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A new species of *Cunninghamia* (Cupressaceae) from the Upper Cretaceous (Maastrichtian) of Hokkaido, Japan

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Abstract

Cunninghamia nakatonbetsuensis sp. nov. is described as a new fossil-species based on a seed cone from the Upper Cretaceous (Maastrichtian) Heitaro-zawa Formation of the Hakobuchi Group, exposed in Heitaro-zawa, Nakatonbetsu Town, Hokkaido, Japan. This newly discovered species has three seeds per the bract-scale complex, a single robust vascular bundle and a resin canal at the base of the bract-scale complex, and a single row of vascular bundles around the middle of the bract-scale complex. These features are shared with other *Cunninghamia* species. This new species shares many characters with extant *C. lanceolata*, such as the trilobed ovuliferous scale, which is fused to the bract except for lateral margins, and branching pattern of vascular bundles in the bract-scale complex. However, it is different from extant and fossil *Cunninghamia* species including *C. lanceolata* by possessing thicker bract-scale complex.

Key words: Cretaceous, *Cunninghamia*, Cunninghamioideae, Cupressaceae, Hakobuchi Group, Hokkaido, seed cone

Introduction

The conifer family Cupressaceae consists of 167 extant species belonging to 30 genera (Farjon 2005, Christenhusz *et al.* 2011, POWO 2023), which includes the former Taxodiaceae but excludes *Sciadopitys* Siebold & Zuccarini (1842: t. 101). The extant Cupressaceae is divided into seven subfamilies (Gadek *et al.* 2000, Liu *et al.* 2022, Yang *et al.* 2022): Cunninghamioideae, Taiwanoideae, Athrotaxidoideae, Sequoioideae, Taxodioideae, Callitroideae (or Actinostroboideae), and Cupressoideae. Molecular phylogenetic analyses suggest that Cunninghamioideae is sister to all other subfamilies within the family, followed by Taiwanoideae, Athrotaxidoideae, Sequoioideae, and Taxodioideae in that order. The largest subfamily, Cupressoideae, and the second largest subfamily, Callitroideae, comprise a clade that is sister to the Taxodioideae (Mao *et al.* 2012, Yang *et al.* 2012, Liu *et al.* 2022, Yang *et al.* 2022).

The Cunninghamioideae exhibits less specialized cone characteristics compared to other subfamilies, such as tapered leafy cone scales with reduced but partially free ovuliferous scales. Anatomical studies have shown that the vascular strands in the bract-scale complex divide horizontally, forming a single line in the middle to distal regions, with diminished adaxial branches (Stopes & Fujii 1910, Satake 1934, Serbet *et al.* 2013). Numerous fossil-genera of this subfamily have been reported worldwide, ranging from the Middle Jurassic to the Late Cretaceous (e.g., Stopes & Fujii 1910, Harris 1953, Atkinson *et al.* 2014a, Shi *et al.* 2014). In contrast, the extant Cunninghamioideae is a monotypic subfamily, comprising only the genus *Cunninghamia* R. Br. in Richard (1826: 80, 149), with two species currently found in East Asia: *C. lanceolata* (Lambert 1803: 52) Hooker (1827: t. 2743) and *C. konishii* Hayata (1908: 194) (LePage, 1990). *Cunninghamia hornbyensis* Brink & Stockey (2009: 90) and *C. taylorii* Serbet, Bomfleur & Rothwell (2013: 472) represent the oldest fossil records of this genus, both discovered in the Upper Cretaceous (Campanian) of Canada (Brink *et al.* 2009, Serbet *et al.* 2009). Although many Cenozoic (mostly Neogene) fossil-species of *Cunninghamia* have been described (Brink *et al.* 2009, Yabe & Yamakawa 2016), no reliable records of this genus are known from the Mesozoic, except for the two species mentioned above.

In this study, we report a new fossil-species of *Cunninghamia* from the Maastrichtian Hakobuchi Group in Heitaro-zawa, Nakatonbetsu town, Hokkaido. Based on these findings, we discuss the evolutionary process of seed cones in genus *Cunninghamia* as well as in the Cupressaceae.

Material and methods

Fossil seed cone

A seed cone was found in a river float collected from the Heitaro-zawa Creek in Nakatonbetsu town, Hokkaido (44.980°N, 142.252°E), within the distribution range of the Heitaro-zawa Formation of the Hakobuchi Group (Ando *et al.* 2001). The presence of *Inoceramus shikotanensis* associated with the seed cone suggests an early Maastrichtian age (Shigeta & Tsutsumi 2019).

The seed cone was sectioned both transversely and longitudinally, and serial sections were obtained using the acetate peel method (Joy *et al.* 1956). Thicknesses of rock matrix were measured before and after making a series of peel sections to estimate the thickness of abraded cone part. Longitudinal sections were assigned slide numbers starting with "b" or "c," while transverse sections were labeled with those starting with "a." The slides and specimens are archived in the Palaeobotanical Collections of the National Museum of Nature and Science (NSM PP) in Tsukuba, Ibaraki, Japan.

Photographs were captured using a BX53 light microscope (Olympus Corporation, Tokyo, Japan) equipped with a DP74 digital camera which is controlled by cellSens Standard software (Olympus Corporation). The images were subsequently processed using Photoshop v23.5.2 (Adobe Inc., San Jose, CA, USA). Amira 3D 2023.2 (Thermo Fisher Scientific, Waltham, MA, USA) was used to generate 3D reconstructions of the cone.

Extant seed cones

Extant seed cones of *Cunninghamia lanceolata* were collected from cultivated trees in Botanical Gardens, Osaka Metropolitan University, Kisaichi, Osaka, Japan. To extract vascular strands, bract-scale complexes were oxidized by Kitchen Haiter (Kao, Tokyo, Japan) in which 6% NaClO is dissolved in a few percent of NaOH solution. Bract-scale complexes were soaked in Kitchen Haiter for 24 hours and rinsed in distilled water twice. The extracted vascular strands were stained with safranin and photographed under dissecting microscope S8APO (Leica, Wetzlar, Germany).

