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DIVERSITY AMONG TAXODIOID CONIFERS: *METASEQUOIA FOXII* SP. NOV. FROM THE PALEOCENE OF CENTRAL ALBERTA, CANADA

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A single species of taxodioid conifers is among the dominant floristic elements at two stratigraphically contemporaneous Paleocene fossil localities in central Alberta, Canada. More than 10,000 compression specimens, including oppositely branched stems, vegetative shoots with decussately arranged leaves, pollen cones, pollen, ovulate cones, seeds, and seedlings, provide data for reconstructing a new species of *Metasequoia*. An *in situ* permineralized stem provides information about wood structure and suggests that the plant was a canopy tree. As is characteristic of taxodioid conifers in general, most compressed organs of the new species are not specifically diagnostic when evaluated as isolated fragments of the sporophyte. However, a combination of characters from several organs demonstrates the occurrence of a distinct species, *M. foxii* sp. nov. The diagnostic combination of characters for this species includes leaf size, pollen cone length, ovuliferous cone scale arrangement, seed size and shape, and characters of the seedlings. Ranges of variation in characters of the new species are compared to those of the currently recognized, well-known species of *Metasequoia*, *M. glyptostroboides*, *M. occidentalis*, and *M. milleri*, and evolutionary diversification within the genus is considered.

Keywords: Cupressaceae, *Metasequoia*, Paleocene, Taxodiaceae.

Introduction

Although taxodioid conifer remains are among the most abundant of Tertiary plant fossils (Florin 1963), they are extremely difficult to identify and characterize as reliable taxonomic species. Taxodioid plant organs commonly display both simple structure and a wide range of variation within a single species, and fossil specimens from different sources often have overlapping ranges of variation in many characters. Taxonomic assignments are further complicated when relatively few specimens are available from a given locality or when the remains of two or more similar species are present in the same fossil assemblage.

Since the initial recognition and characterization of *Metasequoia* Miki (1941) and the subsequent description of the living species *M. glyptostroboides* Hu and Cheng (1948), this genus has been documented as ranging from the Cretaceous to the Recent (Florin 1963). *Metasequoia* is now regarded as one of the most abundant taxodioid conifers in Tertiary sediments of the Northern Hemisphere (Chaney 1948, 1951; Florin 1963). Among conifer fossils with needle-like leaves, the genus *Metasequoia* is relatively easily recognized by opposite/decussate phyllotaxis, by the characteristically opposite branching of the shoots, and by the typically decussate cone scale complexes of the ovulate cones (Sterling 1949; Böcher 1964; Ma and Gu 2000). These characters allow us to distinguish *Metasequoia* fossils from different taxodioid genera with which they otherwise could be confused (e.g., *Parataxodium* Arnold and Lowther 1955). In contrast, delineation of valid species among fossil *Metasequoia* specimens has proven to be exceedingly difficult. Up to the present, more than 20 extinct species have been proposed (Liu et al. 1999), but many of these are based on a relatively small number of specimens and cannot be clearly distinguished from other species. As a result, most of the proposed species have been synonymized (Liu et al. 1999).

Until recently, large numbers of specimens had not been employed to determine the ranges of variation that characterize vegetative and fertile organs for most extinct species of *Metasequoia*. However, in a detailed investigation of *M. occidentalis* (Newberry) Chaney (1951), Liu et al. (1999) examined several hundred vegetative and fertile specimens from the Wuyun Formation in northeast China and established the overall range of variation for each organ of the sporophyte. These authors compared the ranges of variation for all of the organs to the characters of the other proposed species of *Metasequoia* and demonstrated convincingly that most of the extinct species fall within the overall ranges of variation for the organs of *M. occidentalis*.

Liu et al. (1999) recognize only two extinct species of *Metasequoia* plants from Cretaceous and Tertiary sediments of the Northern Hemisphere plus the living species *M. glyptostroboides* Hu and Cheng (1948). *Metasequoia occidentalis* (Newberry) Chaney (1951) is a circumpolar species of compression/impression remains with an extremely long geological range (Yang and Jin 2000), while *M. milleri* Rothwell and Basinger (1979) is based on anatomically preserved specimens from a single Middle Eocene deposit in central British Columbia, Canada. Liu et al. (1999) place virtually all of the other extinct

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species of *Metasequoia* in synonymy with *M. occidentalis*. *Metasequoia milleri* is also quite similar to *M. occidentalis* in most features (Basinger 1981, 1984) but is distinguished by a small number of morphological characters and by anatomical features that differ from those of *M. glyptostroboides* (Rothwell and Basinger 1979; Liu et al. 1999). Internal anatomical characters are not known for *M. occidentalis*.

