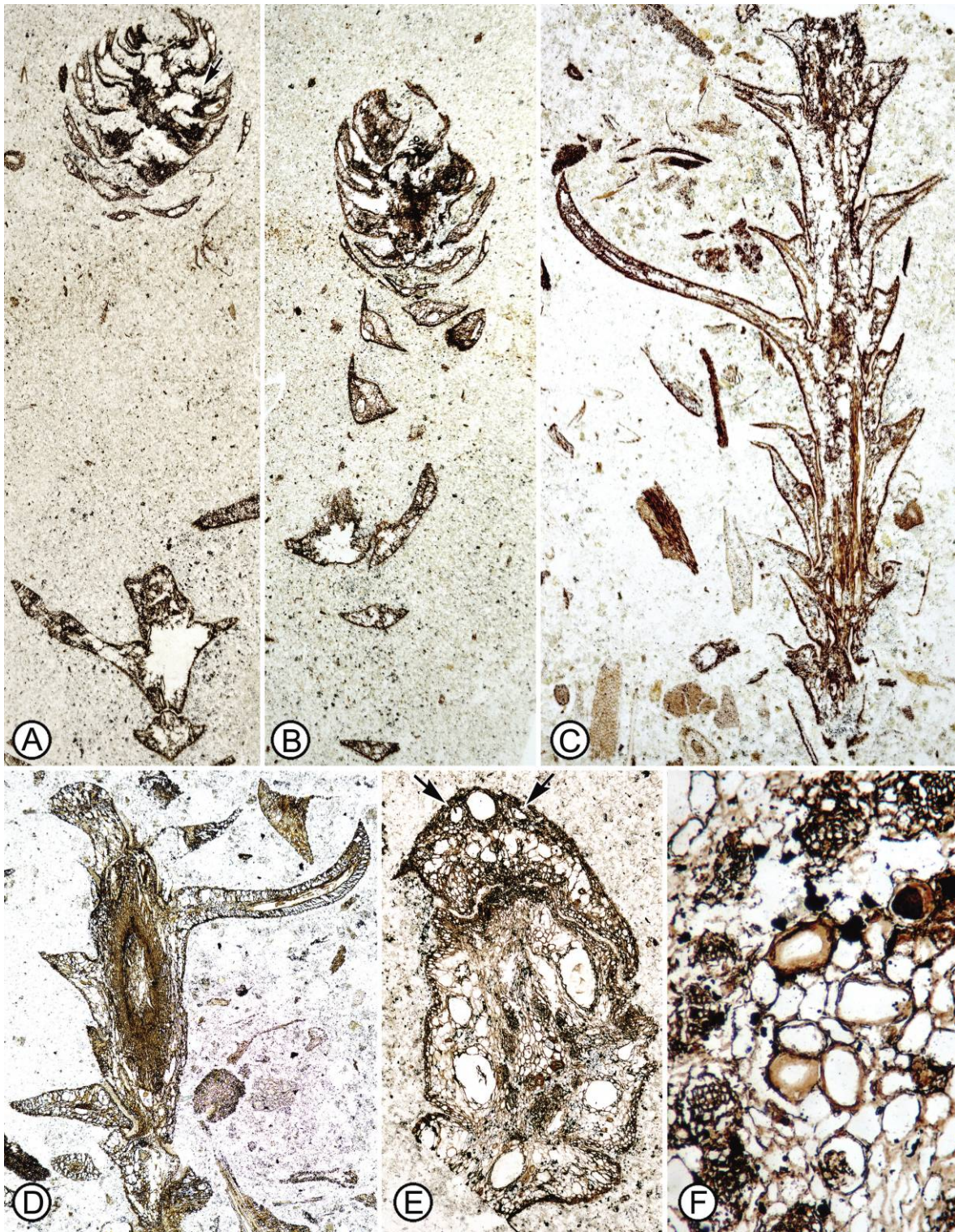


Fig. 1 *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey gen. et sp. nov. *A, B*, Leafy shoot with terminal ovulate cone (holotype) on opposite sides of saw cut, showing general features. Specimen shows shoot with helically arranged leaves subtending terminal cone displaying numerous helically arranged bract scale complexes and immature ovules on adaxial surface of ovuliferous scales. Note small ovule (arrow in *A*). *A* = 23 A bot, no. 16; *B* = 23 B top, no. 1, both, $\times 6$. *C*, Vegetative shoot showing helically arranged needle-like leaves. 25 B bot, no. 13, $\times 7$. *D*, Oblique section of penultimate shoot showing pith, stele, continuous cylinder of wood, and diverging leaves. 15 C top, no. 7, $\times 9$. *E*, Cross section of ultimate stem (holotype) with diverging leaves. Note cauline bundles surrounding pith and ring of resin canals in cortex. Diverging leaf shows large central resin canal and two smaller resin canals (arrows). 23 A bot, no. 4, $\times 62$. *F*, Enlargement of stem in *E* (holotype) showing separate cauline bundles with secondary xylem. Note prominent sclereids in pith. 23 A₂ bot, no. 2, $\times 83$.

