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*Metasequoia* HU et CHENG (Cupressaceae) from the  
Eocene of Axel Heiberg Island, Canadian High Arctic

by

(CHRISTOPHER) YU-SHENG LIU, Johnson City and JAMES F. BASINGER,  
Saskatoon

With 4 plates, 1 text-figure and 8 tables



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## Abstract

A large number of fossilized remains, consisting of leafy branchlets, seed cones, pollen cones, and seeds, of *Metasequoia* (Cupressaceae) recovered from Middle Eocene sediments of the Buchanan Lake Formation, Axel Heiberg Island, Canadian Arctic Archipelago are studied morphologically and anatomically. They are assigned to *M. occidentalis* (NEWBERRY) CHANEY with an emendation, which is proposed to accommodate all the published *Metasequoia* fossils but *M. milleri* ROTHWELL et BASINGER. An emendation is made on the basis of detailed description of the associated leaf-bearing branchlets, leaves, pollen cones, pollen *in situ*, and seed cones, particularly the presence of helically arranged scales in some seed cones, which is a feature no longer represented in the extant *Metasequoia*. The most significant systematic emendation made is the morphology of pollen and arrangement pattern of seed cone scales. A comparison with extant and previously published fossil *Metasequoia* is made in detail and indicates a morphological stasis since Late Cretaceous/Paleocene.

Slight differences from the extant species, however, have been found, such as narrower stomatal bands, smaller stomata, higher stomatal density, presence of hypodermis (like that of *M. milleri*), smaller pollen grains, gemmate exine but with more or less smooth gemmae, and seed cones with, in part, helically arranged scales in the fossil *Metasequoia*. The foliar cuticles of the Arctic fossil were compared with those from the populations representing all the natural distribution areas of *Metasequoia* in central China and the result demonstrates that the fossil shares morphological resemblance most closely to those of the extant *Metasequoia* from an isolated population in central China's Hunan Province, about 100 km southeast of the type locality in Hubei Province, central China. The fossil pollen *in situ* were explained as relatively immature due to only being extracted from the smaller pollen cones and having distinct morphology and anatomy under scanning and transmission electron microscopy. The immature pollen grains have ontogenetic developmental significance, indicating that the spinulate processes of the mature *Metasequoia* pollen are probably developed from smooth gemmae. The helical arrangement of seed cone scales occurs among about 22% of the more than 3200 seed cones surveyed. The size range of seed cones is well correlated to three ecotypic variations in the extant *Metasequoia* and indicates that *M. occidentalis* of Axel Heiberg with larger seed cones (bigger than 2 cm, including large and medium cones) lived in a nearby upland in the Eocene, while those with smaller seed cones (smaller than 2 cm) were distributed in moist or inundated lowlands.

**Key words:** megafossils, pollen *in situ*, cuticle, Eocene, *Metasequoia*, Cupressaceae, Arctic, Axel Heiberg Island, Nunavut, Canada.

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### Authors' addresses:

(CHRISTOPHER) YU-SHENG LIU, Department of Biological Sciences, PO Box 70703, East Tennessee State University, Johnson City, Tennessee 37614-1710, U.S.A. e-mail: liuc@etsu.edu

JAMES F. BASINGER, Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2, Canada. e-mail: jim.basinger@usask.ca

## 1. Introduction

*Metasequoia*, one of the most eminent Chinese monotypic relict conifers, was first named from fossil twigs and cones from Japan (MIKI 1941). Seven years later, its living members were reported from central China (HU & CHENG 1948). The genus is now known to consist of about 5,000 native trees living under a warm temperate climate (YANG & JIN 2000). Nevertheless, *Metasequoia* once covered much of the Northern Hemisphere, from the Late Cretaceous to the Pliocene, and briefly extending into the edges of Europe (FERGUSON 1967, MAI 1994, LEPAGE et al. 2005). Both living and fossil *Metasequoia* have still been actively studied, as evidenced by two recent proceedings (LEPAGE et al. 2005, YANG & HICKEY 2007). Since the genus was established in 1941 (MIKI 1941), a total of 23 fossil species within the genus have been published (CHANEY 1951, LIU et al. 1999 and references cited therein, MASLOVA 2000, STOCKEY et al. 2001). Most species are based upon the external morphology of deciduous shoots, as anatomically preserved specimens are rather rare (MIKI 1941, SVESHNIKOVA 1963, 1975a, b, BASINGER 1981, HUGGINS 1985, LIU et al. 1999, MASLOVA 2000). A desire to decrease the number of fossil species of *Metasequoia*, to few or to even only a single species, has been proposed (CHANDRASEKHARAM 1974, CHRISTOPHEL 1976, LIU et al. 1999); however, others insist that species diversity within the genus may have existed from Late Cretaceous to Pleistocene (KOCH 1963, SERBET & STOCKEY 1991, MAI 1994, YU 1995, STOCKEY et al. 2001).

After careful comparisons of the external morphology between the fossils from the Paleogene of western Canada and extant *Metasequoia glyptostroboides* HU et CHENG (1948), both CHANDRASEKHARAM (1974) and CHRISTOPHEL (1976) concluded that two fossil species, *M. cuneata* (NEWBERRY) CHANEY (1951) and *M. occidentalis* (NEWBERRY) CHANEY (1951), as recognized in western North American strata by CHANEY (1951) and BELL (1957), are basically impossible to separate with certainty. Therefore, they proposed the latter species as a valid name for all fossil *Metasequoia* in North America. A recent thorough review on fossil *Metasequoia* from the Paleocene of northeast China, based on anatomical and morphological analyses of leafy shoots, seeds, and pollen cones, indicates that all previously published *Metasequoia* fossil species, except for *M. milleri* ROTHWELL

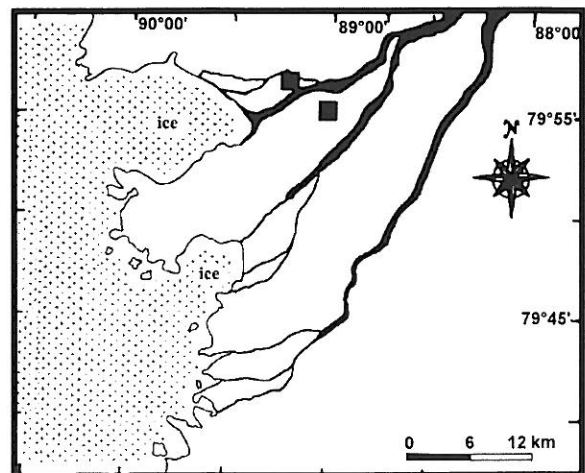
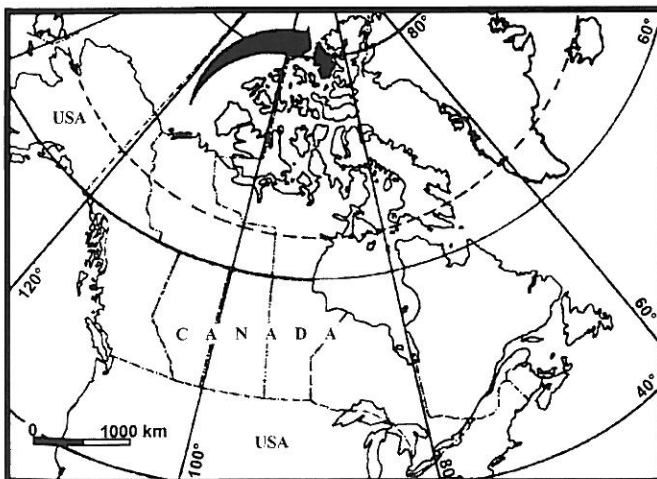
et BASINGER (1979, BASINGER 1981, 1984), which possesses unique anatomy and morphology of pollen cones and leaves, should be combined into one single species, viz. *M. occidentalis* (LIU et al. 1999). This work further supports a hypothesis proposed by BASINGER (1984) that *Metasequoia* has had a morphological stasis since Late Cretaceous/Paleocene, although some diversity among fossil species of the genus has later been documented (STOCKEY et al. 2001). However, LIU et al. (1999) seem not to provide sufficient evidence to support their consolidation; e.g. the pollen cones, from which *in situ* pollen were reported, were not illustrated. Some leaf cuticles are probably taxonomically incorrectly illustrated; i.e. cuticle in their fig. 63 is more similar to that of an angiosperm rather than that of a gymnosperm (Q. LENG, personal communication 2005). In addition, no detailed description on the micromorphology of *in situ* pollen, a rare character for fossil *Metasequoia*, was provided by Liu et al. (1999). Furthermore, their synonymy list is not complete, with some important reports missing, such as *M. occidentalis* from the Paleocene of Greenland (KOCH 1963) and the Miocene of Clarkia, Idaho (HUGGINS 1985). SCHLOEMER-JÄGER (1958) and SCHWEITZER (1974) provided an excellent description on almost every fossil organ of the genus from Spitzbergen, but no work on vegetative anatomy and pollen *in situ* was provided. The most recent new fossil species, *Metasequoia foxii* STOCKEY et al. (2001) from the Paleocene of central Alberta, Canada, was established on the basis of a combination of characters from several organs of more than 10,000 specimens. The significance of this work is that STOCKEY et al. (2001) clearly documented the presence of helical seed cone scales on some of their specimens, although KOCH (1963) made a comment on the occurrence of seed cones with helical scales in fossil *Metasequoia* from the Paleocene of Greenland (for detail, see below). Material from Alberta does not preserve leaf cuticles, one of the most reliable diagnostic characters for systematics of fossil conifers (FLORIN 1931), but their work has provided a solid base for understanding the morphological diversity of *Metasequoia* in the past. However, we have to emphasize the relatively common occurrence of seed cones with helically arranged scales in the fossil record of *Metasequoia*, which appears to indicate that the so-called distinct cone scale arrangement patterns may not be unique to *M. foxii* (for detail, see below; Table 7).

Fossil remains from the Eocene of Axel Heiberg Island, Canadian Arctic Archipelago, mostly preserved as mummified material, make possible an in-depth comparison with their living equivalents and published/figured fossil representatives. *Metasequoia*, one of the most abundant fossil elements of Axel Heiberg Island's Buchanan Lake Formation, has attracted much attention in stratigraphy and floristics (GREENWOOD & BASINGER 1993), forest ecology (WILLIAMS et al. 2003a, b), adaptive physiology (JAGELS & DAY 2004, JAGELS & EQUIZA 2004, VANN et al. 2004), biogeographical history (LEPAGE et al. 2005), cytological and ultrastructural study of leaf chloroplasts (SCHOENHUT et al. 2004), and biochemical analysis (YANG et al. 2005), but its taxonomic work remains to be done. In the present account, we describe the morphology of deciduous leafy shoots, leaves, foliar cuticles, leaf cross sections, seed and pollen cones, seeds, and micromorphology of the *in situ* pollen grains. Based on the new information, an evaluation of *M. occidentalis* is undertaken in order to determine if this is the appropriate name to accommodate all the characters shown by the fossils from Axel Heiberg Island. Finally, a detailed comparison among various fossil species and living *Metasequoia* is made with a view to provide an appropriate taxonomic framework for the genus.

## 2. Material and methods

*Metasequoia* remains occur at 47 sites among 52 catalogued localities of the Middle Eocene Buchanan Lake Formation, Eureka Sound Group, northeastern Axel Heiberg Island, Nunvaut, Arctic Canada (Text-fig. 1) (MCIVER & BASINGER 1999). Morphologically, *Metasequoia* fossils can be roughly separated into two groups on the basis of fossil assemblages in which *Metasequoia* fossils are recorded: one from the "stream sites" (79°57'N, 89°08'W), including flora assemblages recovered from fluvial and floodplain sands and siltstones, where *Metasequoia* remains are generally larger; and the second type from the leaf litters and peats representing the "swamp flora" (79°55'N, 88°58'W), where fossils of leaves and cones are mummified and typically relatively smaller (MCIVER & BASINGER 1999). These remains include deciduous shoots, seed cones, seeds, and pollen cones.