Cuticular characters are considered by many authors to be important for distinguishing among different species of fossil conifers. Cuticles may be helpful for distinguishing among species of *Metasequoia* as well (Sveshnikova 1963; Huggins 1985). However, many *Metasequoia* fossils, including those described here, do not display cuticular remains.

The overall diversity of *Metasequoia* appears to be extremely low, but from the information presently at hand, one cannot distinguish between the hypotheses that (1) the genus *Metasequoia* has consisted primarily of a single, ubiquitous species throughout the Upper Cretaceous, Tertiary, and Quaternary and (2) that the fossil evidence described to date is merely inadequate to distinguish among two or more extremely similar species. The purpose of our study is to describe more than 10,000 *Metasequoia*-like compression specimens from two localities of the same age in central Alberta, Canada, and to assess the specific identity of the specimens. The new material allows us to test the above hypotheses using an extremely large collection of specimens and reveals the existence of a previously unrecognized species, *M. foxii* sp. nov., with unique ranges of variation for the characters of several organs. As a result, we now have a means for recognizing distinct species of *Metasequoia* from the fossil record and for beginning to assess specific diversity and patterns of evolution within the genus.

Material and Methods

Fossils were collected from the Munce's Hill (a.k.a. "One Jaw Gap"; Fox 1990) and Gao Mine localities east of Red Deer, Alberta, Canada (Falder et al. 1999). Most specimens occur as oxidized coalified compressions and impressions in more or less flat-lying, buff to light gray, medium-grain sandstones interbedded with finer sandstones and mudstones of the Paskapoo Formation. As was stressed in an earlier study of Munce's Hill plant fossils (Rothwell and Stockey 1991), size of the collected compression specimens is restricted by the highly fractured nature of the sediments. Therefore, only a small number of large specimens have been investigated (e.g., figs. 2, 3). These were uncovered on bedding planes, measured, and photographed (fig. 2) but could not be collected intact.

We selected 10,147 specimens of *M. foxii* for preparation, examination, and measurement from the University of Alberta Paleobotanical Collections. These include one upright trunk, 2536 vegetative shoots, 123 shoots bearing pollen cones, 2373 ovulate cones, 3263 seeds, and 1850 seedlings in a broad range of developmental stages (Falder 1999; Falder et al. 1999). Some specimens were prepared with fine needles to reveal details of leaf margins and tips, bud scales, pollen cones, ovuliferous cones, cone scale complexes, seeds, and seedlings. Coalified plant material was removed from pollen cones with needles and macerated as described by Rothwell and Stockey (1991) to obtain pollen.

Some large specimens were photographed in the field. Negatives of these photographs were digitized using a Polaroid Print Scan 35 slide scanner. Pollen for scanning electron microscopy was prepared following the methods of Rothwell and Stockey (1991).

There is one permineralized trunk at the Munce's Hill locality. The specimen is preserved upright in the sediment and is apparently *in situ*. It crops out of the face of the road cut ca. 2 m above the layers that yield the most abundant coalified compressions but still within the sediments that yield compressed *Metasequoia* fossils. Fragments of the trunk were collected and returned to the University of Alberta for study. Cell walls of the wood have been more or less leached away, and the wood is highly cracked and easily broken. Because the wood is too delicate to either section or polish, fragments were fractured in transverse, radial, and tangential planes. Wood fragments and pollen were mounted on stubs, coated with 100 Å of gold using a Nanotek sputter-coater, and studied by scanning electron microscopy using a Japan Electron Optics scanning microscope 6301 at 5 kV.