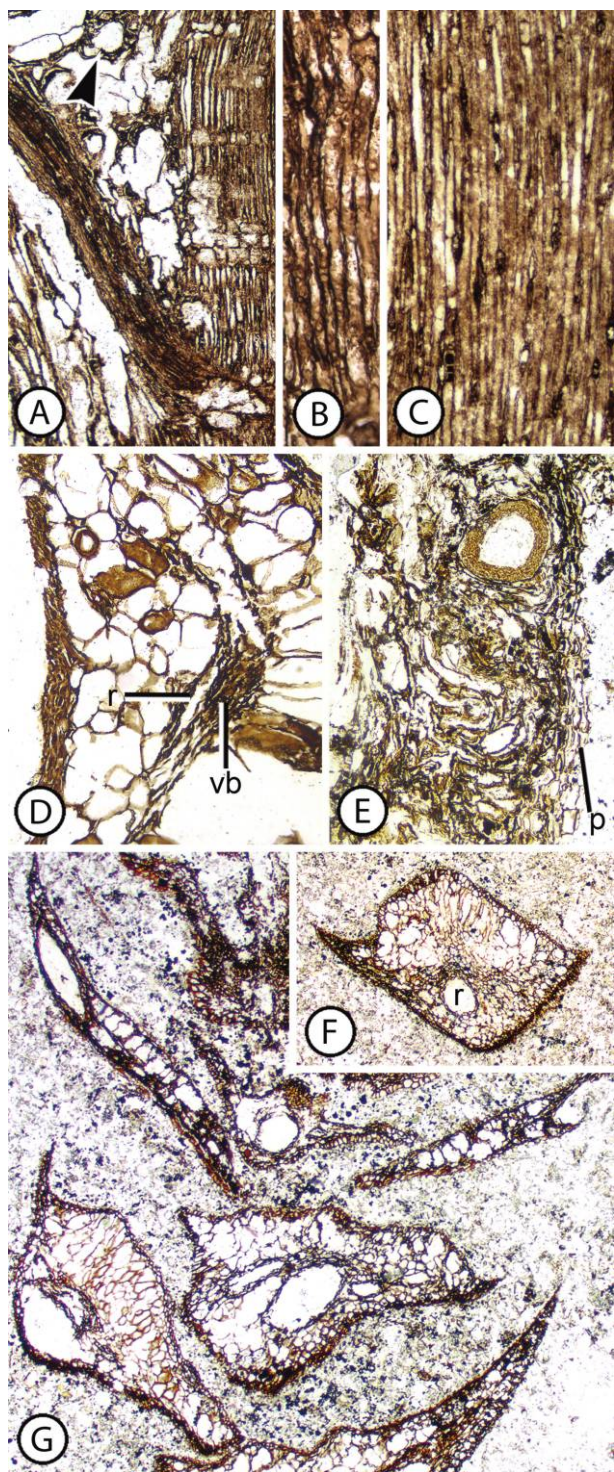


Fig. 2 *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey gen. et sp. nov. **A**, Radial section of vegetative shoot displaying leaf trace divergence associated with abaxial resin canal. Note rays, one to five cells high, in vascular cylinder and nest of sclereids (arrowhead) among large parenchyma cells of inner cortex. 15 C top, no. 7, $\times 445$. **B**, Radial section of wood showing tracheids with uniseriate bordered pits. 15 C top, no. 87, $\times 700$. **C**, Tangential section of wood showing secondary tracheids and uniseriate rays. 15 C top,

numerous similarities of *Hubbardiastrobus* to the genus *Cunninghamia*.

Description

Hubbardiastrobus cunninghamioides is represented by two orders of leafy branches with helically arranged needle leaves and terminal ovulate cones (fig. 1A–1E). Leaves are decurrent and closely spaced, such that nearly the entire outer surface of the stems consists of leaf bases (fig. 1E). Within the Apple Bay collections there are two cones that are attached to a leafy shoot system (i.e., holotype, fig. 1A, 1B; UAPC-ALTA P13,099 C bot, not figured), demonstrating that the vegetative and fertile organs are the same species. Specimens consist of penultimate and ultimate leafy branches that are up to 5.5 cm long and 9–18 mm wide, two of which bear terminal ovulate cones. Ultimate stems are up to ~ 2.5 mm in diameter, with penultimate branches measuring up to 3.0 mm.

Vegetative Stems

Cross sections of stems reveal a central pith, 160–300 μm in diameter, surrounded by a ring of ~ 11 endarch vascular bundles (fig. 1E, 1F) that represent a combination of cauline bundles and leaf traces, suggesting a $3/8$ phyllotaxis. Pith consists of parenchyma cells 36–72 μm in diameter and scattered thick-walled sclereids (fig. 1F) measuring 36–70 μm in cross sections. Most pith cells are parenchymatous with a few showing dark contents (fig. 1F). Culine bundles of ultimate shoots are separated by pith rays and show about six rows of secondary tracheids, 8–12 μm in diameter (fig. 1F). In penultimate shoots the wood forms a continuous cylinder around the pith (fig. 1D) that is up to 340 μm thick. Secondary xylem consists of radial rows of small tracheids 8–14 μm in diameter and uniseriate rays 1 to ~ 10 or 12 cells high (fig. 2A, 2C). Tracheid walls are incompletely preserved, but noncontiguous, uniseriate, circular bordered pits can be identified on the radial walls (fig. 2B).

The stem cortex is largely parenchymatous, with a conspicuous ring of resin canals 125–200 μm in diameter (fig. 1E). Resin canals have a prominent epithelial lining. Cortical parenchyma is similar to that in the pith, except that the walls are less conspicuous (fig. 1E). As with the pith, there are a few scattered sclereids (fig. 2E). Toward the periphery of the stem, the cells become smaller and have thicker, more prominent walls (fig. 1E). Epidermis is largely absent, probably as a result of pre-preservation abrasion. Older stems with a continuous cylinder of wood have cortical cells that have been distorted

no. 68, $\times 600$. **D**, Oblique cross section of leaf showing sclerotic hypodermis (left), histology of mesophyll, and vascular bundle (vb) immediately adaxial to central resin canal (r). Note sclereid and resin-filled cells in mesophyll. 15 B bot, no. 2, $\times 45$. **E**, Longitudinal section of stem cortex with large sclereid and periderm (p) at right. 15 C top, no. 85, $\times 65$. **F**, Slightly oblique cross section of leaf showing central resin canal (r) and one lateral resin canal at immediate left (holotype). 23 A bot, no. 23, $\times 20$. **G**, Tangential section of leaves diverging from stem immediately proximal to attached ovulate cone (holotype). Note differences in number of resin canals (i.e., one to three) in leaves. 23 A bot, no. 23, $\times 25$.