Systematic Palaeobotany

Cunninghamia nakatonbetsuensis S.Y.Jiang & T.Yamada, *sp. nov.* (Figs. 1–4).

Holotype:—JAPAN. Hokkaido: Nakatonbetsu town, Heitaro-zawa Creek, River float at 44.980°N, 142.252°E, 70 m elevation, 10 June 2005, NSM PP-9178 (NSM PP!).

Diagnosis:—Seed cone ovoid, ca. 35 mm long and ca. 30 mm wide. Bract-scale complexes swollen to form a mound around the apical third, supplied with a single vascular strand from cone axis, which firstly divides into abaxial and central adaxial bundles; central adaxial bundle bifurcating once horizontally; abaxial bundle dividing horizontally into 8–10 smaller bundles; 2 lateral adaxial bundles, each branched from abaxial bundle on a lateralmost side; resin canal placed both adaxial and abaxial to the vascular strands. Ovuliferous scale fused to bract except for each lateral margin; apical part trilobed.

Stratigraphic horizon:—the lower Maastrichtian Heitaro-zawa Formation of the Hakobuchi Group.

Etymology:—The specific epithet is named after the town where the sample was collected.

Slides:—NSM PP-9178-a01–a14, b01–b69, c01–c34.

Morphological and anatomical characters of *Cunninghamia nakatonbetsuensis*

Seed cone:—A conical to ovoid in shape, measuring approximately 35 mm in length and over 30 mm in diameter (Figs. 1A, B). The bract-scale complexes are arranged helically. In the specimen, 29 bract-scale complexes were preserved, but the total number would have been over 40 if all complexes were preserved.

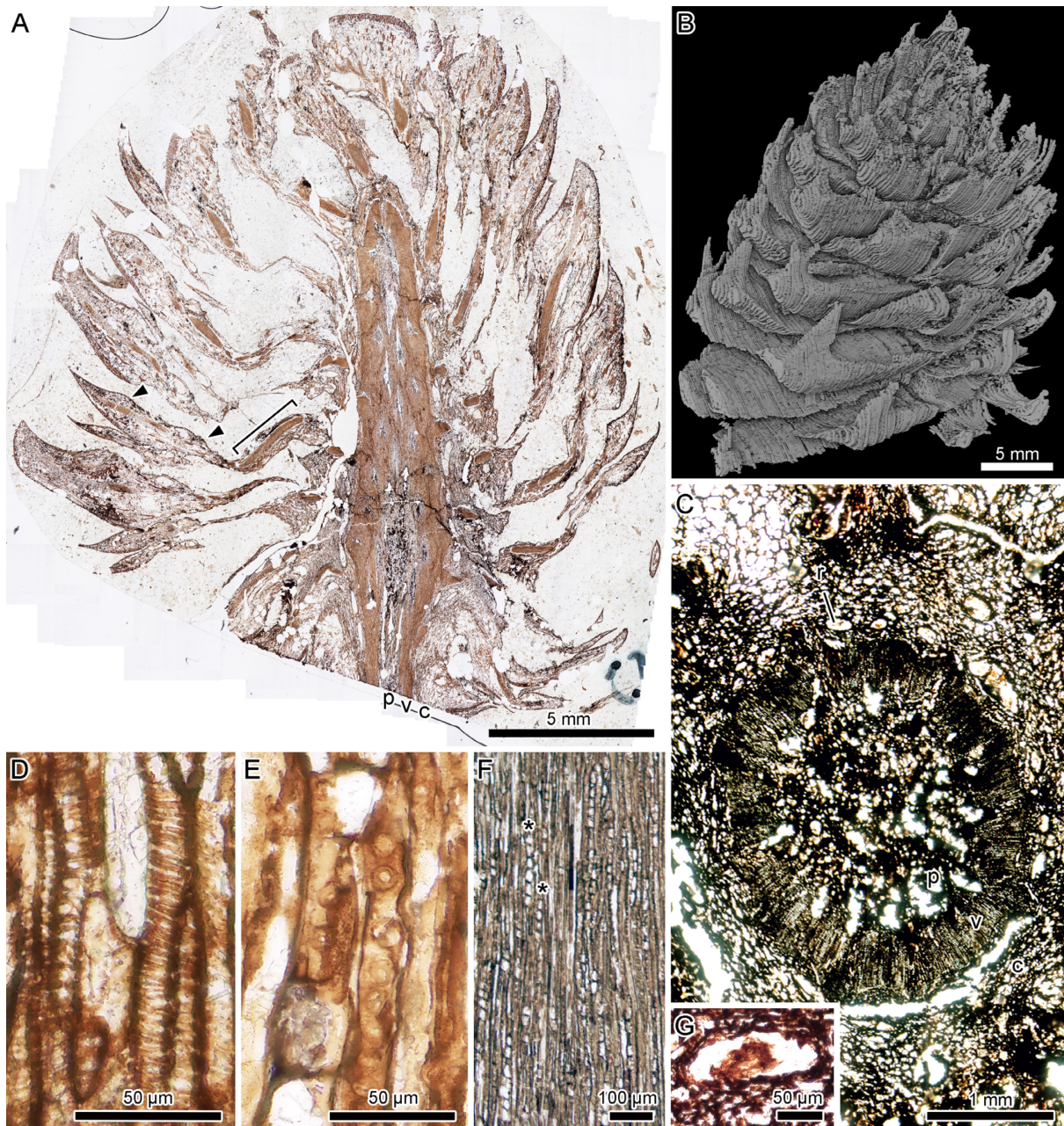


FIGURE 1. *Cunninghamia nakatonbetsuensis*. **A.** Longitudinal section of seed cone. A ovuliferous scale would be attached on the surface between two arrowheads. Bracket shows a stalk-like part of cone scale. Slide #c34. **B.** 3D reconstructed image of cone. **C.** Cross section through the basal part of cone. Slide #a14. **D.** Primary xylem tracheids in cone axis. Slide #c32. **E.** Secondary xylem tracheids in cone axis. Slide #c34. **F.** Rays (asterisks) in secondary xylem of cone axis. Slide #c34. **G.** Close-up of C, showing a resin canal in cortex with resin residue inside. Abbreviations: c, cortex; p, pith; r, resin canal; v, vascular tissue.