Digital image capture was conducted with MicroLumina digital scanning cameras at the University of Alberta and Ohio University (Leaf Systems, Bedford, Mass.) employing reflected light with either a Nikon macro lens, a Zeiss Stemi-2000C dissecting microscope, or a Zeiss WL compound microscope. All images were stored as TIFF files and were processed using Adobe Photoshop 4.0. Plates were constructed using Adobe Photoshop and printed on a Yashika disublimation printer. Specimens are housed in the Paleobotanical Collections, University of Alberta (UAPC P616, S19,627–S20,245; S23,557–S23,670; S24,057–S24,060; S26,129; S26,133; S26,137; S26,217–S26,291; S28,075–S28,202; S28,389–S30,116; S33,287–S33,430; S33,469; S33,470–S33,472; S33,477–S33,504; 33,651; S33,670; S34,261–S34,353; S34,415–S34,416; S35,879; S36,025; S36,111–S36,581; S34,627–S43,769; S46,022–S46,053; S46,583–S47,108; S47,642–S47,994; S48,116–S48,128; S48,157; S48,176–S48,187; S48,803–S48,812; S48,815–S48,817; S48,820–S48,836; S49,180–S49,279; S49,342–S49,364; S49,448–S49,694; S50,555; S50,827–S50,867; S51,333–S51,410; S51,418–S51,841; S52,014–S52,055; S52,091–S52,211; S52,291; S53,727; S53,738; S53,741; S53,745–S53,785; S53,837; S53,846; S53,858; S53,873; S53,877; S53,893–S53,894; S53,925; S53,942–S54,133; S54,140–S53,147; S54,152–S54,157; S54,160–S54,176; S54,183–S54,188; S54,203; S54,210; S54,213; S54,218–S54,223; S54,229–S54,235; S54,239; S54,242–S54,259; S54,270–S54,271; S54,277–S54,279; S54,283–S54,302; S54,318; S54,323; S54,332–S54,338; S54,340–S54,341; S54,348; S54,351–S54,372; S54,385–S54,563; S54,639; S54,642; S54,650–S54,670; S54,679; S54,681; S54,684–S54,685; S54,688–S54,698; S54,704–S54,706; S54,710–S54,716; S54,719–S54,720; S54,726–S54,733; S54,736–S54,749; S54,753–S54,755; S54,757–S54,762; S54,767–S54,772; S54,783; S54,787–S54,789; S54,791; S54,803–S54,804; S54,813; S54,816; S54,838–S54,839; S54,844; S54,848; S54,853–S54,854; S54,857–S54,858; S54,868–S54,879; S54,928–S54,934; S54,937; S54,952; S54,959–S54,996; S55,404–S55,454; S55,518; S55,528; S55,560–S55,561; S55,583; S55,630–S55,640; S55,701–S55,792; S56,006; S56,010; S56,015–

S56,016; S56,023–S56,069; S56,080; S56,082–S56,099; S56,131–S56,159; S56,173; S56,185; S56,199; S56,206; S56,210; S56,226; S56,241; S56,280; S56,308; S56,329; S56,335; S56,340–S56,341; S56,346–S56,347; S56,350; S56,422–S56,429; S56,443; S56,456; S56,458–S56,463; S56,473; S56,475–S56,476; S56,485; S56,490; S56,494; S56,498; S56,501; S56,505; S56,507–S56,509; S56,519; S56,777–S56,790; S56,798–S56,818; S56,865–S56,866; S56,888–S56,894; S57,272–S57,274).

Systematics

Order—Coniferales

Family—Cupressaceae Rich. ex Bartl. sensu *Eckenwalder 1976*

*Genus—*Metasequoia *Hu et W. C. Cheng 1948 nom. cons.*

*Species—*Metasequoia foxii *sp. nov.*

Specific diagnosis. Leaves opposite/decussate, infrequently subopposite; ovate to linear; 2–43 mm long, 0.5–4.5 mm wide, with tips ranging from rounded to mucronate. Pollen cones globose to ovate, 3–8 mm long, 2–5 mm wide; sporophylls decussate; pollen ranging from 17.5 to 24 μm; papillate and orbiculate. Ovulate cones cylindrical to globose, 10–35 mm long, 11–22 mm wide; ovuliferous cone scale arrangement variable, usually helical, less frequently four ranked and decussate; seeds elliptical to cordate, typically widest in midregion, 3.5–9.0 mm long, 2.75–7.0 mm wide; cotyledons 8–21 mm long (mean = 14.1 mm), 1.2–3.0 mm wide (mean = 2.2 mm).

Holotype. Cone attached to long stem; S28,476, figure 7.1; deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Etymology. The specific epithet *foxii* is proposed in honor of Richard C. Fox, vertebrate paleontologist, University of Alberta, who has brought to our attention several sources of plant fossils, including the two localities from which specimens of *M. foxii* have been collected.

Localities. Munce's Hill, a road cut 3 km northeast of Canyon Ski Mine Quarry, NW 1/4 sec. 34, T 38, R 26, W 4; and Gao Mine, a road cut on the north bank of Highway 593, 14 km east of Red Deer, sec. 3, T 38, R 26, W 4, in central Alberta, Canada.

Stratigraphic occurrence. Paskapoo Formation.

Age. Late Tiffanian (Ti_4), Paleocene.