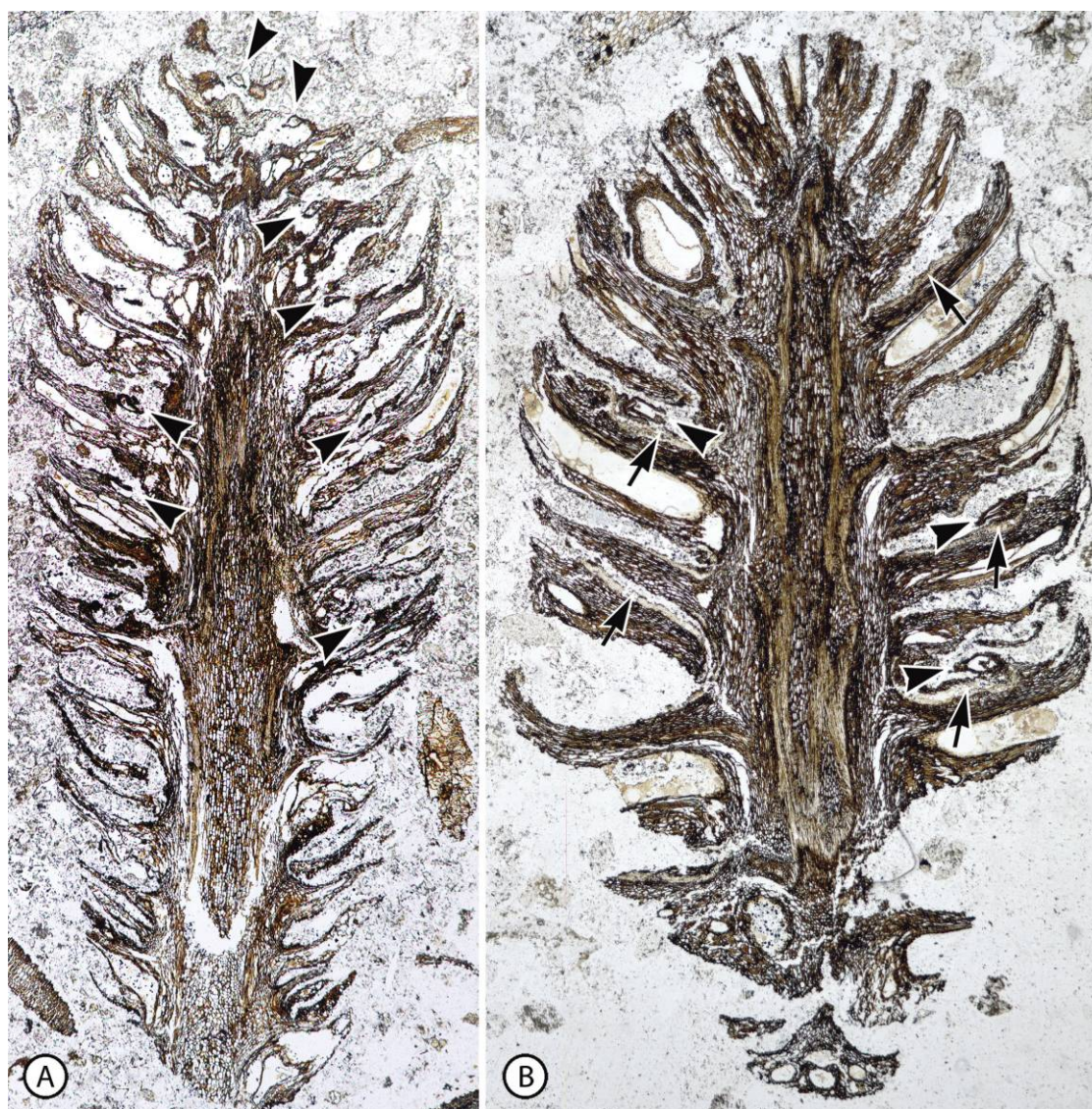


Fig. 3 *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey gen. et sp. nov. Paratype (Oregon State University Paleobotanical Collections specimen P15). *A*, Somewhat oblique longitudinal section of ovulate cone displaying closely spaced bract-scale complexes. Note attached ovules (arrowheads). 15 B top, no. 10, $\times 12$. *B*, Radial longitudinal section of apical region of ovulate cone with large continuous resin canals in bract/scale complexes. Note mature seed with preserved megagametophyte at upper left and three immature or abortive ovules (arrowheads). Note also secondary cortex or periderm in position between tissue of bract and scale (at arrows). 16 A bot, no. 10, $\times 14$.

probably as a result of the increase in diameter of the stele (fig. 2E). Such stems also show three or four layers of radially aligned cells with light-colored walls at the periphery that represent periderm (fig. 2E).

Leaves

The stem cortex expands laterally at each of the closely spaced decurrent leaf bases (fig. 1C–1E). In most leaves internal tissues are somewhat degraded and in many places not well preserved, while leaf outlines are clear (fig. 1A–1C). Leaves range 4–7 mm long and are somewhat S shaped, with the tip curving toward the apex of the stem (figs. 1C, 1D, 2G). The leaf trace diverges at a $\sim 30^\circ$ angle (fig. 2A) before bending

outward at the level where the leaf separates. Leaves are 1.4–2.5 mm wide and ~ 0.5 –1.0 mm thick at the base, tapering gradually toward the apex. In cross sections the leaves show an epidermis that is incompletely preserved, apparently because of abrasion, a sclerotic hypodermis (fig. 2D, 2F, 2G) two to four cells thick, a short palisade mesophyll with prominent intercellular spaces (figs. 1D, upper right, 2F, 2G), several layers of spongy mesophyll (fig. 2D), one to three resin canals (fig. 2F, 2G), and an inconspicuous vascular bundle located within a horizontally elongated, narrow band of small cells with dark contents (fig. 2D, 2F, 2G). There also are scattered fibers within the mesophyll (fig. 2D). The horizontally elongated tissue in which the bundle is embedded is made up of

small, dark cells and is comparable to the zone in leaves of *Cunninghamia* that has been interpreted as transfusion tissue (Ghouse and Yunus 1974). However, in *Hubbardiastrobis* we have not been able to identify either thick-walled cells or thickening patterns on the cell walls. A single central resin canal enters the leaf from the decurrent base/stem cortex abaxial to the vascular bundle and extends to near the leaf tip. At about the level of separation of the leaf from the cortex, one or two smaller, laterally positioned resin canals originate de novo and extend distally for some distance (figs. 1E, 2G). However, some leaves apparently have only one resin canal throughout their length.

Ovulate Cones

Six ovulate cones of *H. cunninghamioides* have been discovered at Apple Bay. The attached specimens (fig. 1A, 1B) demonstrate that the cones are borne terminally on branches. As is characteristic of cupressaceous ovulate cones, there is a transition in the morphology of vegetative leaves immediately below the cone to the basal bract/scale complexes (figs. 1B, 2G), and this clearly relates the isolated vegetative shoots to the ovulate cones. Individual cones are cylindrical (fig. 3A, 3B), with a large number of helically arranged bract/scale complexes (figs. 1A, 1B, 4D, 4H), 13–15 mm long with a maximum diameter of 4 mm.

The cone axis is 1.2 mm in diameter, consisting of a parenchymatous pith, ~0.8 mm wide, in which there are scattered sclereids (fig. 4A) like those of the vegetative stems (fig. 1E, 1F). The pith is surrounded by a ring of cauline bundles that are more or less interconnected by secondary xylem to form a nearly continuous cylinder (fig. 4A). Wood is comparable to that of the vegetative stems, consisting of radial files of narrow tracheids 8–12 μm wide and with uniseriate rays 1–13 cells high (fig. 4B). Primary xylem tracheids have helical to scalariform wall thickenings (fig. 4C, left), while secondary xylem tracheids show incompletely preserved uniseriate circular bordered pits (fig. 4C, right). The cortex is largely parenchymatous, but there are two or three layers of hypodermal fibers at the periphery. Epidermis is not well preserved. A prominent resin canal occurs in the cortex of the axis immediately outside each diverging bract/scale trace (fig. 4A).

Bract/scale complexes diverge from the cone axis at angles of 60°–90°, bend apically, and taper to a narrow tip (fig. 3A, 3B). Individual complexes are 2–3 mm long and 2.5–4 mm wide. In tangential sections of the cone, each complex is roughly diamond shaped at the level of divergence (fig. 4H, center) but rapidly expands laterally as it extends away from the cone axis (fig. 4D, 4H). Most of the bract/scale tissue appears to consist of bract, with the scale recognized by three separate free tips located on the adaxial surface in the mid-region of the complex (fig. 4D, 4I). Like that in the cone axis, ground tissue of the bract/scale complex is typically parenchymatous with a few scattered sclereids, except at the abraded periphery where there is a sclerotic hypodermis. Although only one large central resin canal diverges from the cone axis, several additional lateral resin canals originate de novo and form a row of seven to nine in the midregion of the bract/scale complex (fig. 4D).