The fossil remains described in this paper are from the collections accumulated during almost twenty years' extensive field work on the Geodetic Hills fossil forests on Axel Heiberg Island. Details on the local lithology and geological background have been extensively discussed by BASINGER (1991) and RICKETTS (1991, 1994). The fossil forests of the Buchanan Lake Formation have been interpreted as Middle Eocene in age on the basis of regional structure and stratigraphy, palynology (MCINTYRE 1991, RICKETTS 1991, 1994), and more recently brontotherian vertebrates (EBERLE & STORER 1999).



Text-fig. 1. Maps showing location of Axel Heiberg Island, Canadian High Arctic (left); and northeastern Axel Heiberg Island (right) showing two fossil localities (squares) (modified after LIU & BASINGER 2000).

Carefully sorting of small subsamples of delicate leaf litter mats revealed 31 pollen cones, more than 100 dispersed seeds (many seeds are still enclosed in the cone), over 3200 seed cones, and countless deciduous foliage shoots. Leaf litter sites produce almost all of the mummified pollen cones, a majority of seed cones and foliage shoots, while river bank sites contain compressions of one male cone, some seed cones and many deciduous shoots. For comparison, extant materials of *Metasequoia glyptostroboides* from Matsuyama, Japan and *Sequoia sempervirens* from California, provided by the late Dr. E. E. McIVER, were used.

Fossil materials (leaf, pollen cone, seed cone, and seed) for anatomical studies were first treated with 20% HCl for 2 hours, followed by full strength hydrofluoric acid (48%) for 3 days, and cleaned by rinsing with distilled water.

Leaf cuticles of both fossil and extant *Metasequoia* are generally difficult to obtain, as the cuticles are rather thin and easily broken and shrunken in a reagent. An aqueous solution of hydrogen peroxide (15–20%) is found to yield ideal results for the fossils, while an aqueous bleach solution (~3%) works well for the living leaves. After acid treatment, fossil leaves were immersed in the hydrogen peroxide solution for 30 minutes and then rinsed in water. For extant leaves, material was treated by the aqueous bleach solution for at least 10 days at room temperature, and then rinsed in water. Scanning electron microscopy (SEM) stubs and glass slides were prepared for electron microscopic and light microscopic observations, respectively.

Transverse sections of fossil and living leaves of *Metasequoia* were prepared following the routine paraffin methodology (JOHANSEN 1940).

For fossil *in situ* pollen, small- to medium-sized pollen cones were chosen, as large pollen cones usually are mature and most pollen grains are gone. The material was first demineralized for 3 days in 48% hydrofluoric acid, oxidized in full-strength (~5%) commercial bleach for 5 hours, and then macerated to reveal pollen sacs with well-preserved pollen clumps. Maceration required a full day in concentrated nitric acid, followed by washing in distilled water and treatment in dilute ammonia (approximately 10%) for 10 minutes. After washing in distilled water, pollen clumps for SEM were mounted on stubs following the method of ZETTER (1989) and sputter-coated with approximately 200 Å of gold

on an Edwards Sputter Coater S150B for 5 minutes and examined with a JEOL JSM-840A scanning electron microscope.

Pollen clumps for transmission electron microscopy (TEM) were prepared after the method described by RUZIN (1999). Sections were examined with a Philips 410LS transmission electron microscope at 60 KV.

Figured specimens are housed in the Paleobotanical Collection of the Department of Geological Sciences, University of Saskatchewan (USPC).

### 3. Systematics

Thousands of fossil remains, including leaves, shoots, seed cones, and seeds, attributed to *Metasequoia* have been recovered from the Buchanan Lake Formation on Axel Heiberg Island, although no specimens showing organic connection among all organs have been found. This is simply because the mummified fossils are so delicate that large specimens are not likely obtained, especially after drying. They could be related, however, on the basis of consistent association of vast numbers of specimens in different localities on Axel Heiberg Island and presence of decussate leaves on all the branches and shoots (Pl. 1, Figs 1–6). Interestingly, one shoot bearing helically arranged leaves on the upper part has been found (Pl. 1, Fig. 3). This shoot is considered to be *Metasequoia* too, as these helically arranged leaves appear to have been caused by insect galls. Moreover, leaves at the lower part of the shoot are still decussate, characteristic of *Metasequoia*. For the fossil seed cones with no leaves on the peduncle but with fascicled scale leaves at the base or the cones even without peduncle, they are also attributed to *Metasequoia* mainly due to the similarity of cone morphology and shield-like scales. Therefore, it is reasonable to consider these separate fossil organs as remnants of the same species, and in some cases from the same tree.

Taxodioid conifers, which include the genus *Metasequoia*, have been traditionally classified within the Taxodiaceae (CHANEY 1951), but are now included within the Cupressaceae (ECKENWALDER 1976, GADEK et al. 2000, FARJON 2005).

Family: Cupressaceae RICH. ex BARTLING sensu  
ECKENWALDER

Genus: *Metasequoia* HU et CHENG

Species: *Metasequoia occidentalis* (NEWBERRY 1863)  
CHANEY 1951, emend.

- 1863 *Taxodium occidentale* NEWBERRY, Boston Soc. Nat. Hist. 7, p. 516.
- 1951 *Metasequoia occidentalis* (NEWBERRY) CHANEY, Amer. Phil. Soc. Trans. 40, pt. 3, p. 225, pl. 1, fig. 3; pl. 2, fig. 1–3; pl. 4, fig. 1, 2, 9; pl. 5, fig. 1–3; pl. 6, fig. 2; pl. 7, fig. 1–6; pl. 8, fig. 1–3; pl. 9, figs 3, 5–7; pl. 10, fig. 1a, 2a, 3–6; pl. 11, fig. 7–8; pl. 12, figs 1, 2, 5–8.
- 1951 *Metasequoia cuneata* (NEWBERRY) CHANEY, Amer. Phil. Soc. Trans. 40, pt. 3, p. 229, pl. 11, fig. 1–6.
- 1957 *Metasequoia cuneata* – BELL, Geol. Surv. Can. Mem. 293, p. 31, pl. XI, fig. 3, 5, 6; pl. XII, fig. 1–3; pl. XIII, fig. 2; pl. XVII, fig. 1, 7.
- 1958 *Metasequoia occidentalis* – SCHLOEMER-JÄGER, Palaeontographica Abt. B 104, p. 54–61, text-figs 10, 11; pl. 8, fig. 5, 6; pl. 9, fig. 1, 2.
- 1962 *Metasequoia cuneata* – BROWN, U.S. Geol. Surv. Prof. Pap., 375, p. 49–50, pl. 12, fig. 1–14.
- 1963 *Metasequoia occidentalis* – KOCH, Medd. om Grønl., 172, p. 23–32, pl. 2–4; text-figs 7–12.
- 1974 *Metasequoia occidentalis* – CHANDRASEKHARAM, Palaeontographica Abt. B 147, p. 7–8, pl. 2, fig. 15; pl. 3, fig. 17–20; pl. 4, fig. 21–24; pl. 11, fig. 78, 79.
- 1974 *Metasequoia occidentalis* – SCHWEITZER, Palaeontographica Abt. B 149, p. 27, pl. 4, fig. 5, 6; pl. 5, fig. 1, 3–7; pl. 7, fig. 1–7; text-figs 9, 10, 13, 14.
- 1976 *Metasequoia occidentalis* – CHRISTOPHEL, Palaeontographica Abt. B 157, p. 12–17, pl. 4, fig. 23–25; pl. 5, fig. 27–30, 33a, 34.
- 1985 *Metasequoia occidentalis* – HUGGINS, Late Cenozoic history of the Pacific Northwest, p. 125, pl. 6, fig. 3, 4; pl., fig. 3, 4.
- 1999 *Metasequoia occidentalis* – LIU, LI, & WANG, Bot. J. Linn. Soc. 130, p. 275–279, fig. 2–45, 47–53, 55–59, 63, 65, 67, 68, 71, 74.
- 2001 *Metasequoia foxii* STOCKEY, ROTHWELL et FALDER, Int. J. Plant Sci. 162, p. 223, fig. 1–3, fig. 4.3–4.8, 5, 6; fig. 7.1–7.5, 7.7–7.14.

The species was first fully revised by CHANEY in 1951 and subsequently reported in excellent detail by BELL (1957), SCHLOEMER-JÄGER (1958), BROWN (1962), KOCH (1963), CHANDRASEKHARAM (1974), SCHWEITZER (1974), CHRISTOPHEL (1976), and LIU et al. (1999), although anatomical details have been described only by LIU et al. (1999). SCHWEITZER (1974) described well-preserved pollen cones, but failed to recover *in situ* pollen.

Readers can refer to LIU et al. (1999) and LEPAGE et al. (2005) for expanded synonymy lists for *M.*

*occidentalis*. It should be noted that LIU et al. (1999) incorrectly include *Metasequoia europaea* ZALEWSKA (1959), which DOROFEEV & SVESHNIKOVA (1963) excluded from the genus (FERGUSON 1967, MAI 1994), and have overlooked some important works, such as BROWN (1962) and KOCH (1963).

Diagnostic features of vegetative and reproductive organs of *Metasequoia occidentalis* have been provided in great detail by LIU et al. (1999) and STOCKEY et al. (2001); therefore, emendation below includes solely that information added on the basis of the features revealed from the Canadian Arctic specimens.

### 3.1. Diagnosis

Leaves sessile or nearly sessile, with two marginal resin canals in cross section (Pl. 1, Fig. 9); outer surface of periclinal wall of epidermal cells dome-shaped (Pl. 1, Fig. 9). Pollen cones axillary and terminal, opposite racemosely or paniculately arranged, globose to ovate (Pl. 2, Figs 11, 12; Pl. 3, Figs 1–4). Pollen subspheroidal and small (Pl. 3, Figs 6, 7), exine fine granules and coarse tuberculae, with Ubisch bodies (Pl. 3, Figs 7, 9, 10). Section of exine lamellate, with about 8 lamellae (Pl. 3, Figs 11, 12). Seed cones pedunculate. Peduncles several centimeters long with little or no trace of foliage or foliage scars (Pl. 4, Figs 7–10, 14, 16).

## 4. Anatomy and morphology

### 4.1. Leaf-bearing shoots and leaves

Two types of shoots occur in *Metasequoia*, i.e. persistent (leading or long) and deciduous (short) (CHRISTOPHEL 1976). As expected, most shoots from the Axel Heiberg localities are deciduous, as persistent shoots are far less likely to be dropped intact from the tree. Deciduous shoots vary from 1 cm to 10 cm in length, bearing 15–35 pairs of generally decussately leaves departing at angles of about 45°, 60° or 90° (Pl. 1, Figs 2–6). The shoots from the stream site bear fewer (about 4) leaf pairs per centimeter of shoot (Pl. 1, Figs 5, 6), whereas those from the leaf litter sites possess ca. 8–12 pairs per centimeter of shoot (Pl. 1, Figs 1, 2, 4). Clusters of scale-like leaves occur at the base of shoot (Pl. 1, Figs 2–4).

Based on the terms used in literature for the description of *Metasequoia* foliage, three categories of leaf form, linear, ovate, and obovate, were identified by CHRISTOPHEL (1976), and all are present in the

Axel Heiberg Island collections. Leaves are more or less sessile, with twisted bases (Pl. 1, Figs 1–6). Leaf apex is round or mucronate (Pl. 1, Figs 2–6). Leaf size varies greatly (Pl. 1, Fig. 1), although specimens from the stream site are typically larger, to a maximum of ca. 3.3 cm long and 0.3 cm wide (Pl. 1, Figs 5, 6) than those from the leaf litter site, which are as small as ca. 0.6 cm long and 0.1 cm wide (Pl. 1, Figs 1–4).