Cone axis:—Width is about 3.5 mm in the middle part of the cone, but tapering towards the apex (Figs. 1A, B). It consists of concentric tissue layers, including pith, vascular cylinder, cortex, and epidermis, extending from the center to the outer region (Figs. 1A, C). The pith is parenchymatous and measures 0.5–1 mm in width, although it is disintegrated in certain parts of the axis (Figs. 1A, C). Walls of the pith cells are often thickened, but cells are not sclerenchymatous. No resin canals are observed in the pith (Figs. 1A, C).

The vascular cylinder has a diameter of 3–4.5 mm, a thickness of approximately 1.5 mm, and does not contain resin canals and annual rings. The primary xylem is endarch (Figs. 1A, C). Tracheids of the primary xylem have a diameter of 8–10 µm, with scalariform thickenings on their radial walls (Fig. 1D). The secondary xylem consists of tracheids that are 12–15 µm in diameter (Fig. 1E). Bordered pits are arranged in a single row on the tracheid walls (Fig. 1E). Rays of 4–8 cells thick are developed in the secondary xylem (Fig. 1F). The cambium and phloem are mostly disintegrated, resulting in a blank space between the secondary xylem and cortex (Figs. 1A, C). The cortex measures

approximately 0.5 mm in width and consists mainly of parenchymatous cells with scattered sclerenchymatous cells (Figs. 1A, C). A single ring of large resin canals is observed in the inner cortex (Figs. 1A, C). Each resin canal is encircled by 1–2 layers of flattened epithelial cells (Fig. 1G).

Bract-scale complex:—Each complex is ca. 12 mm long (Figs. 1A, 2A) and the margin is slightly serrated (Fig. 2B). The basal part of the complexes is stalk-like, extending for 4–5 mm from the cone axis (Fig. 1A) and measuring less than 4 mm in width (Figs. 2A, C). In the transition zone to the laminar part of the bract-scale complex, each lateral side of the stalk-like part is thinly expanded (Figs. 2A, D). The middle part of the complexes is 7–8 mm in length and over 10 mm in width and flattened-deltoid in cross section (Figs. 2A, E). Each bract-scale complex is swollen adaxially to form a mound around the apical one-third of the complex, while it becomes thinner distal to the mound (Figs. 1A, 2A, F). The apical part of the complexes is pointed and bends slightly upward (Figs. 1A, 2A). The hypodermis is well-developed on both the adaxial and abaxial sides of each complex, composed of 2–4 layers of sclerenchymatous cells, with the abaxial part being thicker than the adaxial one (Figs. 2F, 3B). The cortex mostly consists of parenchymatous cells with scattered sclereids, which are rounded and polygonal (Fig. 2F).