Three ovules or seeds are borne on each bract/scale complex,

each located on the adaxial surface immediately proximal to the position of a free scale tip (figs. 3A, 3B, 4D, 4F, 4I). The scale tissue to which the ovules are attached and from which the free scale tips extend is raised above the adaxial surface of the bract/scale complex forming a small mound (fig. 4G, 4I). There are no interseminal ridges between adjacent ovules/seeds (fig. 4F, 4G). Most ovules (~95%) are immature or abortive, 150–240 μm long, 120–200 μm wide, 60–110 μm thick, with bilateral symmetry and narrow lateral wings (fig. 4B, 4D, 4F, 4G, 4I, left). Nearly all of the ovules and seeds are inverted, with their micropyle pointed toward the cone axis (figs. 3B, 4I). However, a small number of the smallest ovules are erect (fig. 5A), revealing that the ovules of *H. cunninghamioides* probably originated in an erect orientation and became inverted with subsequent development.

Mature seeds (~5%) are up to 710 μm long, 625 μm wide, 390 μm thick, with an integument constructed of thin-walled endotesta, a central zone of sclereids, and an outer zone of thin-walled sarcotesta (fig. 5B–5D). The nucellus is typically represented by one or two layers of cells that either surround a hollow or contain a shrunken cellular megagametophyte (fig. 5B, 5C). Near the ovule apex the nucellus forms a cellular pad (fig. 5C, bottom right). The nucellus appears to be free from the integument to near the base (fig. 5B–5D) but sometimes appears pushed up against the endotesta, making the details difficult to interpret (fig. 5C). No pollen chamber has been observed. One mature seed shows what appears to be a collapsed megaspore membrane (fig. 5B, m). Cellular tissue of the megagametophyte is preserved in one seed (fig. 5C).

Discussion

Although there is considerable variability among basal Cupressaceae, the taxodiaceous genera are generally characterized by helically arranged needle-like leaves (table 1), ovulate cones with numerous separate and helically arranged bract/scale complexes, highly fused bract and scale, and several adaxially borne seeds. Mature seeds range from two to nine and may be borne erect or inverted depending on the genus (Farjon 2005; Schulz and Stützel 2007). *Hubbardiastrobis cunninghamioides* conforms to this basic morphological plan by displaying helically arranged needle-like leaves and terminal ovulate cones with numerous separate and helically arranged bract/scale complexes that have three small free scale tips that separate in the midregion of the bract and three ovules/seeds that are at first erect but become inverted at maturity. In contrast, cupressoid Cupressaceae typically have scalelike leaves, oppositely arranged appendages, and ovulate cones that are small with only a few bract/scale complexes, and the bract/scale complexes may be either separate or fused together forming a cohesive unit at least until seed dispersal (Gadek et al. 2000; Farjon 2005).

Mature seed cones of some basal Cupressaceae with living species (i.e., *Cunninghamia*, *Taiwania*, and *Athrotaxis*) have a diminutive ovuliferous scale, the tip of which may separate from the adaxial surface of the complex (table 2; Stewart and Rothwell 1993; Jagel and Stützel 2001), or there is no free scale tip at all. Some other extant basal Cupressaceae (i.e., *Taxodium* Rich., *Cryptomeria* D. Don, and *Glyptostrobus* Endl., the Taxodiaceae sensu Gadek et al. 2000, Schulz and