Leaves are hypostomatic. Adaxial epidermal cells are elongate, about 25 to 75  $\mu\text{m}$  long and 10 to 25  $\mu\text{m}$  wide, with straight or slightly undulate anticlinal walls (Pl. 1, Fig. 10; Pl. 2, Fig. 1) and a smooth outer surface (Pl. 2, Fig. 7). The long axis of the epidermal cells is parallel to the leaf midvein. On the abaxial surface, pits occur on the outer surface of non-stomatal epidermal cells (Pl. 2, Figs 8, 9). Stomata are superficially distributed in two narrow bands, one on each side of the midrib (Pl. 1, Fig. 7; Pl. 2, Fig. 9), which occupy about 50% of the leaf width (Pl. 1, Fig. 7). Stomata are orientated more or less parallel to the leaf axis (Pl. 2, Figs 8, 9). The stomatal apparatus are 26 to 34  $\mu\text{m}$  long and 15 to 25  $\mu\text{m}$  wide in size, and monocyclic, with usually four subsidiary cells (Pl. 2, Fig. 10). Abaxial epidermal cells are similar in size to those of the adaxial surface, but may have wavy, undulate to somewhat straight anticlinal walls (Pl. 1, Fig. 11; Pl. 2, Fig. 10).

Leaves are dorsiventral, and in cross-section show two marginal resin canals (Pl. 1, Fig. 9). It is unknown if an abaxially median canal is present, because of inadequate preservation. The periclinal wall of epidermal cells bulges outward to become dome-shaped (Pl. 1, Fig. 9). Conspicuous hypodermis is also present, especially under the adaxial epidermis (Pl. 1, Fig. 9). As the fossil leaves have been compressed during fossilization, it is unclear whether mesophyll was differentiated into palisade and spongy tissues (Pl. 1, Fig. 9).

#### 4.2. Pollen cones and pollen *in situ*

Pollen cones are axillary, opposite, and terminal, arranged in racemes or panicles (Pl. 2, Figs 11, 12; Pl. 3, Figs 1–4). They are globose to ovate, and variable in size (2.0–5.5 mm long and 1.1–3.5 mm wide). Each pollen cone possesses about 10 decussate bracts (Pl. 3, Fig. 3). Number of cones per deciduous shoot and details of cone structure, including the number of pollen sacs per microsporophyll, are not known.

Pollen *in situ* is subspheroidal and 13–20  $\mu\text{m}$  long and 13–20  $\mu\text{m}$  wide (Pl. 3, Figs 5–8), which is generally smaller than grains of living and other fossil species (see Table 1). Papillae are generally present. The exine is covered with two types of elements: fine granules; and rather coarse tuberculae (Pl. 3, Figs 7, 9, 10).

Under TEM, the exine includes both sexine and nexine, which are irregular in thickness (Pl. 3, Figs 11, 12). The sexine is about 0.5  $\mu\text{m}$  thick, while the nexine ranges from 0.7 to 1.2  $\mu\text{m}$ . The nexine is rather thick and distinctly lamellate.

Ubisch bodies are sparse and unevenly distributed on the pollen surface, with diameter ca. 0.38–0.46  $\mu\text{m}$  (Pl. 3, Figs 7, 9, 10). Due to the limitation of preservation, it is unknown if all the Ubisch bodies are hollow (Pl. 3, Figs 11, 12).

#### 4.3. Seed cones and seeds

Seed cones of *Metasequoia occidentalis* are ovoid, occasionally elongate (Pl. 4, Fig. 16) and highly variable in size (Pl. 4, Figs 5–12, 14–16). The smallest cones in our collections are ovoid in shape, and only 1 cm in length and 1 cm in width (Pl. 4, Fig. 14), while the largest approach 3.5 cm long and 3.0 cm wide. Stalks are generally not well preserved, and most cones possess short broken stalks. Intact stalks reach 2 to 5.4 cm in length (Pl. 4, Fig. 7). A distinctive feature of the *Metasequoia occidentalis* cones from Axel Heiberg is that many seed cones bear 10–25 woody and peltate cone scales in a helical arrangement (Pl. 4, Figs 5–11, 16), a trait never documented in any living *Metasequoia* (FU et al. 1999), although not rare in fossil cones (for detail, see below). Significantly, seed cones (Pl. 4, Figs 12, 14, 15) having typical decussate scales are found to be associated with helical seed cones, identical in all other respects, in almost every site on Axel Heiberg Island.

Seeds, lying inverted on the adaxial surface of the cone scale, are 3.5–5.5 mm long to 3 to 5 mm wide, with two narrow lateral wings (Pl. 4, Fig. 13), and vary in shape from round to ovate or flat, with the apex of the wing emarginate (Pl. 4, Fig. 13). Each cone scale normally bears about six seeds.

### 5. Discussion

The fossil remains discussed in the present paper are all assigned to the genus *Metasequoia* on the basis

of external morphology, anatomy, and a consistent and close association of leafy shoots, leaves, and pollen and seed cones. Only one other taxon occurs in the deposits with which leaf remains may on occasion be confused, the taxodiaceous genus *Glyptostrobus*, which occurs abundantly with *Metasequoia* in the same deposits (BASINGER 1991). *Glyptostrobus* leaves are highly polymorphic, with five morphological variants recognized by CHRISTOPHEL (1976), among which crypto-taxodioid and taxodioid types are superficially similar to leaves of *Metasequoia*. *Glyptostrobus* leaves, however, are always helically arranged, while in *Metasequoia* leaves are regularly decussate in arrangement. In addition, leaf cuticles of the two genera are basically similar, especially in the structure of the stomatal apparatus, but the stomata of *Glyptostrobus* are randomly oriented, whereas those of *Metasequoia* are generally parallel to the leaf axis (VICKULIN et al. 2003, MA et al. 2004). Furthermore, seed and pollen cones of *Glyptostrobus* are quite different from those of *Metasequoia*.

About 22% of over 3200 fossil seed cones of *Metasequoia occidentalis* from Axel Heiberg have helically arranged cone scales (for detail, see below), which seems at odds with the definition of the genus (see MIKI 1941, HU & CHENG 1948); however, other characters, such as morphology of seed-cone scale and peduncles, are indistinguishable from those of extant *Metasequoia* (see also STOCKEY et al. 2001). After delving into the literature, we realize that the presence of helically arranged seed cone scales in other fossil *Metasequoia* from Greenland, East Asia and western North America is in fact not rare (for detail, see Table 7). By considering the overlapping morphology and anatomy of leaves, pollen *in situ*, pollen cones and seed cones among *Metasequoia* fossils from different localities in the world, it is concluded that the fossil remains of *Metasequoia* from Axel Heiberg represent a single biological species. It is apparent that this species is consistent with remains found elsewhere in Greenland, East Asia and North America and referred to as *Metasequoia occidentalis*.

*Metasequoia foxii*, a new species from the Paleocene of central Alberta, Canada, was recently reported by STOCKEY et al. (2001), with emphasis on the presence of helical scales in seed cones. Other characteristics considered by STOCKEY et al. (2001) to distinguish *M. foxii* from *M. occidentalis* include higher wood rays ( $\leq 113$ ), wider leaves (up to 4.5 mm),

fewer sporophylls in pollen cones (18–24), longer seeds (up to 9 mm) and shorter length of seedling branches and stem leaves. Seedling fossils of *Metasequoia* are not known from Axel Heiberg; however, the wood fossils of *Metasequoia*, though very common, have not been studied taxonomically. Other than characters of seedlings and woods, the characters of *M. foxii* overlap with those known for *Metasequoia occidentalis* (see Table 1).

There has been much debate about the taxonomic diversity of living *Metasequoia* since 1948, when the living *M. glyptostrobooides* was first established. So far, one new variety, *M. glyptostrobooides* var. *caespitosa* Y. H. LONG et Y. WU (LONG & WU 1984) and one new species, *M. honshuenensis* J. SILBA et F. T. CALLAHAN, II (SILBA 2000) have been reported. The new variety, reported from Guanghwashe, Qianjiang County, Hubei Province, central China, may be diagnosed by characters such as a shrubby habit without a prominent main stem, male cones usually terminating determinate branchlets (rarely axillary to leaves), and more microsporophylls per pollen cone (ca. 30–50) (LONG & WU 1984). However, it has been synonymized under the original species in the most recent review (FU et al. 1999), because these characters fall within the wide range of morphology of the species. On the other hand, the new species, *M. honshuenensis*, is documented from a cultivated tree in Riverside Municipal Park, near Grants Pass, Oregon, U.S.A. (SILBA 2000). It is characterized by having gigantic seed cones (up to 35 mm in diameter) and very long peduncles (up to 85 mm in length). According to the measurements of FU et al. (1999) on Chinese *M. glyptostrobooides*, seed cones vary greatly, from 9 × 5.5 mm at pollination, expanding to 14–25 × 16–23 mm when mature, revealing that the size of seed cone may not taxonomically reliable. The validity of *M. honshuenensis* is doubtful. As relevance of morphological variability in evaluation of modern species concepts is still debated, it is not surprising that arguments continue concerning diversity vs. morphological stasis in fossil *Metasequoia*. In light of the recent review on the species of fossil *Metasequoia* by LIU et al. (1999), we conclude that the fossils from Axel Heiberg are appropriately identified by the name of *M. occidentalis*. It follows that *M. foxii* from central Canada must be treated as a synonym of *M. occidentalis*. Detailed comparisons between the fossils and extant *Metasequoia* are given below (see also Table 1).



Table 1. Comparison of *Metasequoia*: fossil and extant species.

Features	<i>Metasequoia occidentalis</i>		<i>Metasequoia milleri</i> <sup>2</sup>	<i>Metasequoia glyptostroboides</i> <sup>3</sup>	<i>Metasequoia foxii</i> <sup>3</sup>
	Material from Axel Heiberg	Material from China <sup>1</sup>			
<b>Leaf</b>					
Size (mm)	6–33 × 1–3	2–16 × 0.2–2.5	–	8–35 × 1–2.5	2–43 × 0.5–4.5
Phyllotaxy	Decussate	Decussate	Decussate	Decussate	Opposite/Decussate
Shape of pinna	Linear, ovate, and obovate	Linear, ovate, and obovate	Linear	Linear, ovate, and obovate	Ovate to linear
Number of resin ducts	3	–	1 or 3	3	–
Palisade mesophyll	Poorly developed	–	Absent	Well developed	–
Hypodermis	Present	–	Present	Absent	–
Upper epidermal cell walls	Straight to slightly wavy	Wavy	Slightly wavy	Straight to wavy	–
Size of upper epidermal cells (µm)	25–75 × 10–25	20–67 × 8–22	100 × 20	50–110 × 20–25	–
Lower epidermal cell walls	Straight to deeply wavy	Wavy	Slightly wavy	Wavy	–
Size of lower epidermal cells (µm)	50–75 × 10–15	20–67 × 8–22	100 × 20	50–75 × 10–25	–
Size of stomata (µm)	26–34 × 15–24	18–27 × 15–18	40 × 15	45–50 × 30–35	–
Stomatal band	narrow	–	broad	broad	–
Stomatal density on band (no. stomata/0.001 mm <sup>2</sup> )	15	–	–	8–10	–
Percentage of stomatal band per ½ leaf width	25%	–	–	50%	–
Stomatal orientation to leaf axis	Parallel	Random	Parallel	Parallel	–
Position of stomata	Superficial	–	Slightly sunken	Superficial	–
<b>Pollen cone</b>					
Attachment	Laterally and terminally	Laterally and terminally	Laterally and terminally	Laterally and terminally	Laterally and terminally
Size of cone (mm)	2–5.5 × 1.1–3.5	2.2–4.5 × 1.8–3.2	1–3 × 1.2–2.9	4.3 × 1.9–3.5	3–8 × 2–5
<b>Pollen</b>					
Papilla	Not obvious	Moderate length, erect	Moderate length, erect	Moderate length, bent	Papillate
Size of pollen (µm)	12.6–20 × 12.6–20	19.2–24	19–27	27.8–33.1	17.5–24
<b>Seed cone</b>					
Size of seed cone (mm)	10–35 × 10–30	8–40 × 6–34	25 × 17	6–25 × 6–25	10–35 × 11–22
Shape of seed	Round ovate, cordate	Cordate or skull-like	Broadly ovate	compressed-obovoid	Elliptical to cordate
Size of seed (mm)	3.5–6 × 3–7	3–6 × 2.3–4	5 × 4	5 × 4	3.5–9 × 2.75–7
Orientation of seeds	Inverted	–	Inverted	Inverted	–
No. seeds per scale	~ 6	–	4	5–9	–

<sup>1</sup> Most based on LIU, LI & WANG (1999)<sup>2</sup> from ROTHWELL & BASINGER (1979) and BASINGER (1981, 1984)<sup>3</sup> from STERLING (1949), FLORIN (1952), HIDA (1962), SRINIVASAN & FRIIS (1989), YING et al. (1993), FU et al. (1999), LIU et al. (1999), LENG et al. (2001), and our measurements<sup>4</sup> from STOCKEY et al. (2001).