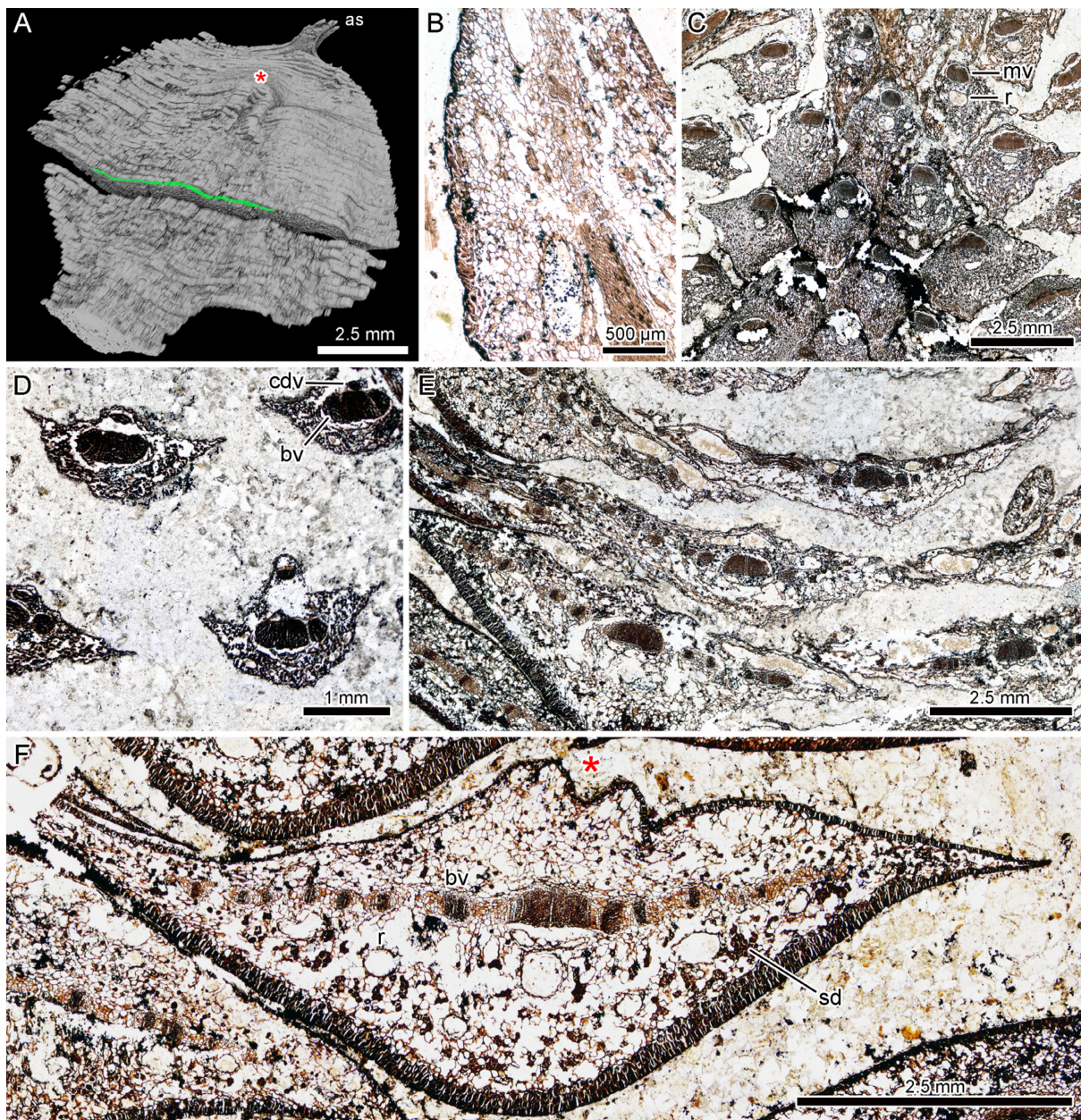


FIGURE 2. Anatomy of bract-scale complex in *Cunninghamia nakatonbetsuensis*. **A.** 3D reconstructed image of bract-scale complex with adaxial face up. Red asterisk shows a mound. Lobes of ovuliferous scale are coloured green in a section. **B.** Paradermal section showing serrate margin. Slide #c21. **C.** Cross section through basal stalk-like part. Slide #c30. **D.** Cross section through middle stalk-like part. Slide #c20. **E.** Cross section through middle part. Slide #c4. **F.** Cross section through swollen part (red asterisk). Slide #b31. Abbreviations: **as**, apical spine; **bv**, abaxial vascular bundle; **cdv**, central adaxial vascular bundle; **mv**, main vascular bundle; **r**, resin canal; **sd**, sclereid.

Ovuliferous scale is fused to a bract except for the lateral sides (Fig. 3A). It is trilobed, as indicated by two longitudinal grooves on the adaxial side of bract scale (Fig. 3A). Adaxial epidermis of the bract is often degraded possibly due to detachment of the ovuliferous scale (Fig. 3B). The degraded part suggests the apex of the ovuliferous scale would have located proximal to the mound of the bract-scale complex (Fig. 3B). Seeds are lost except for a complex in which two unitegmic seeds remain on the adaxial side. Each ovule is positioned laterally, with no ovule in the central position. This indicates that the ovule has been lost in the central lobe, while the ovule is retained in the two lateral lobes of the trilobed ovuliferous scale. Therefore, it is expected that three ovules are present per bract-scale complex. The unitegmic seeds appear to be abortive, judging from their small sizes (Fig. 3C). The seeds have an elliptical shape in cross-section. Serial sections suggest that the micropyle directs basally. Outer and inner layers of integument consist mainly of sclerotic and parenchymatous cells, respectively (Fig. 3C). The preservation of the seeds is poor, making it difficult to identify the nucellus (Fig. 3C).