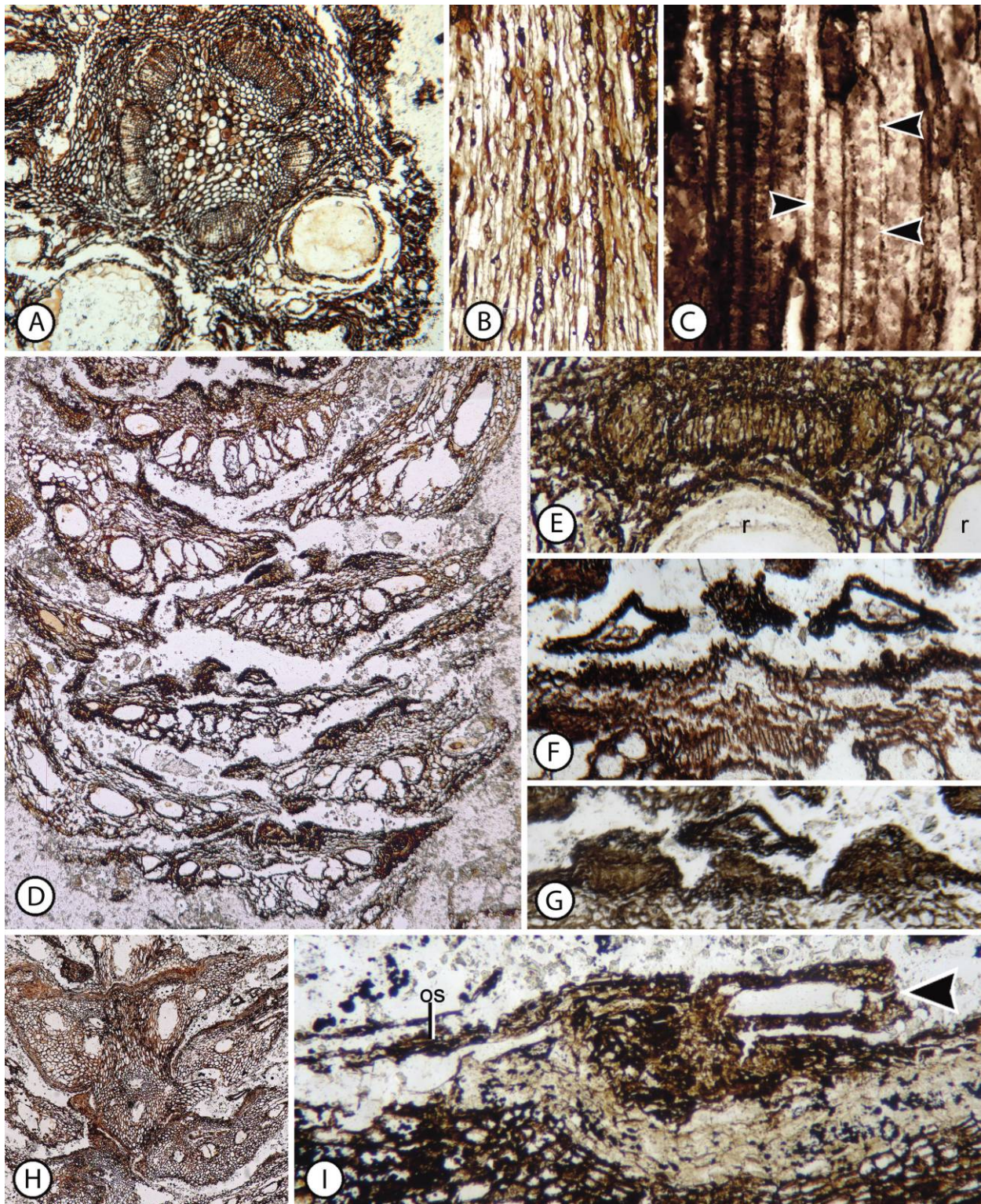


Fig. 4 *Hubbardiastrobus cunninghamioides* Atkinson, Rothwell et Stockey gen. et sp. nov. **A**, Cross section of ovulate cone showing pith, stele, and cortex. Stele has developed sufficient secondary vascular tissue to form nearly complete cylinder of wood. Note prominent sclereids in pith and cauline resin canals in cortex. 16 A₂ bot, no. 21, × 33. **B**, Tangential section of wood in cone axis showing uniseriate rays, one to 13 cells high. 16 A bot, no. 1, × 250. **C**, Radial section of cone vascular cylinder showing helical/scalariform thickenings of the primary xylem (left) and uniseriate bordered pits on secondary xylem (right; arrowheads). 16 A bot, no. 17, × 416. **D**, Transverse sections of bract/scale complexes indicating three separate scale lobes and with ovules located on adaxial side of bract/scale complex. 15 A bot, no. 2, × 18. **E**, Transverse section

Stützel 2007) produce ovulate cones in which the ovuliferous scale is longer than the bract, the ovuliferous scale shows evidence of free distal tips, and the seeds are erect on the bract/scale complex. The scale tips are the longest and most obvious in *Cryptomeria* (pl. 31, figs. 6, 7 of Farjon 2005) but are also obvious in *Glyptostrobus* (i.e., pl. 34, figs. 2, 7–10 of Farjon 2005). In *Taxodium* they are quite subtle but are discernible on the surface of mature cones (i.e., pl. 32, fig. 9; pl. 33 of Farjon 2005). Genera of the Sequoioideae sensu Gadek et al. (2000; Schulz and Stützel 2007; i.e., *Sequoiadendron* Buchholz, *Sequoia* Endl., and *Metasequoia* Miki) lack a conspicuous ovuliferous scale and have a large swelling of the bract that closes the cone (pl. 28, fig. 8; pl. 29, figs. 7, 8; pl. 30, figs. 6, 7 of Farjon 2005), and mature seeds are always inverted (Gadek et al. 2000; Jagel 2001; Farjon 2005; Schulz and Stützel 2007).

The most basal extant genera of Cupressaceae, *Cunninghamia*, *Taiwania*, and *Athrotaxis* (Gadek et al. 2000; Farjon 2005; Schulz and Stützel 2007), share many similarities with *Hubbardiastrobus* (table 2). All have helically arranged needle-like leaves and terminal ovulate cones with a large number of helically arranged bract/scale complexes that are separate from each other and that consist mainly of bract. Ovules are erect initially, but seeds are inverted at maturity (Jagel 2001; Farjon 2005; Schulz and Stützel 2007). The leaves of *Hubbardiastrobus*, like those of *Cunninghamia*, extend away from the stem at a wide angle. Juvenile leaves of *Taiwania cryptomerioides* Hayata have a similar morphology, but mature leaves of that species are shorter and appressed to the stem (Farjon 2005). The leaves of *Athrotaxis cupressoides* D. Don and *Athrotaxis latifolia* Hook. also are relatively short and appressed to the stem, while those of *Athrotaxis selaginoides* D. Don are somewhat longer and intermediate in orientation between those of the other *Athrotaxis* species (Farjon 2005) and those seen in *Hubbardiastrobus*. In both *Athrotaxis* (Abb 56 of Jagel 2001) and *Hubbardiastrobus*, the ovules originate in an upright position but become inverted before maturity (cf. Abb. 56 of Jagel 2001 and figs. 3, 4I, 5C). Ovulate cones of *Athrotaxis* produce three to six ovules/seeds per bract/scale complex (Farjon 2005), whereas the number of ovules/seeds in *Hubbardiastrobus* is consistently three. Also, *Athrotaxis* lacks free ovuliferous scale tissue whereas the scale of *Hubbardiastrobus* has three free tips.

Hubbardiastrobus also differs from *Taiwania* in several important cone characters. The ovuliferous scale of *Taiwania* is completely fused to the bract at maturity (Liu and Su 1983; Farjon and Ortiz García 2003) while the scale of *Hubbardiastrobus* has three distinct free scale tips and cones of *Taiwania* have one to two seeds per bract/scale complex (Farjon 2005) and those of *Hubbardiastrobus* have three. In addition,

the resin canals of *Taiwania* branch within the bract but those of *Hubbardiastrobus* arise de novo within the bract.

Hubbardiastrobus shares the largest number of characters with living and extinct species of Cunninghamioideae. *H. cunninghamioides* and species of *Cunninghamia* have similarly shaped needle leaves with a laterally expanded band of trans-fusion-like tissue located between the vascular bundle and the central resin canal (Ghouse and Yunus 1974; Brink et al. 2009). The ovulate cones of both have numerous helically arranged bract/scale complexes with the ovuliferous scale fused to the bract except for the tip, and typically there are three seeds per bract/scale complex. Both also have seeds that are inverted at maturity (table 1). These numerous similarities reveal that *Hubbardiastrobus* represents an extinct genus of Cupressaceae, subfamily Cunninghamioideae.

Hubbardiastrobus can be distinguished from living species of *Cunninghamia* by three, separate, free tips of the ovuliferous scale, whereas in mature *Cunninghamia* cones there is a single, three-lobed free scale tip (Farjon 2005; Serbet et al. 2013). Interestingly, immature ovulate cones of *Cunninghamia lanceolata* show three separate scale tips (Abb. 52B of Jagel 2001) like those of *Hubbardiastrobus*, but mature cones of *C. lanceolata* do not. Also, in *Cunninghamia* the first division of bract/scale trace is vertical while that of *Hubbardiastrobus* is horizontal, and the resin canals of *Cunninghamia* branch within the bract while new canals of *Hubbardiastrobus* arise de novo. Both leaf and cone size of *H. cunninghamioides* are smaller than for all extinct and living species of *Cunninghamia* (tables 1, 2).