### 5.1. Leaf-bearing shoots and leaves

Leaves and leafy deciduous branchlets are the most commonly preserved organs of *Metasequoia* on Axel Heiberg Island, and most allow for cuticular study.

The sterile shoots are morphologically identical in all aspects to those of the extant *Metasequoia*. SCHWEITZER (1974) reported that the average internodal distance between sequential needles in *M. occidentalis* is a little greater than in *M. glyptostroboides*,

which was considered by him to be the only relevant difference between foliage of *M. occidentalis* and the extant species. This difference, however, seems not to really exist, and some shoots from our collections are identical to those of the extant *Metasequoia*. Generally, shoots with smaller cones have more space between adjacent leaves (Pl. 3, Figs 1, 4), while those with bigger cones are correlated with more closed spaced leaves (Pl. 2, Figs 11, 12; Pl. 3, Figs 2, 3).

Morphologically, the leaves show no significant difference from those of the living *Metasequoia* and other fossil taxa such as *M. foxii* (Table 1). Although *M. foxii* was reported to have wider leaves, the values overlap with those of *M. occidentalis*.

The phyllotaxis of the fossil is clearly decussate (Pl. 1, Figs 2–6). Although several authors doubted the reality of decussate phyllotaxis in *Metasequoia* (MAEKAWA 1948, GREGUSS 1956, SCHWARZ & WEIDE 1962), later work has proven unambiguously decussate phyllotaxis in *Metasequoia* (FU et al. 1999, FARJON 2005).

Foliar cuticular features are generally important taxonomic characters in the taxodiaceous genera (SVESHNIKOVA 1963). Several fossil species of *Metasequoia* have been established mainly based on cuticle characters (e.g. SVESHNIKOVA 1963, 1967, 1975a, b, MASLOVA 2000). However, the validity of these “species” seems to lack strong supporting evidence. Significantly, recent work on cuticle micromorphology of extant *Metasequoia* reveals that infraspecific variation occurs among the natural populations in central China, including that of the type locality of *M. glyptostrobooides* (LENG et al. 2001, LENG 2005; Table 2).

LENG et al. (2001) and LENG (2005) recognized two different types of lower cuticle in extant *Metasequoia* – Uneven and Even types – based on the nature of the periclinal wall. Leaves of *Metasequoia* from Hubei (including the type locality), Sichuan, and part of Hunan provinces in central China display the Uneven Type of lower cuticle, while those from a remote village in Luota town of Hunan province, about 100 km southeast of the type locality, possess the Even Type of lower cuticle. It is necessary to note that the first cultivated *Metasequoia* trees were grown from the seeds collected at the type locality in Hubei province (see ANDREWS 1948, MERRILL 1948). *Metasequoia* trees have since been cultivated globally (SATO 1998/1999). As most international comparative work is based on these cultivated trees, there is a good reason to assume that paleobotanists use living material that does not represent the full range of cuticle morphology present in the extant species (see SVESHNIKOVA 1963, 1975a, b). These living comparative samples are known to possess only the Uneven lower cuticle morphotype.

Most interesting is that the lower cuticle from published fossil *Metasequoia* appears to be of the

Table 2. Differences of lower cuticle in the living populations of *Metasequoia* under SEM observation (after LENG et al. 2001, LENG 2005).

Character	Uneven Type	Even Type
Internal Surface:		
Non-stomatal zone		
Epidermal cells	elliptic	rectangular
Anticlinal walls	variable in thickness*	distinct
Periclinal walls	uneven	even
Stomatal zone		
Anticlinal walls	variable in thickness*	distinct
Periclinal walls	uneven	even
Subsidiary cells	undistinguishable from epidermal cells	distinct
Stomata	rectangular	elliptical
External Surface:		
Non-stomatal zone	outline indistinct	outline recognizable
Epidermal cells	uneven	even
Periclinal walls	outline indistinct	outline recognizable
Stomatal zone	shaped like two parallel flanges	shaped elliptically
Epidermal cells		
Florin rings		
Natural distribution	widely in the 3 provinces of central China: Hubei (incl. type locality), Hunan, and Sichuan	only in one site at Paomu village, Luota town, Hunan Province

\* Anticlinal wall variable in thickness, making the boundary of cells indistinct, rarely distinct.

Table 3. Summary of fossil *Metasequoia* lower cuticle types in published literature, including only those with lower cuticle illustrated. The type of lower cuticle is recognized based on LENG et al. (2001).

Taxon	Lower cuticle type	Age	Literature
<i>Metasequoia cuneata</i>	Even type	Late Cretaceous	SVESHNIKOVA 1967
<i>M. paradoxa</i>	Even type	Late Cretaceous	SVESHNIKOVA 1967
<i>M. asiatica</i>	Even type	Late Cretaceous	SAMYLINA 1988
<i>M. disticha</i>	Even type	Late Cretaceous	ABLAEV 1974
<i>M. disticha</i>	Even type	Tertiary	SVESHNIKOVA 1963
<i>M. nathorstii</i>	Even type	Paleogene	SVESHNIKOVA 1975a, b
<i>M. sp.1</i>	Even type	Paleogene	SVESHNIKOVA 1975a
<i>M. kryshstofovichii</i>	Even type	Paleogene	SVESHNIKOVA 1975b
<i>M. snatolana</i>	Even type	Late Paleocene	MASLOVA 2000
<i>M. occidentalis</i>	Even type	Eocene	LIU & LI 2000
<i>M. milleri</i>	Even type	Middle Eocene	BASINGER 1981
<i>M. disticha</i>	Even type	Miocene	KLIMOVA 1975
<i>M. occidentalis</i>	Even type	Miocene	HUGGINS 1985
<i>M. occidentalis</i>	Even type	Late Miocene	HORIUCHI 1996
<i>M. disticha</i>	Even type	Pliocene	MIKI 1941

Even Type (LENG 2005, also see Table 3), although this observation must be considered tentative, as our judgment is solely based on checking illustrations in publications. Most illustrations do not allow precise estimation due to lack of high quality SEM micrographs. It is possible, however, that Even Type cuticle might represent an ancestral character, and perhaps that most living populations of *Metasequoia*, including the type locality population, are a later derivation from that of a more ancient morphotype represented by the isolated population in Luota town of Hunan Province.

Overall, the leaves of *M. occidentalis* from Axel Heiberg are morphologically and anatomically similar to fossils documented by LIU et al. (1999) and LIU & LI (2000) from China. A minor difference requires consideration. LIU et al. (1999) claimed that the Chinese fossils from the Paleocene Wuyun Formation of Jiayin County in northeast China include leaves with randomly distributed stomata on the abaxial surface of leaves, which is different from *M. glyptostrobooides* (Table 1) and our fossils. This character, however, could be a misinterpreted based on contamination of their samples with dicotyledonous leaves (Q. LENG, personal communication 2005). Unfortunately, illustrations provided by LIU et al. (1999) are not clear enough to resolve this issue. In addition, SVESHNIKOVA (1975b) proposed an evolutionary trend of epidermis morphology in fossil *Metasequoia*. She suggested that, over time, the orientation of stomata evolved from a random arrangement to regular and parallel to the vein, and anticli-

nal walls of epidermal cells change from straight to wavy. Our collections do not support her latter hypothesis, as anticlinal walls of epidermal cells are highly variable, and both of the forms recognized by SVESHNIKOVA are seen in our collections (Pl. 1, Fig. 10, 11). Thus, the feature of anticlinal walls appears not to be of taxonomic significance in the classification of fossil *Metasequoia*.

Leaf cuticles of *Metasequoia* from Axel Heiberg closely resemble those of extant *M. glyptostrobooides*, with the exception of some differences in the size of stomata, width of stomatal band, and stomatal density (Table 1; Pl. 1, Fig. 7, 8). The Arctic fossils have smaller stomata, narrower stomatal bands, and higher stomatal density than *M. glyptostrobooides* (Table 1). Among these differences, smaller stomata are also shown in Chinese fossil material (LIU et al. 1999), but *M. milleri*, another well recognized fossil species due to its unique preservation, has stomata of similar size to *M. glyptostrobooides* (BASINGER 1981). Cell size is believed to correlate with DNA content and thus with chromosome number, so that the study of fossil stomata permits the estimation of ploidy levels (MASTERSON 1994). BASINGER (1981) therefore suggested that *M. milleri* had ploidy similar to that of extant *Metasequoia*. Smaller stomata in the Arctic and Chinese fossil *Metasequoia* may suggest that *Metasequoia* of the Late Cretaceous and Paleogene included members with ploidy levels lower than those of any extant members. Furthermore, *Metasequoia* from Axel Heiberg has higher stomatal density than *M. glyptostrobooides* (Table 1). This reduction in

density from fossil to extant species may be a response to higher paleo-CO<sub>2</sub> levels, a trend well documented among seed plants by ROYER (2001).

There are only two reports dealing with cross sections of fossil *Metasequoia* leaves (HARR & TING 1976, BASINGER 1981). As BASINGER (1981) reviewed, silicified leaves and shoots of *Metasequoia* from the Paleocene Fort Union Group in North Dakota (HARR & TING 1976) are not clearly illustrated, and are therefore difficult to compare with the Arctic fossil and the extant *M. glyptostrobooides*. *Metasequoia milleri* from the Eocene of British Columbia preserves the best and most complete anatomical record (BASINGER 1981). There are typically three, rarely just one, resin ducts in the leaves of *M. milleri*, while the Axel Heiberg leaves appear somewhat different in revealing only two resin ducts (Table 1), although preservational limitations preclude identification of an expected central abaxial resin duct in cross sections of the Arctic *Metasequoia* leaves. Nevertheless, these two fossils also share a number of characters, such as the presence of hypodermis, which is not found in the extant *Metasequoia* (YAO & HU 1982). However, cross sections of the fossil leaves from Axel Heiberg show that the periclinal wall of epidermal cells bulge outward to become dome-shaped (Pl. 1, Fig. 9), a feature typical of living *Metasequoia* within taxodiaceous conifers (YAO & HU 1982).

The present study does not support the hypothesis of SVESHNIKOVA (1963, 1975a, b), who suggested that the differences between the fossil and the modern species are most evident in leaf cuticle; in fact, the differences between leaves of fossil and living *Metasequoia* are apparent only in cross section.

## 5.2. Pollen cones

While dealing with well reserved permineralized pollen cones of *Metasequoia milleri* from the Middle Eocene of British Columbia, ROTHWELL & BASINGER (1979) noted that sporangia of relatively mature cones contain a large number of subspheroidal, papillate pollen grains, while some cones have small, nearly spherical grains with little or no exine ornamentation. Only one pollen cone in the Axel Heiberg collection has been found to yield *in situ* pollen (Pl. 2, Fig. 11), and this cone is smaller (2.5 × 2 mm) than most others (typically 3.5–5.5 × 2.1–3.5 mm), and is considered somewhat immature. Mature cones contain no pollen, probably because they were ma-

ture and grains were already shed, while the smallest cones (ca. 2 × 1.1 mm, Pl. 3, Fig. 1) were likely too immature to have produced pollen. Such size differences in fossil pollen cones of *Metasequoia* were also documented by CHANEY (1948), who noticed that the staminate cones from the Oligocene Bridge Creek flora of Oregon are much smaller than those from Elko, and appear to represent a less-mature stage; in the living species there is a similar range in size. A specimen from Elko shows six spikes in close association, as in the living species. CHANEY did not report any *in situ* pollen. Morphologically, the pollen cones show no differences from those of either living (*M. glyptostrobooides*) or other fossils (including *M. foxii*) (Table 1). The pollen cones of *M. milleri* are described as having helically arranged sporophylls, which differentiates this taxon from other known members of the genus.