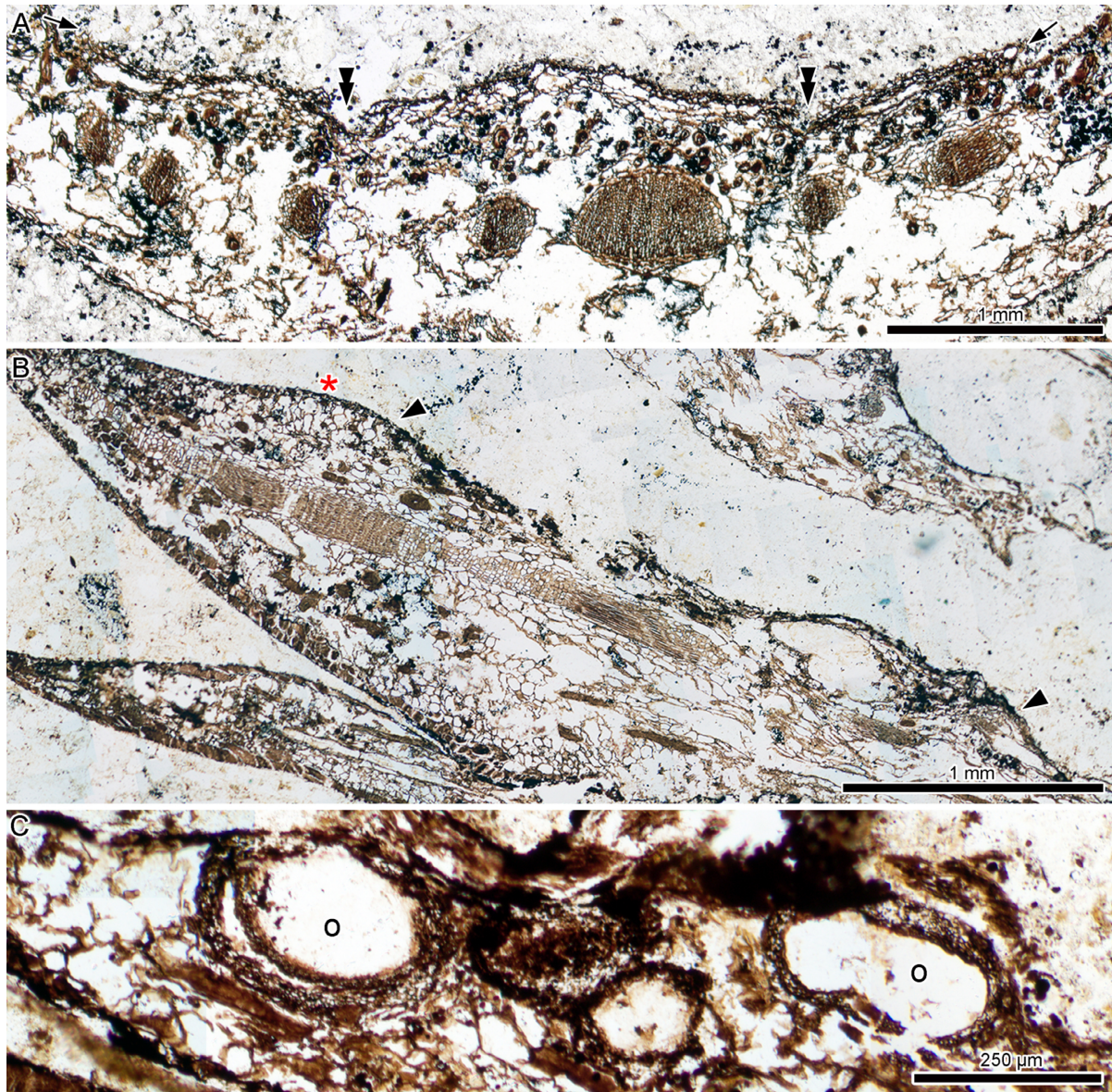


FIGURE 3. Anatomy of bract-scale complex in *Cunninghamia nakatonbetsuensis*. **A.** Cross section of bract-scale complex highlighting marginal free parts (arrows) and grooves (double-arrowheads) between lobes of ovuliferous scale. Slide #c34. **B.** Close up of 1A, showing a disintegrated region of cone scale (between two arrowheads), possibly formed by detachment of ovuliferous scale. Red asterisk shows a mound. Slide #c34. **C.** Cross section of bract-scale complex with two aborted ovules (o). Note that two circular structures in the middle are not ovules but hollow made by disintegration.

A single vascular trace, which is elliptical in cross-section, supplies each bract-scale complex from the cone axis (Fig. 2C). The trace is collateral, with adaxial xylem and abaxial phloem (Fig. 4A). The trace remains undivided for approximately 1–1.5 mm from the axis. Primary xylem tracheids are present on the adaxial side of the strand, while secondary xylem tracheids with secondary thickenings are located on the abaxial side of the primary xylem (Fig. 4A).

Crushed phloem cells are found abaxial to the secondary xylem (Fig. 4A). The vascular trace divides vertically to abaxial and central adaxial bundles through the intercalation of parenchymatous tissue at approximately 1–1.5 mm from the axis (Fig. 4B). The central adaxial bundle is smaller than the abaxial one (Figs. 2D, 4B) and divides laterally (Figs. 4C, D). The primary xylem in the central adaxial bundle is oriented towards that of the abaxial bundle (Fig. 4B), indicating an inverted orientation in the adaxial bundle. The abaxial bundle divides laterally several times, eventually forming 8–10 bundles (Figs. 3A, 4C, D). Transfusion tissue develops between each abaxial vascular bundle, as well as on adaxial and abaxial sides of them (Figs. 2F, 4E). Each of the lateralmost derivatives of the abaxial bundle divides vertically to give rise to a lateral adaxial bundle (Figs. 4D, F). The central and lateral adaxial bundles are likely to supply the ovules, although the supply was not observable in the specimen.