There have been numerous descriptions of fossil conifers from the Mesozoic and Cenozoic that are intriguingly similar to extant *Cunninghamia* in morphological and anatomical details and that extend back to the Late Jurassic (Stopes and Fujii 1910; Miki 1941; Harris 1943; Szafer 1958; Matsuo 1970; Givulescu 1972; Miller 1975, 1977, 1990; Kimura and Hor-iuchi 1978; Meng et al. 1988; Walther 1989; Miller and Crabtree 1989; Golovneva 1994; Ohana and Kimura 1995; Palamarev and Ivanov 1998; Otto et al. 2003; Van der Ham et al. 2004; Dolezych and Schneider 2007; Brink et al. 2009; Du et al. 2012; Rothwell et al. 2012; Yabe and Yamakawa 2012; Serbet et al. 2013). These include species that are preserved as compressions or impressions, several anatomically preserved ovulate cones with or without a subtending leafy shoot, and one Upper Cretaceous suite of anatomically preserved remains that has been characterized as an extinct species, *Cunninghamia taylorii* Serbet, Bomfleur et Rothwell (Serbet et al. 2013). Specimens of *C. taylorii* consist of leafy shoots, ovulate cones, and pollen cone-bearing shoots, confirming that crown group species of *Cunninghamia* were well established by the Late Cretaceous.

of bract/scale complex near base, showing vascular trace dividing into three bundles and abaxial resin canals. 16 A₂ bot, no. 25, × 100. F, Cross section of bract/scale complex with three ovules. Note narrow lateral wings of ovules. 15 B top, no. 84, × 70. G, Slightly more distal cross section of bract/scale complex in F, showing central ovule and three scale tips. Note that central ovule is situated slightly more distally than lateral ovules seen in F. 15 B top, no. 86, × 70. H, Tangential section of ovulate cone near level of bract/scale complex divergence, with increasing numbers of resin canals in successively more distal views. 16 B bot, no. 49, × 10. I, Longitudinal section of bract/scale complex showing inverted ovule with micropyle (arrowhead) facing cone axis and free tip of ovuliferous scale (os). Note light-colored secondary cortex between positions of bract and scale. 16 A bot, no. 30, × 100.

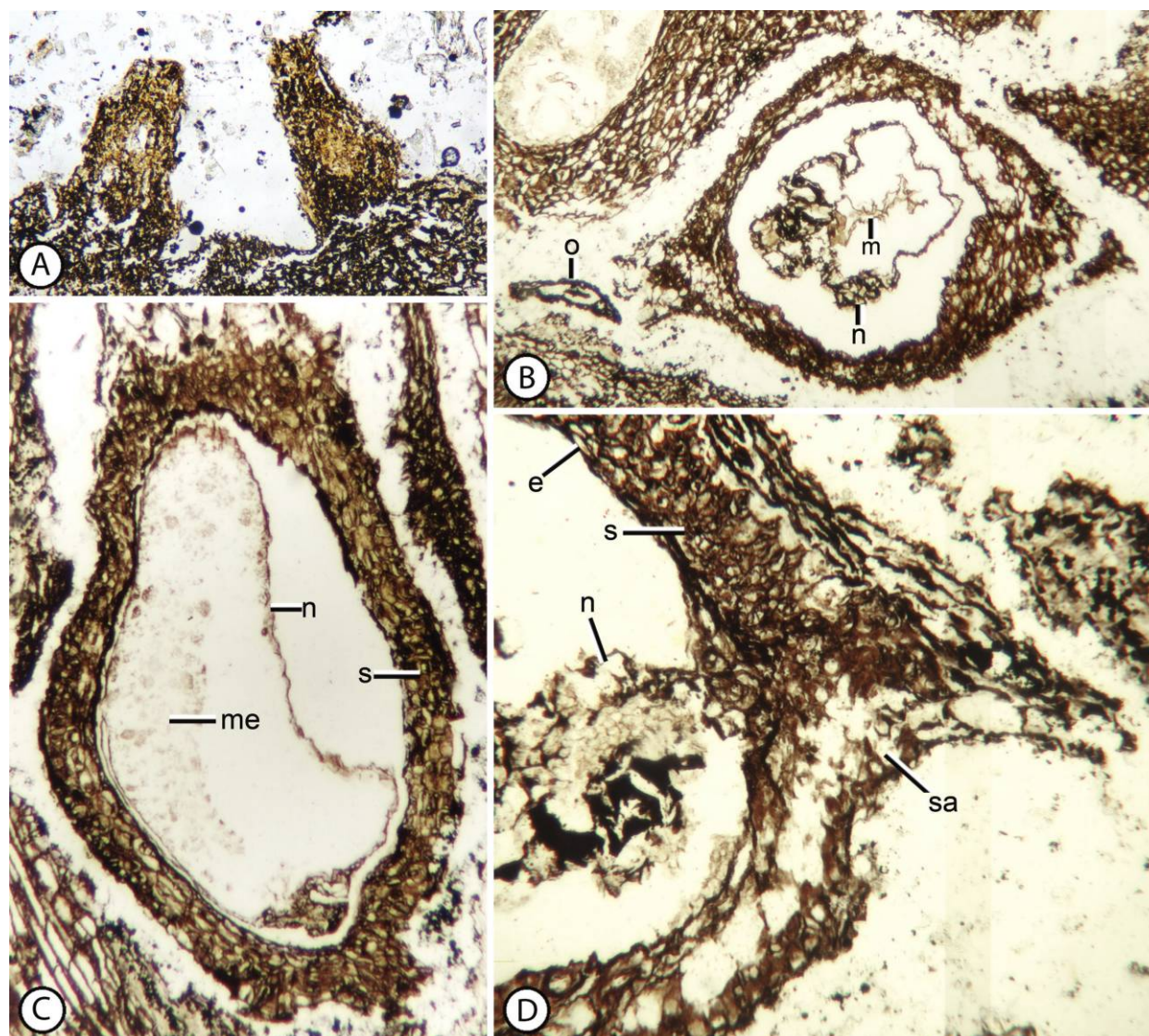


Fig. 5 *Hubbardiastrobis cunninghamioides* Atkinson, Rothwell et Stockey gen. et sp. nov. *A*, Cross section in midregion of bract scale complex of holotype showing attachment of two relatively erect immature ovules. 23 B top, no. 6, $\times 45$. *B*, Cross section of large, relatively mature ovule or seed at right and small immature (possibly abortive) ovule (*o*) at left. Note narrow lateral wings and well-developed integument of mature seed. Also note shrunken nucellus (*n*) with apparently cellular apex (*left*) and amber megaspore membrane (*m*). 16 A₂ bot, no. 32, $\times 45$. *C*, Longitudinal section of large, relatively mature seed with micropyle and apparently cellular nucellar apex facing cone axis (toward bottom of photo), nucellus (*n*), and cellular megagametophyte (*me*). Note thick-walled cells of sclerotesta (*s*). 16 A bot, no. 10, $\times 72$. *D*, Cross section of relatively mature seed in *B* showing sclerotesta between inner thin-walled cells of endotesta (*e*) and outer layers of sacrotesta (*sa*). 16 A₂ bot, no. 25, $\times 122$.

Resolving the systematic relationships of many *Cunninghamia*-like fossils described in older records remains difficult because of differing modes of preservation, the different plant organs that are known for the extinct species, and the heterogeneity of characters displayed by the various species (Bosma et al. 2012). For example, there is an extensive record for *Cunninghamia*-like fossils in Japan ranging from the Cretaceous to the Pleistocene (Miki 1941; Matsuo 1967, 1970). Most of these fossils consist of compressions of leafy shoots whose close systematic affinities remain uncertain (Kimura and Horiuchi 1978). Other *Cunninghamia*-like fossils preserved as

compression/impressions are assigned to the genus *Cunninghamites* Presl. *Cunninghamites* was originally proposed for leafy vegetative conifer shoots, but ovulate cones have subsequently been discovered for a few species that extend throughout the Cretaceous (Kvaček 1999; Bosma et al. 2012). Other Triassic and Jurassic fossils that were previously assigned to *Cunninghamites* are now recognized as species of *Palissya* Endlicher or *Elatocladus* Halle and are of less certain affinities to cunninghamioid Cupressaceae (see Bosma et al. 2012 for a detailed review).