## 5.3 Pollen *in situ*

The study of pollen *in situ* is considered critical to classification of fossil *Metasequoia* (BOULTER & KVAČEK 1989). LIU et al. (1999) reported pollen grains that they considered to be *in situ* and were slightly larger than those from Axel Heiberg Island. These Chinese pollen cones were not illustrated, however, and the so called *in situ* pollen grains, which are not clearly illustrated, appear to form a pollen clump, and they are difficult to compare with the *in situ* pollen from Axel Heiberg.

The relatively immature pollen from Axel Heiberg has exine characters that differ from those of the extant and other (apparently more mature) fossil *Metasequoia* (cf. ROTHWELL & BASINGER 1979, YING et al. 1993). Like the fossil and extant mature pollen of *Metasequoia*, the exine from Axel Heiberg is gemmate, but the gemmae are more or less smooth, and most like those of *M. foxii* (see STOCKEY et al. 2001), while exine of the extant *Metasequoia* typically has spinulate processes (YING et al. 1993). A comparison of exine morphology of extant taxodiaceous genera and the Arctic fossil is presented in Table 4, and indicates that the Arctic fossil pollen is distinct from all other taxodiaceous grains in external morphology, but our interpretation of immaturity of these *in situ* pollen grains explains this distinctiveness (cf. ROTHWELL & BASINGER 1979). This suggests that the spinulate processes on the surface of gemmae, as shown on the exine of mature pollen grains in *Metase-*

Table 4. Comparison of exine surface under SEM between extant taxodiaceous genera and *Metasequoia occidentalis* of Axel Heiberg (compiled from XI 1986, 1988, XI & WANG 1989, YING et al. 1993, STOCKEY et al. 2001).

Genus	Coarse ornamentation	Fine ornamentation
<i>Cryptomeria</i>	verrucate, surface of verrucae smooth	same as those of coarse ornamentation
<i>Cunninghamia</i>	tuberculate	tuberculate with spinules unevenly distributed over exine surface
<i>Glyptostrobus</i>	tuberculate, ridges with micro-granulate	same as those of coarse ornamentation processes
<i>Metasequoia</i>	tuberculate	gemmate, gemmae with spinulate processes
<i>Sequoia</i>	tuberculate	tubercles which are fused laterally, forming the wavy, undulate tectum, the inside of which is filled with granules
<i>Sciadopitys</i>	rugulate, rugula with clear and micro-granulate	same as those of coarse ornamentation granula
<i>Taiwania</i>	tuberculate, tubercles rather irregular	same as those of coarse ornamentation in shape and unequal in size
<i>Taxodium</i>	tuberculate	granulate and striate
Fossil <i>Metasequoia</i> from Axel Heiberg	tuberculate	granulate, granula smooth
<i>Metasequoia foxii</i>	verrucate (= tuberculate)	granulate, granula smooth

*quoia*, are deposited late in the ontogenetic development of pollen exine.

Evidence for developmental immaturity of the fossil pollen is also present in the TEM of exine (Table 5). The fossil pollen from Axel Heiberg, like that of *M. milleri*, possesses thicker nexine and thinner sexine (Pl. 3, Figs 11, 12), although both nexine and sexine are thicker than that of *M. milleri*. This is in contrast to the extant *Metasequoia* pollen, where the sexine is as thick as, or thicker than, the nexine (YING et al. 1993). Taxodiaceous pollen has distinctly lamellate structure under TEM (XI & WANG 1989). The nexine of grains of *M. occidentalis* from Axel Heiberg typically has less than 8 lamellae (Pl. 3, Figs 11, 12), whereas the nexine of extant *M. glyptostrobes* consists of 10–15 rather thick lamellae (XI 1988, XI & WANG 1989). Due to the limitation of fossil pollen preservation, it is unclear if each lamella of the fossil pollen possesses a tripartite structure, a distinct feature in grains of the living *M. glyptostrobes* (XI 1988, XI & WANG 1989). The smaller number of lamellae in the fossil pollen of the Axel Heiberg specimen is similar to that of grains of *Taxo-*

*dium ascendens* and *Sequoia sempervirens*, although the lamellae in *Sequoia* are unequal in thickness, while those in the fossil are equally thick. While the fossil pollen from Axel Heiberg is thus more similar to *Taxodium* in the aspect of TEM structure, particular in the continuous and distinct spaces between the lamellae (Table 5), nevertheless, in more than twenty years of intensive collecting, not a single *Taxodium* macrofossil has ever been found in the Axel Heiberg Island beds.

It is not clear if the Ubisch bodies on the exine surface of *M. occidentalis* from Axel Heiberg possess a hollow center, as do other conifers (ROTHWELL & BASINGER 1979, TAYLOR 1990), although the somewhat smooth surface on the orbicules and the lack of microspinulate processes make the grains different from those of living and some other fossil *Metasequoia* (ROTHWELL & BASINGER 1979, XI & WANG 1989). The presence of Ubisch bodies in *M. occidentalis* may suggest that the plant had secretory or parietal tapetum (see PACINI et al. 1985). Studies by PACINI et al. (1985) suggest that tapetum type and plant habitat appear to be closely correlated (TAYLOR

Table 5. Comparison of pollen nexine under TEM between selected living taxodiaceous genera and fossil *Metasequoia occidentalis* from Axel Heiberg Island (after XI 1986, 1988, XI & WANG 1989, YING et al. 1993, YU & FU 1996).

Genus	Number of lamellae	Tripartite structure	Note
<i>Cryptomeria</i>	16, thickest, lamellae distinct	evident	most lamellate
<i>Cunninghamia</i>	6–8, thin, lamellae indistinct	none	
<i>Glyptostrobus</i>	6–7, rather thick, equal in thickness	indistinct	
<i>Metasequoia</i>	10–13, rather thick lamellae; outermost one being the thickest	distinct (nearly every lamellae possessing a white line in its fork or fuse middle, especially 3–4 outer lamellae)	lamellae usually together
<i>Sequoia sempervirens</i>	8–9, which are unequal in thickness and gradually decrease in the thickness inwards	indistinct	remarkable differences from <i>Metasequoia</i> in ultrastructure of nexine
<i>Taiwania</i>	5–6, rather thin lamellae, of which the outermost one is slightly thicker than the others	unknown	the space between the lamellae is continuous and the boundary is distinct
<i>Taxodium ascendens</i>	8–10	distinct	rather similar to that of <i>Metasequoia</i>
fossil <i>Metasequoia</i> from Axel Heiberg	8, equal in thickness	unknown	

1990), with parietal type appearing to be characteristic of plants in drier habitats (PACINI et al. 1985). This seems not to be true for *M. occidentalis* in the Eocene of Axel Heiberg, as there is clear evidence that the Eocene flora in the High Arctic received an abundance of moisture (BASINGER 1991).

The pollen grains of *M. occidentalis* from Axel Heiberg show close resemblance with those of *M. foxii* in exine morphology, and deviate somewhat in character from those of extant *Metasequoia* under SEM and TEM, although it must be kept in mind that the pollen is interpreted as immature, and therefore its morphology may have undergone further maturation.

#### 5.4. Seed cones and seeds

Like the seed cones of *M. foxii*, those of *M. occidentalis* of Axel Heiberg are also represented by two types of cone-scale arrangement. Based on a statistical survey of more than 3200 seed cones recovered from all three facies-controlled assemblages in the area, viz. leaf litter floras, channel sands floras, and

siltstone floras, about 22% of seed cones have helically arranged scales, while 32% have the typical decussate scales seen in extant *Metasequoia* (Table 6). The seed cones from swamp localities like B' (220), 184, and 185 (University of Saskatchewan geological locality letter and number for Axel Heiberg Island) show a high proportion of cones with helical scales; whereas those from other swamp localities such as N and O produce more seed cones with decussate scales. Therefore, the presence of the two types of scale arrangement appears to be unrelated to specific fossil assemblages. While both types of cone-scale arrangement are found intermingled, it is not clear if these cones could be borne on the same branch.

Fossil *Metasequoia* seed cones, like those of extant *M. glyptostrobooides*, had long been documented as solely having decussate scales, without any exception (MIKI 1941, CHANEY 1951, FU et al. 1999). When cones are preserved longitudinally, a decussate condition has usually been assumed, and deviation typically attributed to preservational distortion. Very few had suspected variation in cone-scale arrangement in fossil *Metasequoia* (KOCH 1963), although

Table 6. Statistics of seed cone scale arrangement of *Metasequoia occidentalis* from Axel Heiberg. The location is identified by a University of Saskatchewan palaeobotanical locality letter and number (see LEPAGE 1993, MCLIVER & BASINGER 1999).

Location	No. helical cones	No. undetermined cones	No. decussate cones	Total
B'	20	125	8	153
B'/G'	23	16	0	39
G'	1	5	22	28
I	0	28	4	32
L or N	0	40	0	40
N	0	39	14	53
O	0	28	15	43
184	130	141	13	284
184/185	277	438	48	763
185	22	66	6	94
226	8	56	4	68
244	0	154	637	791
246	0	1	4	5
247	0	6	9	15
522	4	29	6	39
527	0	36	2	38
553	21	30	7	58
564	6	28	4	38
565	0	15	8	23
566	0	50	163	213
570	6	109	39	154
770	6	1	13	20
Arctic97	8	0	0	8
Arctic99	176	0	0	176
Locality unknown	0	30	3	33
Subtotal	708	1471	1029	3208
Percentage	22%	46%	32%	100%

in fact this variation does exist (STOCKEY et al. 2001).

It is not always possible to evaluate what the actual pattern of scale arrangement of fossil coniferous seed cones may be. If the fossil preservation allows examination of both sides of a seed cone, as in the case of those from central Alberta (STOCKEY et al. 2001) and Axel Heiberg (Pl. 4, Figs 5–12, 14–16), it is likely that the pattern of scale arrangement may be discerned. In the seed cones of extant *Metasequoia* (Pl. 4, Figs 1, 2) and *Sequoia* (Pl. 4, Figs 3, 4), the recognition of the pattern is fairly straightforward if attention is paid to the relationships between any single scale and all adjacent scales. Following the same criterion, a survey on more than 3200 fossil seed cones of *M. occidentalis* from Axel Heiberg was made (Table 6).

While the presence of helically arranged seed cone scales has never been documented in extant *Metasequoia* (see FU et al. 1999), it is apparent that this condition was fairly common in fossil members

of the genus (for detail, see below). As early as in 1963, KOCH (1963: 31) mentioned that some of his fossil *Metasequoia* seed cones from Atanikerdluk of Greenland bear spirally arranged scales. Unfortunately, he did not illustrate them; therefore, his report was long ignored. KOCH (1963) felt that these fossils might represent a different species from CHANEY'S *M. occidentalis*. A similar opinion on past diversity within the genus *Metasequoia* was also expressed by STOCKEY et al. (2001), who introduced a new species (*M. foxii*) based on material from central Alberta, Canada, although they appeared unaware of KOCH'S observation of 40 years earlier. After reviewing many illustrated fossil *Metasequoia* seed cones from the literature, we have realized that the occurrence of helical seed cone scales appears to be quite common in fossils ascribed to *Metasequoia occidentalis* from across North America and Asia (Table 7). As seed cones with helical scales are a common variant in *M. occidentalis*, this feature no longer serves to dis-

Table 7. Summary of the seed cone scale arrangement in published fossil species of *Metasequoia*. Information is solely based on illustrations and plates in the publications (D – cones with decussate scales; H – cones with helical scales; ? – cone scale arrangement hard to define).