Results

Permineralized Stem and Large Branches

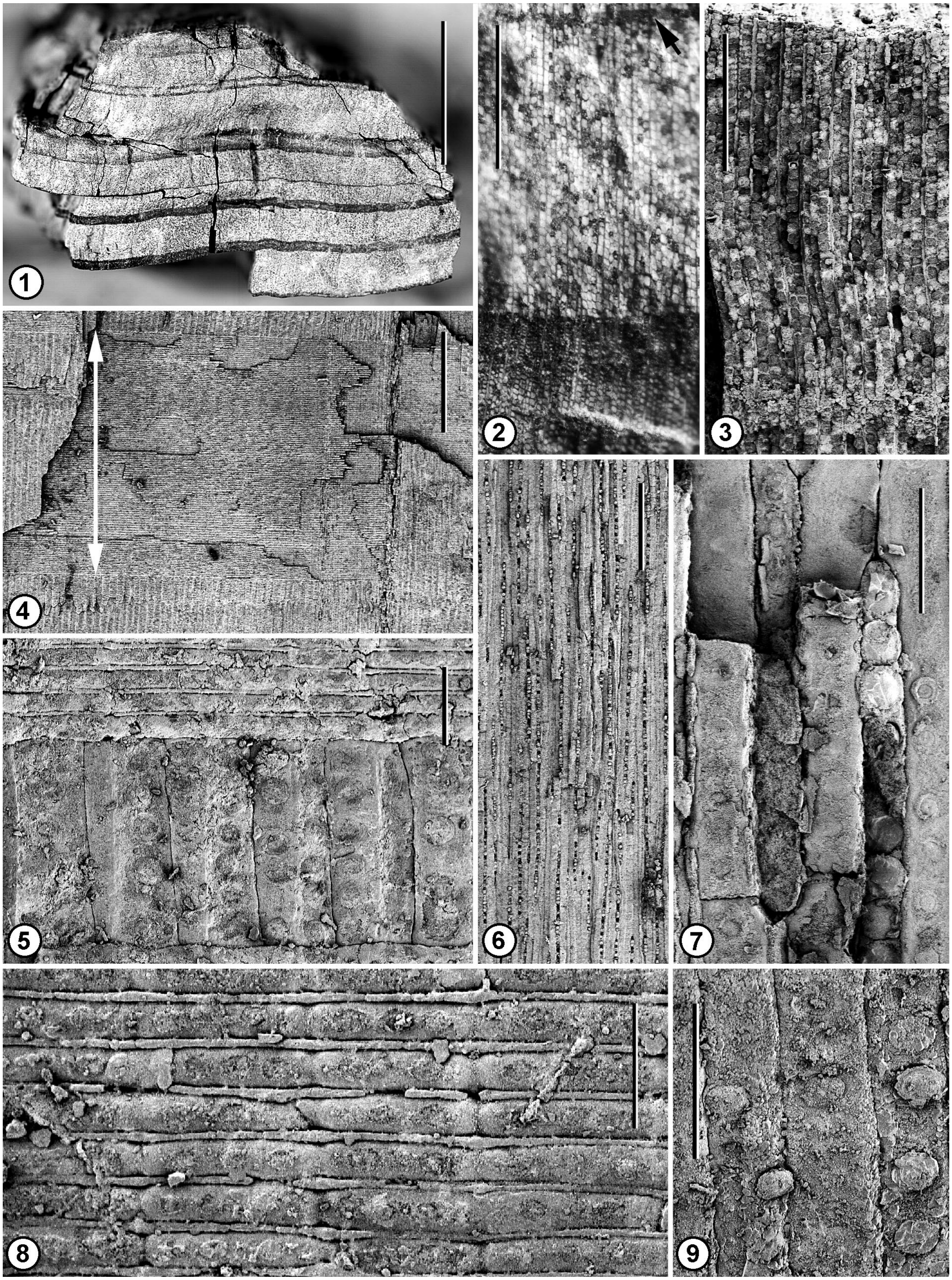
Material at Munce's Hill consists primarily of compressions, but one upright, permineralized trunk crops out at the face of the road cut. This stump is ca. 30 cm in diameter at the exposed upper end. Numerous concentric light bands and alternating narrower dark bands are present in end views of the wood (fig. 1.1), indicating the presence of growth rings. The thickness of the light bands is highly variable (fig. 1.1), ranging up to 6 mm. The dark bands are also of variable thickness (figs. 1.1–1.3). Dark bands comprise cells that typically diminish in radial diameter toward the periphery of the stem (figs. 1.2, 1.3), as is characteristic of annual growth rings. The centrifugal change from large cells in the light bands to small cells of the dark bands is gradual in some rings (fig. 1.2, at bottom; fig. 1.3, at top) and abrupt in others (fig. 1.2, at arrow near top; fig. 1.3, near bottom) but is always abrupt at the inner margin of a light band. This suggests that rate of growth toward the end of a growth period was highly variable but that initiation of a new growth period was characteristically abrupt. Some dark bands have small cells at both the inner and outer margins and cell sizes that intergrade to larger diameters toward the center of the dark band. Other dark bands consist of as few as two or three radial rows of small cells. These features suggest that some of the growth rings are traumatic, rather than annual, and may have resulted from fluctuations in water availability during a single growing season.