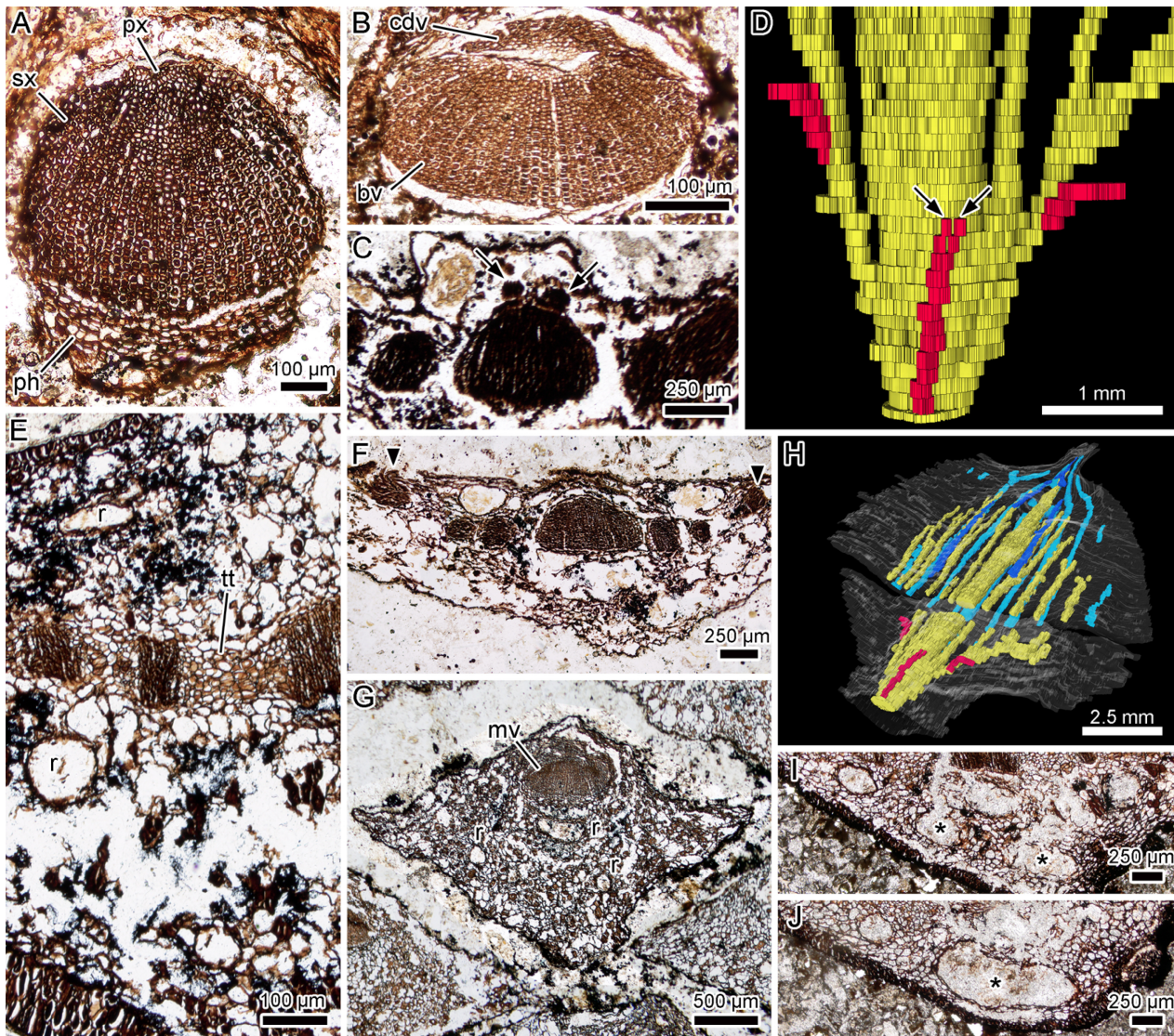


FIGURE 4. Anatomy of vascular bundles and resin canals in *Cunninghamia nakatonbetsuensis*. **A.** Cross section of main vascular bundle just diverging from vascular cylinder of cone axis. Slide #c27. **B.** Cross section of main vascular bundle with the central adaxial bundle diverging. Slide #c28. **C.** Cross section of bract-scale complex with central adaxial strand dividing (arrows). Slide #c13. **D.** 3D reconstructed image of vascular system in basal part of bract-scale complex. Adaxial vascular bundles are coloured red and abaxial bundles in yellow. Note bifurcate central adaxial bundle (arrows). Arrowhead shows lateral adaxial vascular bundle. **E.** Resin canals adaxial and abaxial to vascular strands. Note transfusion tissue connecting vascular strands. **F.** Cross section of bract-scale complex with two lateral adaxial bundles (arrowheads) diverging. Slide #c5. **G.** Cross section through stalk-like part of bract-scale complex. Slide #c27. **H.** 3D reconstructed images of vascular system and resin canal system. Cone scale is positioned with the adaxial side up and the apical direction to the right. Resin canals abaxial or adaxial to a row of vascular strands are coloured cyan or blue, respectively. Vascular bundles are coloured as 4D. **I, J.** Cross sections of the same bract-scale complex through its apical part. Section in J (slide #b56) is apical to that in I (slide #b53). Two abaxial resin canals are fused as they run into more apical part (asterisks). Abbreviations: **bv**, abaxial vascular bundle; **cdv**, central adaxial vascular bundle; **mv**, main vascular bundle; **ph**, phloem; **px**, primary xylem; **r**, resin canal; **tt**, transfusion tissue.

A large resin canal is supplied to the bract-scale complex from the resin canal system of the axis. It is located abaxial to the vascular strand and nearly circular in shape (Fig. 2C). Several resin canals originate *de novo* on both the adaxial and abaxial sides of the vascular strand (Figs. 2E, F, 4G, H). Although the distribution of abaxial resin canals is somewhat variable, the number of abaxial resin canals is approximately equal to that of vascular strands in the middle part of the bract-scale complexes (Figs. 2F, 4H). In the apical part, the number of the resin canals are decreased due to fusion among adjacent resin canals (Figs. 4H, I, J).