Taxon	Cone scale arrangement	Age	Literature
<i>Sequoia dakotensis</i>	D, ?	Late Cretaceous	DORF 1942
<i>Metasequoia cuneata</i>	D	Late Cretaceous	BELL 1957
<i>M. sp.1</i>	?	Late Cretaceous	SVESHNIKOVA 1967
<i>M. sp.2</i>	H(?)	Late Cretaceous	SVESHNIKOVA 1967 (pl. VII, fig. 6)
<i>M. asiatica</i>	D	Late Cretaceous	SAMYLINA 1988
<i>M. sp.</i>	H	Late Cretaceous	SAMYLINA 1988 (pl. XXII, fig. 7)
<i>M. sp.</i>	?	Tertiary	DOROFEEV 1972
<i>M. sp.</i>	?	Tertiary	ZHILIN 1974
<i>M. disticha</i>	D	Tertiary	KRASSILOV 1976
<i>M. disticha</i>	H(?)	Tertiary	KRASSILOV 1976 (pl. X, fig. 5)
<i>M. nathorstii</i>	?	Paleogene	SVESHNIKOVA 1975a
<i>M. occidentalis</i>	D	Paleocene	BROWN 1962
<i>M. occidentalis</i>	D	Paleocene	KOCH 1963
<i>M. occidentalis</i>	H*	Paleocene	KOCH 1963 (pl. 4, fig. 5)
<i>M. occidentalis</i>	D, ?	Paleocene	CHANDRASEKHARAM 1974
<i>M. occidentalis</i>	?	Paleocene	SCHWEITZER 1974
<i>M. occidentalis</i>	D	Paleocene	BUDANTSEV 1983
<i>M. occidentalis</i>	D	Paleocene	BOULTER & KVACEK 1989
<i>M. occidentalis</i>	D, ?	Paleocene	LIU et al. 1999
<i>M. occidentalis</i>	D, ?	Paleocene-Eocene	HICKEY 1977
<i>M. sp.</i>	?	Early Eocene	DENK et al. 1999
<i>M. occidentalis</i>	D	Eocene	HUZIOKA & TAKAHASI 1970
<i>M. disticha</i>	H	Eocene	WGCP 1978 (pl. 7, fig. 6)
<i>M. occidentalis</i>	?	Eocene	LIU & LI 2000
<i>M. disticha</i>	H	Eocene	ZHANG et al. 1980 (pl. 194, fig. 2)
<i>M. milleri</i>	D	Eocene	BASINGER 1984
<i>M. sp.</i>	?	Eocene	WEHR & SCHORN 1992
<i>M. occidentalis</i>	D	Oligocene	CHANEY 1951 (pl. 7, figs 1, 2)
<i>M. occidentalis</i>	H	Oligocene	CHANEY 1951 (pl. 7, fig. 3; Pl. 12, fig. 1)
<i>Sequoia langsdorfi</i> **	D	Oligocene	KRYSHTOFOVICH et al. 1956
<i>M. occidentalis</i>	?	Oligocene	BECKER 1960
<i>M. occidentalis</i>	?	Oligocene	TANAI 1970
<i>M. occidentalis</i>	?	Oligocene	MANCHESTER & MEYER 1987
<i>M. sp.</i>	? (fig. 5)	Oligocene	MEYER & MANCHESTER 1997
	D (fig.6)		
<i>M. occidentalis</i>	D	Oligocene-Miocene	BECKER 1969
<i>M. occidentalis</i>	?	Miocene	CANRIGHT 1972
<i>M. sp.</i>	?	Miocene	DOROFEEV 1972
<i>M. disticha</i>	?	Miocene	KLIMOVA 1975
<i>M. occidentalis</i>	?	Miocene	HORIUCHI 1996
<i>M. disticha</i>	D	Pliocene	MIKI 1941

\* KOCH (1963: 31) only mentioned the presence of helical scale cones from Atanikerdluk, Greenland, and he did not provide a detailed systematic description.

\*\* This illustrated seed cone from the Oligocene of Kazakhstan should be assigned to the genus *Metasequoia* due to the presence of a long and naked peduncle.

tinguish *M. foxii* from the ubiquitous *M. occidentalis*, and therefore *M. foxii* is a later synonym.

It is not known why the seed cones with helical scales, common in the fossil *Metasequoia* from the Late Cretaceous to Oligocene, finally disappeared in

the extant *Metasequoia*. STERLING (1949) pointed out that the male sporophylls of extant *Metasequoia* are not strictly decussate. Therefore, decussate arrangement in organs of *Metasequoia* might not be an exclusive character in fossil or extant members.



Table 8. Comparison of the three ecotypic variations of living *Metasequoia* (after LI 1998/1999).

Ecological type	Large cone	Medium cone	Small cone
Cone size (cm)	2.2 × 2.0	2.0 × 1.8	1.5 × 1.4
Seed size (mm)	6 × 5	5.3 × 4.8	4.8 × 4.2
Ecological preference	mountain slope drought-tolerant	wide; medium drought-tolerant	ditch or creek drought-intolerant
Growth rate	fast	medium	slow

Realization in the current study that helical arrangement of seed cone scales in fossil *Metasequoia* is a widespread phenomenon raises questions as to why this was not recognized earlier. The reports of KOCH (1963) and STOCKEY et al. (2001) associated the character with *Metasequoia*, but as an exception to the otherwise unchallenged and defining decussate morphotype, and necessitating segregation from other fossil remains of the genus. It seems that the demonstrably decussate arrangement of seed cone scales in extant *Metasequoia glyptostroboides*, in the context of such strong morphological consistency in pollen, seeds, leaves, wood, and habit, demanded that fossil cones shared this feature as well. Even the extraordinarily well preserved materials from Axel Heiberg Island presented a challenge, with arrangement of scales indeterminate in nearly half of the cones. Where the search image is for decussate arrangement, it has been easy to overlook the evidence that is before our eyes, and cones not consistent with the preconceived model dismissed as poorly preserved, crushed, or distorted.

Except for the nature of seed cone scale arrangement, the morphology of Arctic *Metasequoia* fossil seed cones and seeds is very much like that of the extant *M. glyptostroboides* (Table 1). It has long been noted, however, that considerable variation in size of seed cones and seeds exists among both living and fossil *Metasequoia* (Pl. 4, Figs 5–12, 14–16) (Table 8), and that environmental variants appear to be represented in extant *Metasequoia*. Large seed cones are correlated with trees of mountain slopes, which are more drought tolerant and develop a broader canopy; while small seed cones are borne on trees that grow along streambanks, and are less tolerant of drought (LI 1998/1999). A similar environmental correlation is found among fossil *Metasequoia* from Axel Heiberg Island. Three broad categories of depositional environments were recognized in the Buchanan Lake sediments by BASINGER (1991): *in situ*

autochthonous accumulations of lignitic leaf litter and woody remains, including stumps; allochthonous leaf localities, with remains preserved as compressions in fine-grained silts or shales; and allochthonous accumulations of cones, woody fruits, seeds, and woody debris within fine to coarse fluvial sands. Among the fossil sites on Axel Heiberg, the large and medium seed cones of *Metasequoia* (greater than 2 cm) are found in sites 180, 184, 226, 527, and 564, which are all from the latter environment, and interpreted by (BASINGER et al. 1994) as derived from 'upland' sites within some hundreds of meters to a few kilometers at most from the sites of deposition, but likely representing somewhat elevated and well drained habitat. Small seed cones (smaller than 2 cm) are abundant in leaf litter mats, such as sites 244, 566 and Level G', which represent local wetland vegetation and may be used to determine composition of swamp forest communities (BASINGER et al. 1994).

It is also interesting to note that the Axel Heiberg *M. occidentalis* with largest seed cones generally have larger leaves, while those with small seed cones have smaller leaves. These probably represent various ecotypes of fossil *Metasequoia* in the Arctic in the Middle to Late Eocene. This work again implies that characters of size difference must be applied in classification with great caution. The establishment of a new living species by SILBA (2000), *M. honshuenensis*, therefore, might not be well supported.

## 6. Conclusions

Through the extensive comparison between various vegetative and reproductive organs of fossil *Metasequoia* from Axel Heiberg Island and those of the extant and previously published fossil *Metasequoia*, we conclude that the Axel Heiberg fossils, along with all published fossil species (except *M. milleri* due to different mode of preservation), represent a single fossil species, viz. *M. occidentalis* with

emendation. This taxonomic treatment supports the conclusions proposed by LIU et al. (1999), and includes *M. foxii* (STOCKEY et al. 2001) as a synonym of *M. occidentalis*. Although several distinct characters were recognized for the fossil species *M. occidentalis*, most notably the helical arrangement of seed cone scales and ultrastructure of pollen exine, morphology and anatomy of other organs of this fossil species appears to have changed little with time and persist in the extant species, suggesting a morphological stasis. Constraints and stabilizing selection are proposed to be the two major mechanisms for evolutionary stasis (WILLIAMSON 1987). As seems likely from sedimentological evidence, habitats occupied by *M. occidentalis* and *M. milleri*, were similar to those now occupied by *M. glyptostroboides*; thus, persistent habitat preference may have exerted stabilizing selection and led to morphological stasis (cf. WEN 1999).

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## Plate 1

- Figs 1–7; 9–11. Fossil *Metasequoia occidentalis* (NEWBERRY) CHANEY from Axel Heiberg Island, Canadian High Arctic.
- Fig. 1. Numerous overlapped deciduous shoots in leaf litter recovered from level N, showing the mummified preservation. Scale bar = 1 cm.
- Fig. 2. Deciduous shoot from level B' leaf litter. Note the clusters of scale-like leaves at the base. Scale bar = 1 cm. USPC-5962.
- Fig. 3. Deciduous shoot from level B' leaf litter, showing a gall developed near the top of shoot. Note the leaves around the gall appear to be helically arranged, but all the leaves on the lower part of shoot are the typical decussate arrangement, a character diagnostic to *Metasequoia*. Note the clusters of scale-like leaves at the base of shoot. USPC-5969.
- Fig. 4. Deciduous shoot from level N leaf litter. Note the clusters of scale-like leaves at the base of shoot. Scale bar = 1 cm. USPC-5965.
- Fig. 5. Incomplete deciduous shoot from the stream fossil site, a floodplain deposit, showing larger and longer leaves on the shoot than those from swamp-forest leaf litter. Scale bar = 1 cm. USPC-5820.
- Fig. 6. Incomplete short shoot from the stream fossil site. Note the larger and longer leaves on the shoot than those from leaf litter. Scale bar = 1 cm. USPC-5967.
- Fig. 7. Close-up of adaxial side of an arbitrary leaf from level B' leaf litter, showing a relatively narrow stomatal band (S) on each side of the midrib (M). Scale bar = 1 mm.
- Fig. 9. Transverse section of a fossil leaf from level B' leaf litter, showing a resin canal (R), dome-shaped epidermal cells, and two stomata (S) on the adaxial side of leaf. Scale bar = 20  $\mu\text{m}$ .
- Fig. 10. Upper cuticle under Light Microscopy (LM) of fossil leaf from the level B' of leaf litter, showing undulate to straight anticlinal walls of epidermal cells. Scale bar = 25  $\mu\text{m}$ .
- Fig. 11. Lower cuticle under LM of fossil leaf from level B' leaf litter, showing the regular orientation of stomata and undulate to straight anticlinal walls of epidermal cells. Scale bar = 30  $\mu\text{m}$ .
- Figs 8, 12–15. Extant *Metasequoia glyptostroboides* HU et CHENG for comparison, collected from Matsuyama Japan.
- Fig. 8. Close-up of adaxial side of a leaf, showing a relatively wide stomatal band (S) on each side of midrib (M). Scale bar = 1 mm.
- Fig. 12. Lower cuticle under LM of extant leaf, showing the regular orientation of stomata. Scale bar = 45  $\mu\text{m}$ .
- Fig. 13. Outer surface of upper cuticle under Scanning Electron Microscopy (SEM), showing wrinkled periclinal walls. Scale bar = 10  $\mu\text{m}$ .
- Fig. 14. Closeup of Fig. 13 under SEM, showing smooth periclinal walls. Scale bar = 10  $\mu\text{m}$ .
- Fig. 15. Inner surface of upper cuticle under SEM, showing undulate anticlinal walls. Scale bar = 10  $\mu\text{m}$ .