Features of the wood have been determined from fractured surfaces. In these views, leaching of the silicate matrix between the cell walls and the cell lumens is clearly evident (e.g., fig. 1.8), and the fractured surfaces typically represent either casts of the cell lumens or molds of the degraded inner surfaces of the cell walls. The wood is made up of tracheids and interspersed parenchymatous rays (figs. 1.2–1.9). No evidence of resin canals, xylem parenchyma, or ray tracheids has been found.

Tracheids in the "spring wood" (i.e., light bands; fig. 1.2) are typically rectangular-hexagonal in cross sections (figs. 1.2, 1.3), ranging from 27 to 55 μm in maximum tangential diameter. Those in the narrower and darker bands of "summer wood" are more rectangular, with rounded corners (figs. 1.2, 1.3), and these cells diminish to as little as 18 μm in radial dimension at the periphery of a growth increment (fig. 1.2, near bottom; fig. 1.3, at top). Pitting typically consists of relatively crowded, opposite, biseriate, bordered pits (fig. 1.5) on radial walls of tracheids, but uniseriate pits are also found in some areas of the radial walls on the smaller tracheids (fig. 1.9). Most pits are circular, but some are oval (figs. 1.5, 1.9). Pits measure 17–25 μm in diameter. Circular bordered pits also occur on tangential tracheid walls, where they are frequent, but not crowded, and uniseriate (fig. 1.7). Pits on the tangential tracheid walls are somewhat smaller than on the radial walls and measure 11–15 μm.

Rays are uniseriate and may be extremely tall, ranging from 10 to 113 cells high (figs. 1.4, 1.6). The mean height of 25 rays counted is 49.4 cells. Ray cells are radially elongated and rectangular to trapezoidal in radial sections, with end walls that are usually transverse and, less often, oblique (fig. 1.8). Fractured ray cells in tangential views are nearly round (fig. 1.7) and 18–22 μm in diameter. Cross-field pitting is taxodioid, with a single row of round-oval, degraded pits preserved on radial walls of the ray cells (fig. 1.8).

Compressed branches of *M. foxii* up to 1.5 m long have been exposed on the same bedding planes as *in situ* specimens of the filicalean fern *Onoclea sensibilis* (figs. 2.1, 2.2; Rothwell and Stockey 1991). One large specimen consists of a branch 0.7 m long and 2 cm wide at the base, with opposite branches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10 cm from the proximal end and an ovulate cone attached to a terminal branch near the distal end (figs. 2, 3). A second ovulate cone is preserved slightly distal to the attached cone (fig. 2.1, at farthest right). It also terminates a branch, but possible attachment of this branch to the larger system is obscured under the matrix (fig. 2.2). Both ovulate cones conform to the characters of *M. foxii* that are described below, and both fall within the ranges of size variation for the species (described below).

Leafy Shoots

Leafy shoots of *Metasequoia* show a wide range of growth variation. In *M. glyptostroboides* the largest leafy branches are compound, consisting of two orders of branching (fig. 3.1). Leaves of the penultimate order are typically larger than those of the ultimate order, and penultimate leaves are separated by longer internodes than those on ultimate branches (fig. 3.1). Somewhat smaller branches also have large leaves but are unbranched and display shorter internodes. The smallest branches are equivalent to the ultimate branches of the compound shoots, with relatively short leaves and internodes. These different leafy branches have been referred to as long shoots and short shoots by some authors (e.g., Florin 1952; Schwarz and Weide 1962; Böcher 1964), but they are not equivalent to the long and short shoots of other conifers (Liu et al. 1999). Our observations of living trees at Ohio University and the University of Alberta reveal that these different shoot morphologies intergrade completely, as suggested by Böcher (1964).