There are several permineralized fossil species from Creta-

Table 1

Morphological and Vegetative Features of Cunninghamioideae and Related Fossils

Character taxon	Diameter of pith (µm)	Secretory		Sclereids or fibers in pith	Sclereids or fibers in cortex	Leaf length (mm)	Leaf serrations	Incurved leaf tips (falcate)	Leaf tip shape	Positions of stomata	Resin canals	Lateral extending transfusion tissue	Fibers or sclereids in leaf	Sclerotic hypodermis in leaf
		cells in pith and cortex	Sclereids											
<i>Austrohamia minuta</i> ^a	?	?	?	?	?	6–7	Absent	Present	Rounded	?	?	?	?	?
<i>Austrohamia acanthobracteata</i> ^b	?	?	?	?	?	3–7	Absent	Present	Rounded	?	?	?	?	?
<i>Elatides williamsonii</i> ^c	?	?	?	?	?	6–12	Absent	Present	Rounded	Hypostomatic	?	?	?	?
<i>Sewardiodendron laxum</i> ^d	?	?	?	?	?	10–22	Absent	Absent	Pointed	Hypostomatic	?	?	?	?
<i>Hubbardiastrobos cunninghamioides</i>	160–300	Both	Sclereids	Sclereids	Sclereids	4–7	?	Present	Pointed	?	1–3	Present	Fibers	Present
<i>Cunninghamia hornbyensis</i> ^e	1600	Pith	None	None	None	21–50	Absent	Present	Pointed	Epistomatic	1–5	Present	Fibers	Present
<i>Cunninghamia taylorii</i> ^f	1680	Both	None	None	None	8–20	Present	Present	Pointed	Hypostomatic	3	Present	Present	Present
<i>Cunninghamiostrobos goedertii</i> ^g	160–700	None	None	None	None	23	Present	Absent?	Pointed	Hypostomatic	3–5	Present	Sclereids	?
<i>Cunninghamiostrobos huebertii</i> ^h	?	?	?	Fibers	Fibers	8	Not seen	?	Pointed	Amphistomatic	3	Present	Fibers	Present
<i>Cunninghamia lanceolata</i> ^{e,f,i}	800–1000	?	None	None	None	30–60	Present	Absent	Pointed	Hypostomatic	1	Present	Absent	Present

^a Escapa et al. 2008.

^b Zhang et al. 2012.

^c Harris 1943.

^d Yao et al. 1998.

^e Brink et al. 2009.

^f Serbet et al. 2013.

^g Miller 1990.

^h Miller 1975.

ⁱ Farjon 2005.

Table 2
Ovulate Cone Characters of Basal Cupressaceae

Character taxon	Age	Cone shape	Size (cm)	Bract/ scale fusion	No. seeds per scale	Interseminal ridge	Free tips of ovuliferous scale	First division of cone scale complex trace vertical	No. resin canals at origin to cone scale complex	Resin canal system	No. resin canals with bract trace at divergence	Resin canal branching in bract	Resin canals adaxial to vascular strands
<i>Hughmillerites juddii</i> ^a	Late Jurassic	Ovoid	3.0–4.3 × 2.2–3.6	Except at tip	3	Present	3	Absent	1	Discontinuous	1	Absent	Present
<i>Hubbardiastrobus cunninghamioides</i>	Early Cretaceous	Cylindrical	1.3–1.5 × .4	Except at tip	3	Absent	3	Absent	1	Continuous	1	Absent	Absent
<i>Cunninghamiostrobus hueberi</i> ^b	Cretaceous	Ovoid	3.0–3.5 × 2.5	Except at tip	3	Absent	1	Present	3	Continuous	3	Present	Present
<i>Cunninghamiostrobus yubariensis</i> ^c	Cretaceous	Cylindrical	6.5 × 2.5	Throughout	3	Absent	0	Present	3	Continuous	3	Present	Present
<i>Parataiwania nihongi</i> ^d	Cretaceous	Ellipsoid	2.2 × 1.6	Except at tip	4	Absent	1	Absent	3	Continuous	1	Absent	Absent
<i>Cunninghamia taylorii</i> ^e	Late Cretaceous	Ovoid	3 × 2.3	Except at tip	3	Absent	1	Present	1	Continuous	1	Present	Absent
<i>Cunninghamiostrobus goedertii</i> ^f	Oligocene	Ovoid	4.0 × 3.0–4.5	Except at tip	3	Absent	1	Present	3	Continuous	3	Present	Present
<i>Cunninghamia lanceolata</i> ^{a,e,g}	Extant	Ovoid	2.5–4.0 × 2.5–3.5	Except at tip	3	Absent	1	Present	1	Continuous	1	Present	Absent
<i>Athrotaxis selaginoides</i> ^g	Extant	Ovoid	1.5–3.0 × 1.5–3.0	Throughout	3–6	Absent	0	Present	1	?	3	Present	Present

^a Rothwell et al. 2011.

^b Miller 1975.

^c Ohana and Kimura 1995.

^d Nishida et al. 1992.

^e Serbet et al. 2013.

^f Miller 1990.

^g Farjon 2005.

ceous deposits that are similar to, but do not show the entire suite of, cunninghamioid characters. The bract and ovuliferous scale of ovulate cones assigned to *Mikastrobus hokkaidoensis* Saiki et Kimura (1993) from the Upper Cretaceous of Japan are highly fused, but there is a single free scale tip as in species of *Cunninghamia* and *Cunninghamiostrobus hueberi* Miller (table 2). The vascular system of the cone scale in *M. hokkaidoensis* is described as being more similar to that of *Taiwania* than *Cunninghamia* (Saiki and Kimura 1993), and there is no *Cunninghamia*-like transfusion tissue between the vascular bundle and central resin canal in the leaf. *Mikastrobus hokkaidoensis* has four or five seeds per bract/scale complex, as compared to three in *Hubbardiastrobus* and other members of the Cunninghamioideae (table 2). Therefore, *M. hokkaidoensis* has been assigned to the Taiwaniioideae (Saiki and Kimura 1993; Stockey et al. 2005a).

The extinct monotypic genus *Parataiwania* (i.e., *Parataiwania nihongii* M. Nishida, Ohsawa et H. Nishida), represented by an ovulate cone from the Upper Cretaceous of Japan, is also considered to be a genus of Taiwaniioideae (Nishida et al. 1992; Stockey et al. 2005a). Bract/ovuliferous scale fusion is similar in *Parataiwania* and *Hubbardiastrobus*, but *Parataiwania* has one free scale tip rather than the three separate scale tips that characterize *Hubbardiastrobus* (table 2). Also, there are four seeds per bract/scale complex in *Parataiwania* rather than three as in *Hubbardiastrobus*, *Cunninghamia*, *Cunninghamiostrobus* Stopes et Fujii, and *Hughmillerites* (table 2).