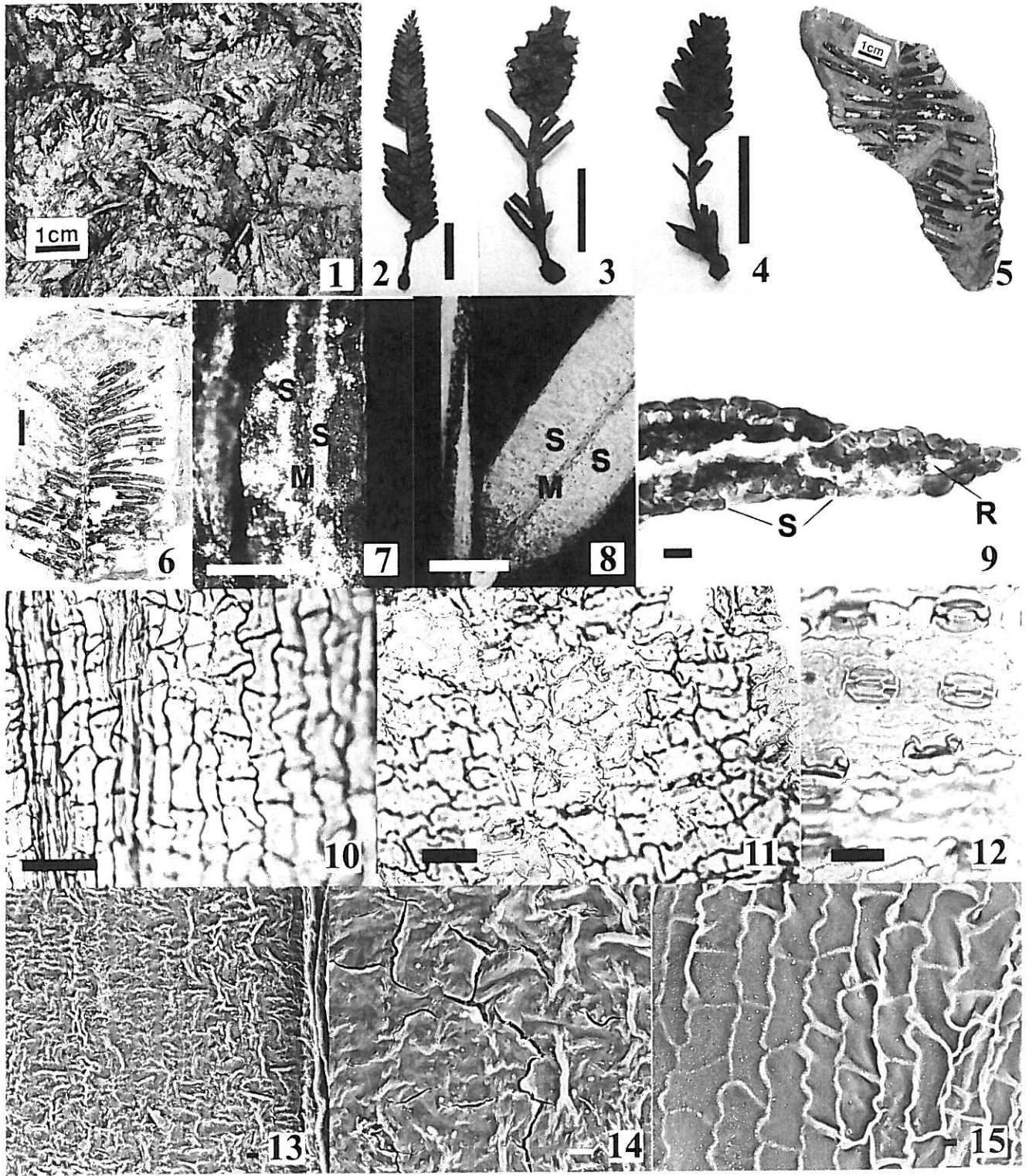


Plate 1. LIU, C.Y.-S. & BASINGER, J.F.: *Metasequoia* HU et CHENG from the Eocene of Axel Heiberg Island.

## Plate 2

Figs 1; 7–12. Fossil *Metasequoia occidentalis* (NEWBERRY) CHANEY from Axel Heiberg Island, Canadian High Arctic.

- Fig. 1. Inner surface of upper cuticle of leaf from level B' leaf litter under SEM, showing undulate anticlinal walls of epidermal cell. Scale bar = 10  $\mu\text{m}$ .
- Fig. 7. Outer surface of lower cuticle of leaf from the stream fossil site under SEM, showing stomatal band in the middle (S) between midrib (Mid) and margin of leaf (Mar). Scale bar = 100  $\mu\text{m}$ .
- Fig. 8. Outer surface of lower cuticle of leaf from level B' leaf litter under SEM, showing numerous elliptical stomata (S) and outlines of recognizable epidermal cells. Note the presence of elliptical Florin rings, marked by S. Scale bar = 10  $\mu\text{m}$ .
- Fig. 9. Outer surface of lower cuticle of leaf from B' leaf litter under SEM, showing about seven stomatal rows and the presence of elliptical Florin rings. Note that the stomata are not sunken and the outlines of pitted epidermal cells are clearly visible in the non-stomatal zone. Scale bar = 10  $\mu\text{m}$ .
- Fig. 10. Inner surface of lower cuticle of leaf from level B' leaf litter under SEM, showing three elliptical stomata in the center and lower left of the figure and monocyclic (usually 4) subsidiary cells, typical for the Even Type of lower cuticle, first recognized from an isolated population of extant *Metasequoia* in central China. Scale bar = 10  $\mu\text{m}$ .
- Fig. 11. Shoot with subtending small pollen cones from level B' leaf litter. Only one cone is preserved, which is the only pollen cone found to yield *in situ* pollen. USPC-5945. Scale bar = 1 cm.
- Fig. 12. Shoot with large pollen cones from level B' leaf litter. Note that these cones appear empty and contain no *in situ* pollen. USPC-5943. Scale bar = 1 cm.
- Figs 2–6. Extant *Metasequoia glyptostroboides* HU et CHENG for comparison, collected from Matsuyama of Japan.
- Fig. 2. Outer surface of lower cuticle under SEM, showing wrinkled periclinal walls and the indistinct outlines of epidermal cells. Note the Florin rings shaped like two parallel flanges, a character documented in Uneven Type of lower cuticle in *Metasequoia*. Scale bar = 10  $\mu\text{m}$ .
- Fig. 3. Outer surface of lower cuticle under SEM, showing "papillae-like" bulges. Scale bar = 10  $\mu\text{m}$ .
- Fig. 4. Inner surface of lower cuticle under SEM, showing that stomata are rectangular in shape and periclinal walls are uneven, characters typical for Uneven Type of lower cuticle of *Metasequoia*. Scale bar = 10  $\mu\text{m}$ .
- Fig. 5. Inner surface of lower cuticle under SEM, showing a close-up of one stoma. Note the stoma is about rectangular in shape and periclinal walls of epidermal cells are uneven. Scale bar = 1  $\mu\text{m}$ .
- Fig. 6. Inner surface of lower cuticle under SEM, showing epidermal cells with uneven periclinal walls on non-stomatal zone. Scale bar = 10  $\mu\text{m}$ .



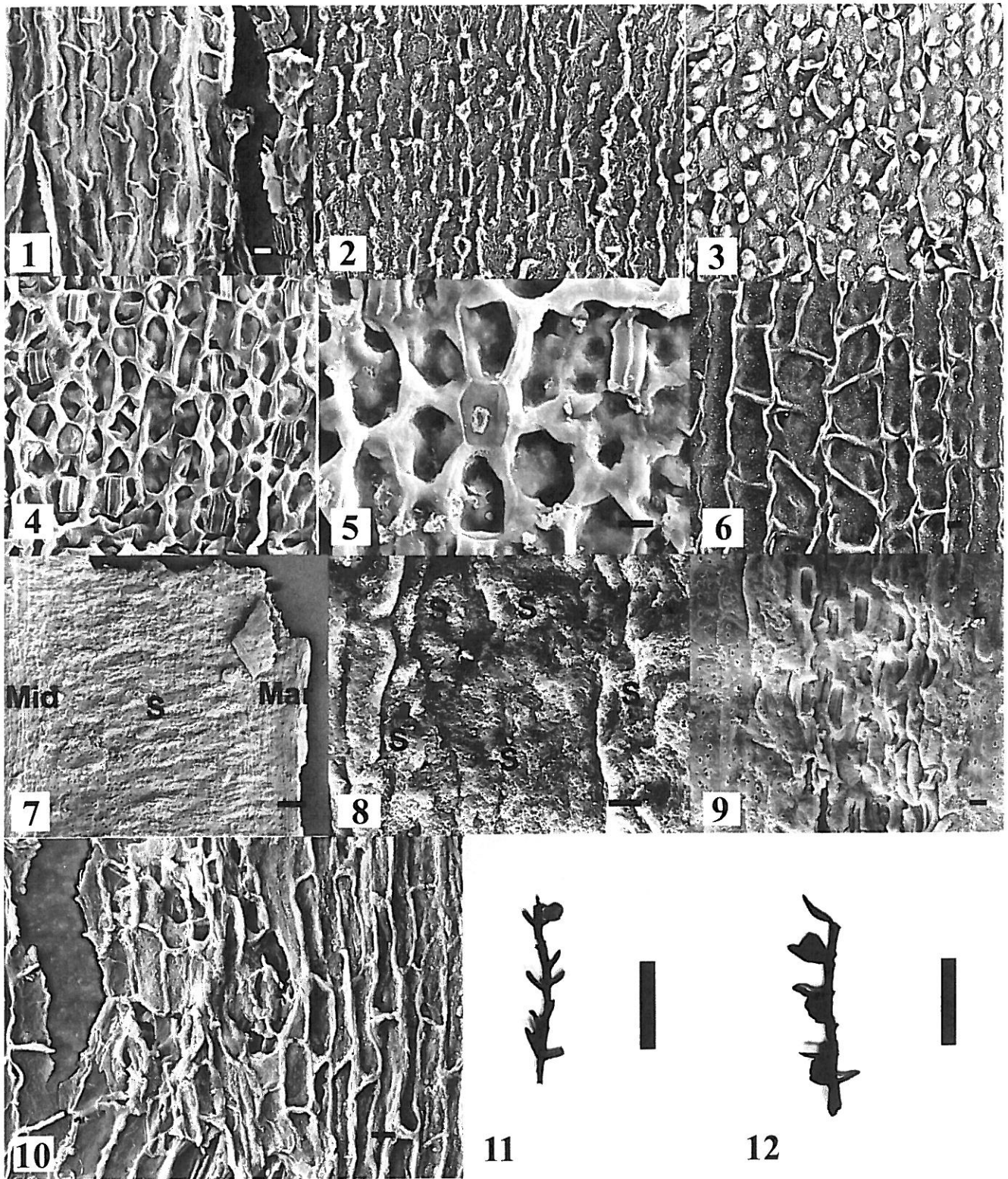


Plate 2. LIU, C.Y.-S. & BASINGER, J.F.: *Metasequoia* HU et CHENG from the Eocene of Axel Heiberg Island.

### Plate 3

Figs 1–12. Fossil *Metasequoia occidentalis* (NEWBERRY) CHANEY from Axel Heiberg Island, Canadian High Arctic.

- Fig. 1. Shoot with premature pollen cones yielding no *in situ* pollen, from level B' leaf litter. Note the tiny size of these pollen cones, interpreted to have been too immature for pollen grains to have been developed. USPC-5944. Scale bar = 1 cm.
- Fig. 2. Shoot with subtending mature pollen cones from level B' leaf litter. The cones seem to contain no *in situ* pollen. USPC-5954. Scale bar = 1 cm.
- Fig. 3. Shoot with large subtending and apical pollen cones from level B' leaf litter. No *in situ* pollen grains have been found in these cones. USPC-5955. Scale bar = 1 cm.
- Fig. 4. Shoot with subtending small and probably immature pollen cones from level B' leaf litter. USPC-5956. Scale bar = 1 cm.
- Fig. 5. Pollen clumps extracted from the pollen cone illustrated in Pl. 2, Fig. 11 (USPC-5943), under LM, showing well preserved *in situ* pollen. Note the occurrence of papillae (P). Scale bar = 15  $\mu$ m.
- Fig. 6. Close-up of part of one pollen clump from Fig. 5 under LM, showing one separated *in situ* pollen. Scale bar = 15  $\mu$ m.
- Fig. 7. Close-up of one *in situ* pollen grain from the pollen clump, illustrated in Fig. 6, under SEM, showing the fine granules and Ubisch bodies on the exine. Scale bar = 1  $\mu$ m.
- Fig. 8. SEM of pollen clumps from the pollen cone pictured in Pl. 2, Fig. 11. Scale bar = 10  $\mu$ m.
- Fig. 9. Close-up of the exine of three *in situ* pollen grains extracted from the pollen cone illustrated in Pl. 2, Fig. 11. Note the fine granules on the exine. Scale bar = 1  $\mu$ m.
- Fig. 10. Close-up of the exine from one pollen grain in Fig. 8, showing the typical granular exine. Scale bar = 1  $\mu$ m.
- Fig. 11. Transmission Electron Micrograph (TEM) of *in situ* pollen grain extracted from the pollen cone illustrated in Pl. 2, Fig. 11. Note the eight distinct lamellae (L) in nexine and numerous Ubisch bodies on the exine. Scale bar = 1  $\mu$ m.
- Fig. 12. TEM of another *in situ* pollen grain extracted from the pollen cone illustrated in Pl. 2, Fig. 11, showing that the nexine has eight distinct lamellae (L) and many Ubisch bodies on the exine. Scale bar = 1  $\mu$ m.