A similar range of variation in leafy shoot morphology is present among specimens of *M. foxii* (figs. 4.3–4.7) but was not initially recognized (Falder et al. 1999) because of the small size of the rocks on which most of our specimens are preserved. Leaves of compound specimens appear opposite/decussate. As in the other species of the genus (e.g., figs. 4.1, 4.2), they are decurrent and twist at the level of divergence to form a single plane (cf. figs. 4.3, 4.4). Twisting of the internodes also contributes to the planar form of the branches (Böcher 1964). Leaves on penultimate branches are distinctly larger than those on the ultimate shoots (figs. 4.3, 7.13). Unbranched shoots with large leaves are also sometimes planar (fig. 4.6), but on other specimens the leaves partly retain their decussate orientation (fig. 4.4). Simple shoots with the smallest leaves have short internodes (figs. 4.5, 4.7) and can be distinguished from ultimate branches of compound shoots by a swollen base (cf. figs. 4.3, 4.5) that results from bud scales remaining attached at the base of all *Metasequoia* branches that grew from a dormant bud (figs. 4.4, 4.5). This latter feature is characteristic of deciduous shoots of the other *Metasequoia* species and reveals that *M. foxii* had a proleptic growth pattern that is similar to that of *M. glyptostroboides*. In some specimens the pair of leaves immediately distal to the bud scales is much shorter than the remainder of the leaves on the shoot (fig. 4.4, at arrows), but in most specimens the basal foliar leaves are similar to others near the base of the branch (fig. 4.5).

Phyllome

Metasequoia foxii produces a wide range of leaf morphologies in different parts of the phyllome and in this respect is similar to *M. glyptostroboides* (Böcher 1964). The various leaf types range in shape from deltoid to elliptical to linear depending on their position on the plant (figs. 4.2–4.8, 5.1–5.5), and microsporophylls display a terete shank and spatulate distal lamina (figs. 6.4–6.8). Cotyledons (fig. 5.1), seedling stem leaves (figs. 5.1–5.3), seedling branch leaves (fig. 5.3; Falder 1999), leaves on penultimate leafy shoots (figs. 4.3, 7.13), leaves on ultimate leafy shoots (figs. 3.2–3.8; figs. 4.4, 4.5; fig. 6.13), leaves on penultimate branches of shoots that produce pollen cones (figs. 5.1–5.3), bud scales at the bases of ultimate branches (figs. 4.4, 4.5) and pollen cones (figs. 5.1–5.4), and microsporophylls (figs. 5.4–5.8) all have characteristic ranges of variation in length, width, and morphology of the apex. Each displays smooth margins and a single midvein (figs. 3.8, 4.1–4.3). Cotyledons (fig. 4.1), seedling stem leaves (figs. 4.1, 4.3), leaves subtending pollen cones (figs. 5.1, 5.2), leaves subtending ovulate cones (fig. 6.4, at arrowheads), and bud scales (figs. 5.1–5.4) are oriented with their adaxial surface parallel to the surface of the stem. As in the living *M. glyptostroboides* (figs. 4.1, 4.2), leaves on seedling branches (fig. 5.3) and ultimate foliar shoots of *M. foxii* are decurrent and twist at the level of divergence from the shoot to form a planar branch (e.g., figs. 4.3–4.8, 5.3–5.5). However, in some specimens of *M. foxii* the degree of twisting was apparently inadequate to bring all of the leaves into the same plane (fig. 4.4). Except for the deltoid bud scales, leaves expand in width immediately distal to the level of divergence from the stem (e.g., figs.

Fig. 1 Permineralized wood. Fig. 1.1, Fragment of wood showing growth rings on transverse face. P616A ×2.3; bar = 1 cm. Fig. 1.2, Split surface showing cross section of wood, with periphery at top. Thick zone of summer wood from one growth increment (at base) below and complete growth ring above. Note gradual reduction in tracheid size toward end of growth increment in broad zone of summer wood (at base). Complete growth increment is terminated by narrow zone of summer wood (at arrow) only two to three cells thick. P616A ×25; bar = 1 mm. Fig. 1.3, SEM of fractured wood surface showing cross section with uniseriate rays separating files of tracheids. Note smaller tracheids that form narrow, ill-defined zone of summer wood near base and gradual reduction of tracheid size in broader zone of summer wood at top. P616B ×0.45; bar = 0.5 mm. Fig. 1.4, SEM of fractured surface showing radial view of wood. Double-headed arrow indicates vertical extent of an extremely tall ray. P616C ×17; bar = 1 mm. Fig. 1.5, SEM of radial surface showing tracheids with opposite, biseriate, circular/oval bordered pits on short segments of tracheids that pass below two rays. P616C ×270; bar = 50 μm. Fig. 1.6, SEM of fractured tangential wood surface showing height of uniseriate rays between groups of one to four tracheids. P616D ×30; bar = 0.5 mm. Fig. 1.7, Closer SEM view showing ray cells in cross section and scattered circular bordered pits on tangential walls of tracheids. P616C ×430; bar = 50 μm. Fig. 1.8, SEM view of ray cells in radial section showing transverse and oblique end walls and uniseriate cross-field pitting. Note how degradation of cell walls facilitates splitting between wall and lumen of cells. P616C ×535; bar = 50 μm. Fig. 1.9, Radial view of tracheid walls showing bordered pits. P616C ×520; bar = 50 μm.