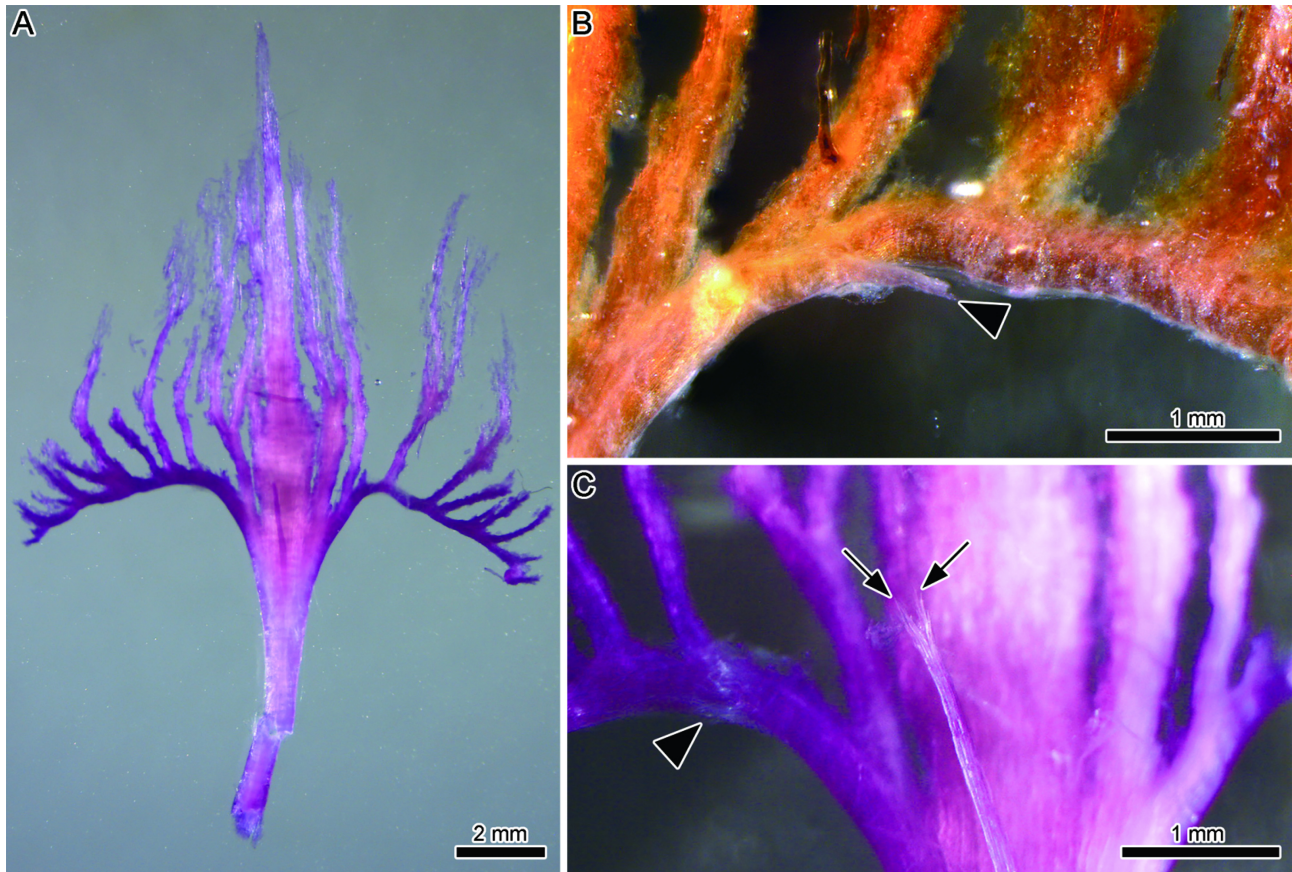


FIGURE 5. Vascular system in bract-scale complex of *Cunninghamia lanceolata*. **A.** Adaxial view of entire vascular system. **B.** Lateral adaxial vascular bundle (arrowhead) branched from lateral abaxial vascular bundle. **C.** Close-up of A showing bifurcation of central adaxial vascular bundle (arrows). Arrowhead shows lateral adaxial vascular bundle.

Discussion

Cunninghamia nakatonbetsuensis shares many characters with extant *C. lanceolata*, such as the cone shape and size, three seeds per the bract-scale complex, and the trilobed ovuliferous scale which is fused to the bract except for lateral margins (Stopes & Fujii 1910, Aase 1915, Satake 1934, Farjon & Garcia 2003, Serbet *et al.* 2013). In particular, the branching pattern of vascular bundles in the bract-scale complexes is closely similar between *C. nakatonbetsuensis* and extant *C. lanceolata*: a central adaxial bundle vertically branches from the main bundle at the base of the bract-scale complex, and a lateral adaxial bundle branches from each lateralmost abaxial bundle (Figs. 4C, D, 5A, B). The central adaxial bundle further bifurcates in both species (Figs. 4C, D, 5A, C). Our observations on extant *C. lanceolata* align with those made by Satake (1934), despite some studies proposing different branching patterns of the adaxial vascular bundles (Ohana & Kimura 1995, Serbet *et al.* 2013). Ohana & Kimura (1995) speculated that bifurcation of the central adaxial bundle in *C. lanceolata* is unlikely because only one ovule is supplied by the central adaxial bundle, but they did not observe the branching pattern in *C. lanceolata*. Serbet *et al.* (2013) hypothesized that three ovular traces are formed from the central adaxial bundle through two successive branchings; while they demonstrated the first branching of the central adaxial bundle, they did not provide data supporting the occurrence of the second branching. Aase (1915) observed the branching patterns of vascular bundles in the extant species *C. davidiana nom. nud.*, identifying five to six adaxial vascular bundles. This observation is likely based on either *C. lanceolata* or *C. konishii*, considering these

are the only extant species of *Cunninghamia* accepted so far. However, other studies consistently report fewer than five adaxial vascular bundles in both *C. lanceolata* and a fossil-species *C. taylori* (Satake 1934, Serbet *et al.* 2013, this study). Nevertheless, *C. nakatonbetsuensis* could be distinguished from extant *Cunninghamia* species by thicker bract-scale complex and longer ovuliferous scale (Satake 1934, Serbet *et al.* 2013).

Cunninghamia taylori is reported from the Campanian of Canada, represented by permineralized specimens of leafy shoots bearing seed cones (Serbet *et al.* 2013). Compared to *C. nakatonbetsuensis*, the bract-scale complexes of *C. taylori* are narrower and have a longer apical bract tip. The cone size of *C. taylori* is 30 mm in length and 23 mm in width, indicating that this species has smaller cones than *C. nakatonbetsuensis*. Most fossil *Cunninghamia* species are established based only on leafy shoots (Brink *et al.* 2009). Even when information on seed cone characters is available, it often comes from compressed cones rather than permineralized ones (Walther 1989, Yabe & Yamakawa 2016). These compressed cones, as well as those of *C. taylori*, are distinguished from *C. nakatonbetsuensis* by the absence of a mound on the adaxial side of the cone scales.

The fossil-genus *Cunninghamiostrobus* Stopes & Fujii (1910: 51) was established based on a seed cone collected from the Cretaceous Yezo Group in Oyubari, Yubari City, Hokkaido, Japan, with *Cs. yubariensis* Stopes & Fujii (1910: 51) as the type fossil-species. As the generic name suggests, it was originally diagnosed as "cone scales and axis in anatomical essentials like those of the living genus *Cunninghamia*" (Stopes & Fujii 1910). The diagnosis of the fossil-genus *Cunninghamiostrobus* was later emended by Ogura (1930, 1932) and Ohana & Kimura (1995) based on their own "*Cs. yubariensis*" specimens, rather than the type specimen. These "neotypes" differ from the original *Cs. yubariensis* in terms of conical shape, larger size of the cones, and higher density of cone scales. Therefore, we followed the original generic diagnosis by Stopes & Fujii (1910) which could be applied to all *Cunninghamiostrobus* species described so far (Ogura 1930, Miller 1975, Miller & Crabtree 1989, Ohana & Kimura 1995). Our specimen could be assigned to this fossil-genus by a single robust vascular bundle and a resin canal at the base of the bract-scale complex, uniseriately arranged vascular bundles around the middle of the bract-scale complex, and three adaxial vascular bundles likely supplying the ovules (Stopes & Fujii 1910). However, we refrained from assigning our specimen to this genus due to the confusion surrounding the generic diagnosis. Additionally, the characteristics of the vascular and resin systems in our specimen match better with those of *Cunninghamia* than with those of *Cunninghamiostrobus*, as discussed below.