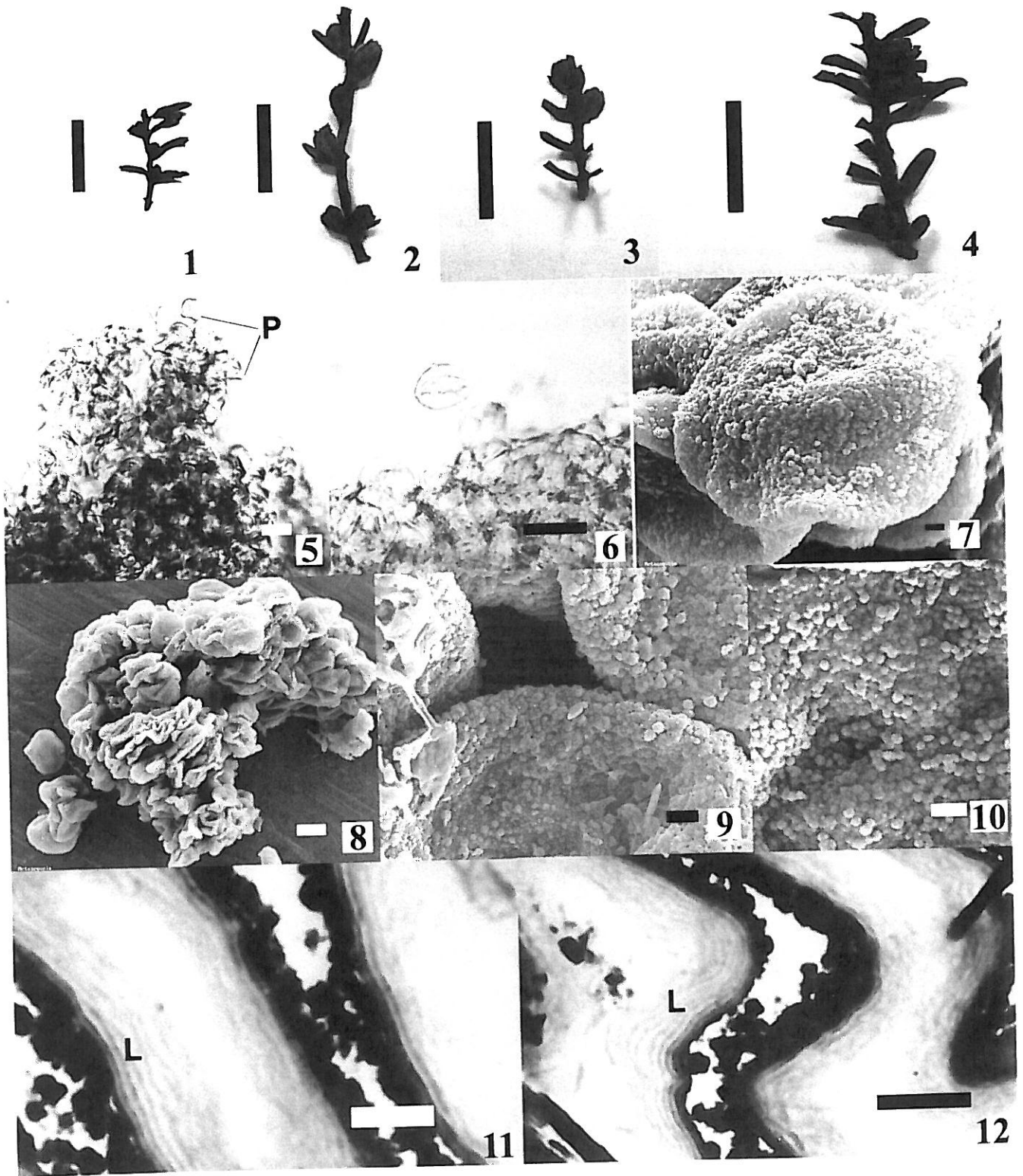


Plate 3. LIU, C.Y.-S. & BASINGER, J.F.: *Metasequoia* HU et CHENG from the Eocene of Axel Heiberg Island.

#### Plate 4

- Figs 1–2. A seed cone of extant *Metasequoia glyptostroboides* HU et CHENG for comparison, collected from Matsayama of Japan.
- Fig. 1. One side of the seed cone, showing both lateral sides of one scale (E) adjacent to four other scales (A, B, C, and D). Scale bar = 1 cm.
- Fig. 2. The other side of the same seed cone as Fig. 1, showing scale (F), which is opposite to Scale E of Fig. 1, also adjacent to the same four scales (A, B, C, and D). This confirms that the arrangement of Scales A–F is decussate. Scale bar = 1 cm.
- Figs 3–4. A comparative seed cone of extant *Sequoia sempervirens* (LAMB. ex D. DON) ENDL., collected from California, U.S.A.
- Fig. 3. One side of the seed cone, showing that both lateral sides of one scale (E) are neighbored by four scales (A, B, C, and D). Scale bar = 1 cm.
- Fig. 4. The other side of the same seed cone as Fig. 3, showing that two scales (F and G) exist within the range framed by the same four scales as those in Fig. 3 (A, B, C, and D). This indicates that the arrangement of Scales A–G is helical. Scale bar = 1 cm.
- Figs 5–16. Various seed cones and one seed of fossil *Metasequoia occidentalis* (NEWBERRY) CHANEY from Axel Heiberg Island, Canadian High Arctic.
- Fig. 5. Seed cone from leaf litter, showing the lateral sides of Scale E is neighbored with four other scales (A, B, C, and D). USPC-5935. Scale bar = 1 cm.
- Fig. 6. The other side of the same seed cone as Fig. 5, after being flipped over. Note two scales (F and G) are laterally encompassed by the same four scales as in Fig. 5 (only A and B visible in the image). This is typical of a seed cone with scales helically arranged. Scale bar = 1 cm.
- Fig. 7. Seed cone from the level B'/G' of leaf litter, showing the helically arranged scales and long and smooth peduncle. USPC-5939. Scale bar = 1 cm.
- Fig. 8. The same seed cone as Fig. 7, showing the other side of the cone. Scale bar = 1 cm.
- Fig. 9. Seed cone from leaf litter, showing the scales are helically arranged. USPC-5940. Scale bar = 1 cm.
- Fig. 10. The same seed cone as Fig. 9, showing the other side of the cone. Scale bar = 1 cm.
- Fig. 11. Seed cone from leaf litter, showing the apical view of the scale. Note the first four scales on the top, marked as a, b, c, and d, are arranged as decussate, while the rest scales, marked as 1 to 5, appear in a helical arrangement. USPC-5942. Scale bar = 1 cm.
- Fig. 12. Seed cone from leaf litter, showing the apical view of decussate scale arrangement. USPC-5947. Scale bar = 1 cm.
- Fig. 13. One dispersed seed from leaf litter, showing the round ovate to cordate shape. Scale bar = 1 cm.
- Fig. 14. Seed cone from leaf litter, showing the decussately arranged scales. USPC-5950. Scale bar = 1 cm.
- Fig. 15. Seed cone from leaf litter, showing the decussately arranged scale from an apical view. USPC-5953. Scale bar = 1 cm.
- Fig. 16. Seed cone from the level N of leaf litter, showing the helically arranged scales. USPC-5941. Scale bar = 1 cm.

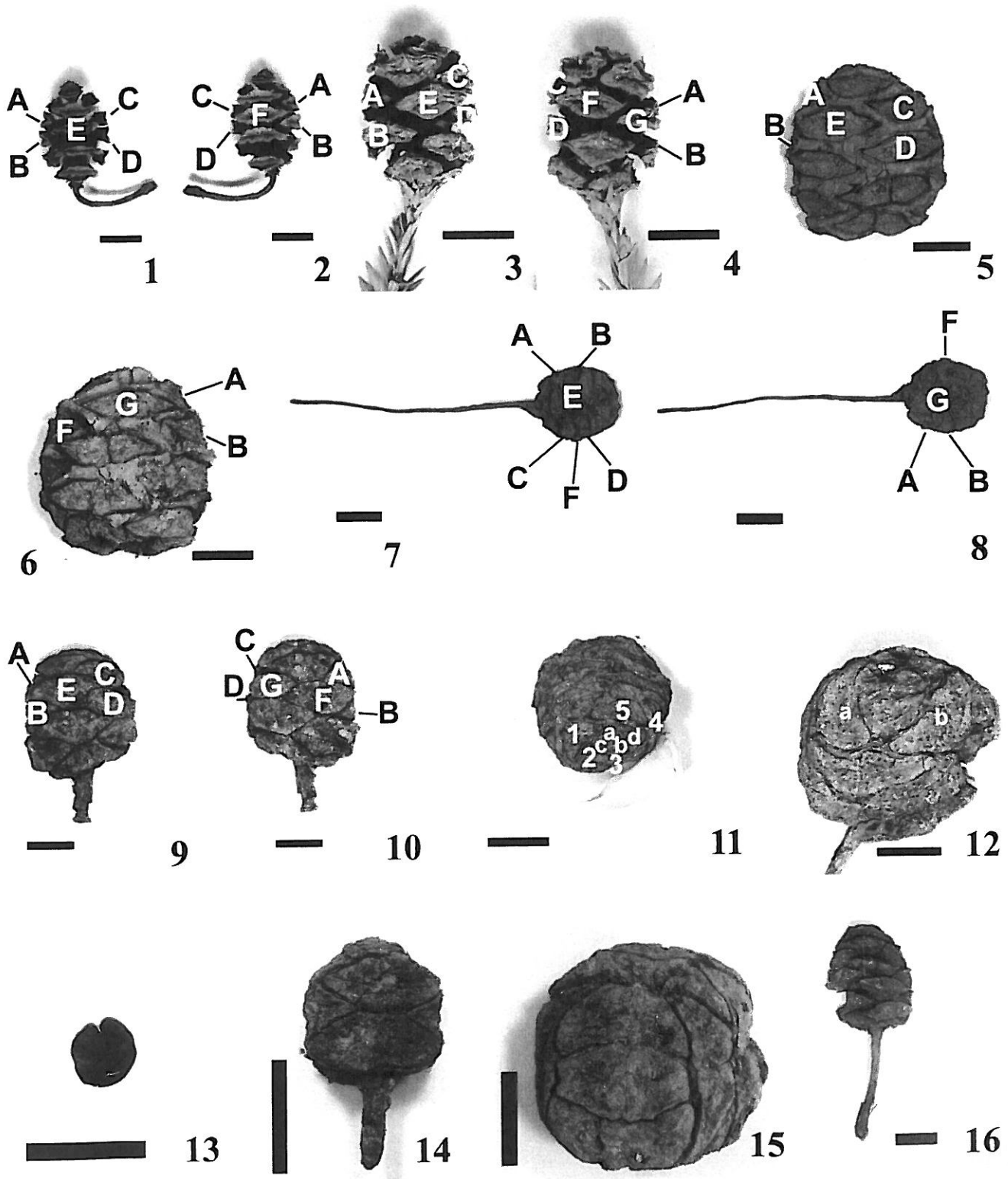


Plate 4. LIU, C.Y.-S. & BASINGER, J.F.: *Metasequoia* HU et CHENG from the Eocene of Axel Heiberg Island.