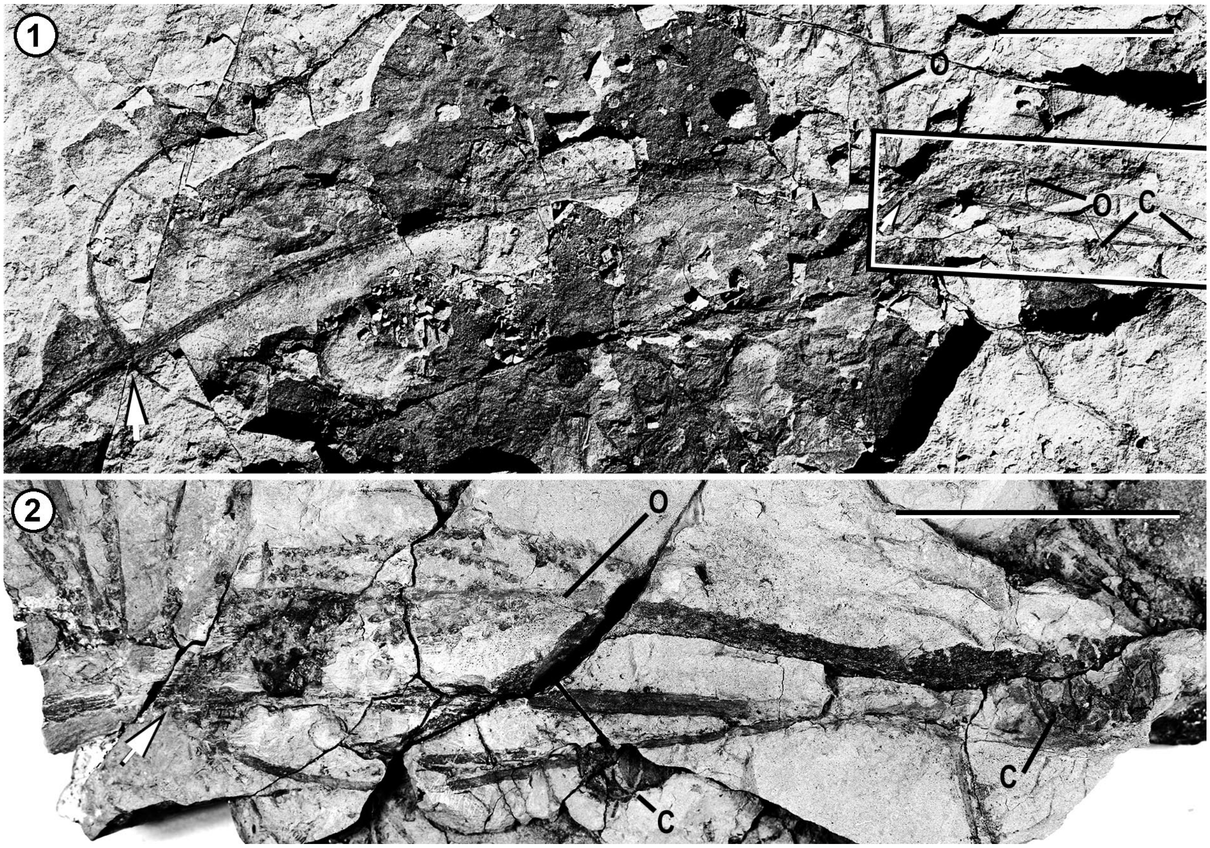

Fig. 2 *Metasequoia foxii* sp. nov. Fig. 2.1, Large stem with opposite branching (at arrows) and cones (at C) exposed on bedding plane along with *in situ* fertile spikes of *Onoclea* (at O). Apical region (in rectangle at right) with attached cone collected and figured below as fig. 2.2; bar = 10 cm. Fig. 2.2, Apical segment of branching specimen in fig. 2.1 showing two ovulate cones (C), one of which (at center) is attached (at arrow) by long stalk. Note associated fertile spike of *Onoclea* (O). S57,272 ×0.75; bar = 5 cm.

4.1–4.3), and the basal twist further accentuates the narrowness of leaf attachment on some branches (e.g., fig. 5.4). As revealed by the living species (fig. 4.2), horizontally oblique dark lines on the stems of the fossils represent margins of the decurrent leaf bases that reflect internodal twisting of the stems (figs. 4.4, 4.5; fig. 5.5).