Cunninghamiostrobus yubariensis shares several similarities with *C. nakatonbetsuensis*, including comparable size and ovoid shape of the seed cone, less crowded cone scales, and fusion of the ovuliferous scale to the bract except for the margin (Stopes & Fujii 1910). However, *C. nakatonbetsuensis* differs from *Cs. yubariensis* in having a thicker cone axis and bract-scale complexes with a distinct stalk-like structure, an adaxially swollen mound, and a vertically pointed apex. These characters also distinguish *C. nakatonbetsuensis* from the "neotypes of *Cs. yubariensis*" by Ogura (1930) and Ohana & Kimura (1995).

Cunninghamiostrobus hueberi Miller (1975: 706) was reported from the Albian of California. This species is similar to *C. nakatonbetsuensis* in terms of ovoid seed cones and incompletely fused bract-scale complexes. However, annual rings are observed in the vascular cylinders of the cone axis of *Cs. hueberi* (Miller 1975), unlike *C. nakatonbetsuensis*. *Cunninghamiostrobus goedertii* Miller & Crabtree (1989: 133) is a fossil-species based on ovulate cones with leafy shoots from the Oligocene of Washington State (Miller & Crabtree 1989, Miller 1990). The central resin canals in *Cs. goedertii* have a larger diameter than those in *C. nakatonbetsuensis*, accounting for more than one half of the scale thickness (Miller & Crabtree 1989). Additionally, the other resin canals in *Cs. goedertii* are larger and aligned in two rows (Miller & Crabtree 1989).

The fossil-genus *Elatides* (Heer 1876: 77) Harris (1953: 22) has laminar bract-scale complexes similar to *Cunninghamia*, although this genus usually has four or more seeds per complex (Harris 1943, 1953, Shi *et al.* 2014, Contreras *et al.* 2019). Similarly, the following *Cunninghamia*-like fossil-species are different from *C. nakatonbetsuensis*; *Pentakonos diminutus* Herrera, Shi, Knopf, Leslie, Ichinnorov, Takahashi, Crane & Herendeen (2017: 21) and *Stutzeliastrobus foliatus* Herrera, Shi, Knopf, Leslie, Ichinnorov, Takahashi, Crane & Herendeen (2017: 27). *Elatides bommeri* Harris (1953: 23) from the Lower Cretaceous of Belgium is an exceptional species of this genus because it has three seeds per complex as in *Cunninghamia* (Harris 1953). However, *E. bommeri* could be distinguished from *Cunninghamia* species including *C. nakatonbetsuensis* in having a single resin duct unbranched for a whole length of the bract-scale complex (Harris 1953).

Several monotypic genera comparable to *C. nakatonbetsuensis* were described from the Upper Cretaceous of Hokkaido, Japan based on permineralized seed cones with numerous helically arranged leafy bract-scale complexes (Nishida *et al.* 1992, Saiki & Kimura 1993, Stockey *et al.* 2020, Atkinson *et al.* 2021). *Mikasastrobus hokkaidoensis* Saiki & Kimura (1993: 83) and *Parataiwania nihongii* Nishida, Ohsawa & Hishida (1992: 2) are distinguished

from cunninghamioids by a ligulate ovuliferous scale and possessing 4–5 ovules per complex. Among them, three seeds per bract-scale complex are found in *Mukawastrobus satoi* Stockey, Nishida & Rothwell (2020: 684) from the Maastrichtian Hakobuchi Group in Mukawa Town, and *Nishidastrobus japonicum* Atkinson, Contreras, Stockey & Rothwell (2021: 464) and *Ohanastrobus hokkaidoensis* Atkinson, Contreras, Stockey and Rothwell (2021: 461) from the Coniacian–Santonian Kashima Formation of the Yezo Group in the Shuparo River area, Oyubari. *Mukawastrobus satoi* is distinguished from *C. nakatonbetsuensis* in numerous conspicuous resin canals in the bract-scale complexes and completely fused ovuliferous scale (Stockey *et al.* 2020). The other two species have an elongate conical cone unlike *C. nakatonbetsuensis* (Atkinson *et al.* 2021).

Hubbardiaastrobus Atkinson, Rothwell & Stockey (2014: 257) (Early Cretaceous: Atkinson *et al.* 2014a) and *Hughmillerites* Rothwell, Stockey, Mapes & Hilton (2011: 49) (Late Jurassic to Early Cretaceous: Rothwell *et al.* 2011, Atkinson *et al.* 2014b) are similar to *C. nakatonbetsuensis* in leafy bract-scale complexes with three seeds, but vascular strands are not divided vertically before horizontal divisions in these genera (Rothwell *et al.* 2011, Atkinson *et al.* 2014a, b).

Cunninghamia nakatonbetsuensis from the Maastrichtian, the last age of Mesozoic era, might provide an important case for understanding the evolution of cupressaceous seed cones, including those of cunninghamioid species. Cupressaceous conifers with foliate bract-scale complexes, including *Cunninghamia*, *Taiwania*, and their related fossil taxa, had greater diversity in the Cretaceous with numerous fossil-genera, although most of them disappeared before the Campanian (Atkinson *et al.* 2021). The number of *Cunninghamia* and *Taiwania* species had declined to two and one, respectively, in the present (Farjon 2005, Yang *et al.* 2012). On the other hand, the genera with peltate or cuneate bract-scale complexes are the most diversified group within the extant Cupressaceae, including over 150 species (Farjon 2005, Yang *et al.* 2012). These members are characterized by secondary growth of the adaxial region of the ovuliferous complex, which fill the spaces among different complexes, resulting in completely closed seed cones (Jagel & Dörken 2015). *Cunninghamia nakatonbetsuensis* from the Maastrichtian presents an adaxially swollen bract, leading to a nearly closed seed cone. If this feature confers some advantage, such as in seed survival or dispersal, its presence in *C. nakatonbetsuensis* might explain why the species survived the massive extinction of cunninghamioids after the Campanian.

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