Vegetative morphology and anatomy of living and extinct *Cunninghamia*, *Cunninghamites* Presl ex Sternberg, and *Cunninghamiostrobus* species have been thoroughly reviewed by Brink et al. (2009), revealing that the vegetative features within this clade have remained surprisingly stable over a long period of time (Brink et al. 2009; table 1). Stems of the various species differ in size and histological features, and the leaves have differing combinations of size and shape, number of veins, number of resin canals, positions of stomata, and presence or absence of serrations along the leaf margins (Brink et al. 2009). The taxonomic distribution of transfusion tissue that occurs between the leaf trace and the central canal in *Cunninghamia* and *Hubbardiastrobus* is not as well known as some other features but appears to be absent from at least some cupressaceous species (e.g., *M. hokkaidoensis*; pl. IV, fig. 2 of Saiki and Kimura 1993). Stem, leaf, and cone size of *Hubbardiastrobus* all fall at the lower end of the range of variation for cunninghamioids (tables 1, 2). Leaf serrations are present in *C. lanceolata*, *Cunninghamia konishii* Hayata, *C. taylorii* Serbet, Bomfleur et Rothwell, and *Cunninghamiostrobus goedertii* Miller, but they are not known to occur in either *Cunninghamia hornbyensis* Brink, Stockey, Beard et Wehr or *H. cunninghamioides* (table 1; Brink et al. 2009; Serbet et al. 2013). Among living and extinct species of Cupressaceae, subfamily Cunninghamioideae, *H. cunninghamioides* is the only species known to have sclereids and secretory cells in both the pith and the cortex (table 1).

Fossil cunninghamioid ovulate/seed cones. Several anatomically preserved cunninghamioids have been described from ovulate cones, some with attached vegetative shoots, and those fossils possess many features that add critical information to our understanding of basal Cupressaceae by having a

novel combination of characters (especially when attached to leafy shoots). Conifers of the genus *Cunninghamiostrobus* are known from the Cretaceous (*C. hueberi* Miller and *Cunninghamiostrobus yubariensis* Stopes & Fujii) and the Oligocene (*C. goedertii* Miller; Stopes and Fujii 1910; Miller 1975; Miller and Crabtree 1989; Ohana and Kimura 1995). All three species of *Cunninghamiostrobus* share with *Hubbardiastrobus* three seeds per bract/scale complex. However, within *Cunninghamiostrobus* ovulate cones there are three resin canals at the origin of bract/scale complex and the resin canals branch within the bract, while in *Hubbardiastrobus* there is only one resin canal at the origin of the bract/scale complex and additional resin canals arise de novo (table 2). Three prominent, free, scale tips like those of *Hubbardiastrobus* do not occur in any of the species *Cunninghamiostrobus*. Rather, there is a single free scale tip in *C. hueberi* and *C. goedertii* and none in *C. yubariensis* (table 2).

As indicated above, there is one anatomically preserved fossil species of *Cunninghamia*, *C. taylorii*, from the Upper Cretaceous of Alberta, Canada, that has been described from leafy shoots, ovulate cones, and pollen cone-bearing structures (Serbet et al. 2013). As with *C. hornbyensis*, the leaves of *C. taylorii* are longer than those of *H. cunninghamioides* (table 1). The cones of *C. taylorii* are also larger than those of *Hubbardiastrobus* (table 2). A single free ovuliferous scale tip is present in *C. taylorii*, as opposed to the three free scale tips seen in *Hubbardiastrobus*. Unlike *Hubbardiastrobus* the resin canals of *C. taylorii* branch inside the bract. The stem pith of *C. taylorii* is similar to that in *C. hornbyensis* and is much larger than the pith of *H. cunninghamioides* (table 1). Histology of the stem of *Hubbardiastrobus* differs from *C. taylorii* in several characters. In *H. cunninghamioides* there are sclereids in the pith and cortex while *C. taylorii* lacks sclerenchyma in those tissues. However, there are secretory cells in the stem pith and cortex in both *C. taylorii* and *H. cunninghamioides*.

Hughmillerites juddii (Seward et Bancroft) Rothwell, Stockey, Mapes et Hilton from the Jurassic of Scotland is the oldest permineralized cunninghamioid described to date (Rothwell et al. 2011), and of all of the fossil cunninghamioid ovulate cones, it appears to be the most similar to *H. cunninghamioides*. Both of these species have three free tips of the ovuliferous scale and also have an ovule/seed associated with each free tip (table 2). At the origin of the bract/scale complex, there is only one resin canal in both *Hughmillerites* and *Hubbardiastrobus*. A primary vertical division of the bract/scale trace is absent in the two genera. One other similarity is that the resin canals in *Hughmillerites* and *Hubbardiastrobus* arise de novo in the bract. However, *Hughmillerites* has interseminal ridges between the ovules/seeds, which are absent in *Hubbardiastrobus*. *Hughmillerites* has resin canals adaxial to the vascular strands in the bract/scale complex while *Hubbardiastrobus* lacks adaxial canals. It is tempting to hypothesize that because *Hughmillerites* and *Hubbardiastrobus* are the oldest and only cunninghamioids that possess three free ovuliferous scale tips, this character may be ancestral within the cunninghamioid clade. The occurrence of separate bract tips in immature ovulate cones of living *C. lanceolata* that are lost with further maturation suggests that loss may have resulted from an altered path of bract/scale development in living and some extinct species (table 2).

Hubbardiastrobus cunninghamioides represents a new genus of conifers in Cupressaceae, subfamily *Cunninghamioideae*, based on a unique combination of characters. The vegetative features include helically arranged falcate leaves, one to three resin canals within the leaves, lateral extending transfusion tissue, fibers in the mesophyll, and sclereids in the stem pith and cortex. The ovulate cone characters include three free tips of the ovuliferous scale, three seeds per scale, no primary vertical division of the bract/scale vascular trace, one resin canal at the origin of the bract/scale complex, resin canals arising de novo, and no resin canals adaxial to the vascular strands.

Discovery of *H. cunninghamioides* further expands our knowledge of the diversity of extinct cunninghamioids during the Early Cretaceous. Due to our growing understanding of mosaic character evolution within the Cupressaceae and the critical combination of characters that ovulate cones contain, features of the *H. cunninghamioides* plant also suggest that the identification of fossil conifers as extinct species of *Cunninghamia* based solely on vegetative features may be suspect. However, novel combinations of vegetative and reproductive

characters, such as those displayed by *Hubbardiastrobus*, do contribute solid data for resolving the overall pattern of phylogeny for Cupressaceae and provide further evidence that the *Cunninghamioideae* played a major role in the initial radiation of the family.

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