Cotyledons are 8–21 mm long (mean = 14.3 mm) and 1.2–3.0 mm wide (mean = 2.2 mm), with more or less parallel sides and a rounded or bluntly pointed tip (fig. 5.1; Falder 1999; Falder et al. 1999). They have length : width ratios in the range of 4–7 : 1. Most cotyledons diminish in width at the base and display a prominent midvein (fig. 5.1).

Leaves on the stems of seedlings are 3–14 mm long (mean = 7.3 mm) and 0.8–2.0 mm wide (mean = 1.2 mm; figs. 5.1–5.3). Stem leaves are more elliptical than the cotyledons, gently tapering toward the base and terminating in a rounded or bluntly pointed tip (figs. 5.1–5.3; Falder 1999; Falder et al. 1999). Their length : width ratios are usually in the range of 4–6 : 1. Leaves on branches of the seedlings (fig. 5.3) are quite similar to those on the stems, measuring 3–11 mm long and showing a rounded to bluntly pointed apex. However, because these leaves twist to produce a planar branch, they appear to be much narrower at the level of divergence from the stem (fig. 5.3) than the stem leaves.

Leaves on penultimate deciduous branches (figs. 4.3, 7.13) are the largest of the phyllome (fig. 5.1–5.5), ranging up to 43 mm long and 4.5 mm wide (table 1). They typically have parallel margins and apices that vary from bluntly pointed to mucronate (figs. 4.6, 5.5), and length : width ratios range up to 16 : 1. Leaves on some ultimate branches approach the length and shape of those on the penultimate branches, but internodes are shorter (figs. 4.6, 5.5). Other ultimate branches have leaves that are similar in morphology to those on the ultimate branches of compound shoots (cf. figs. 4.3, 4.5), being only about half the length of leaves on penultimate branches. The shorter leaves have length : width ratios that typically range from 3.8 : 1 to 5.5 : 1. Leaves toward the end of the spectrum with the lowest length : width ratios have convex lateral margins (fig. 4.7), making the overall leaf shape elliptical. Except for leaves at shoot apices, which are shorter than the rest (figs. 4.3, 4.6), leaves on the ultimate branches tend to fall into one of these two categories. Shoots with intermediate-length leaves are hard to find.

Leaves that subtend pollen cones (figs. 6.1, 6.3) and those on ultimate shoots below ovulate cones (fig. 7.4) appear most similar to those on seedling stems, but such leaves are either incompletely preserved or apparently are abscised prior to fossilization (figs. 6.2, 7.1). As in living *M. glyptostroboides*, long

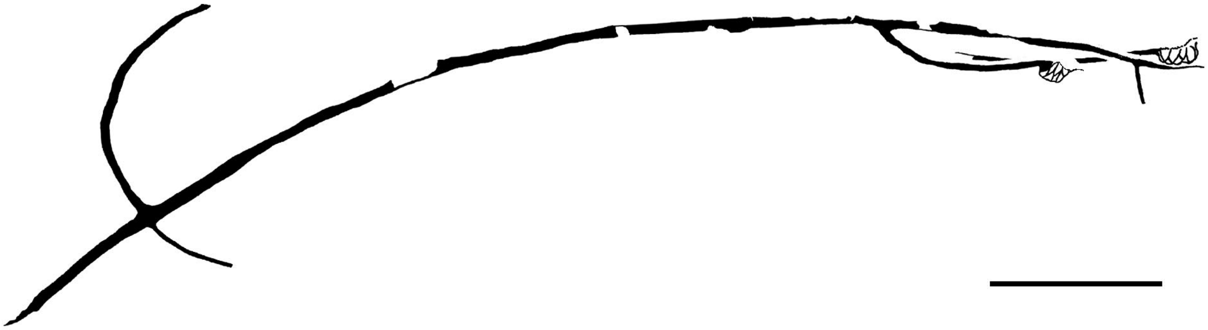

Fig. 3 *Metasequoia foxii* sp. nov. Line diagram of specimen in fig. 2. Branches are preserved at three levels, basal level showing opposite arrangement. One branch bears terminal cone, and a second cone-bearing branch occurs at the same level. Bar = 10 cm.

internodes and early leaf abscission leave ovulate terminal stems with a naked appearance (figs. 7.1, 7.6, 7.7).

Bud scales that remain attached to leafy branches and to ultimate ovulate branches, and bud scales at the bases of pollen cones, are deltoid with pointed tips. These typically are broadly attached, tightly appressed, and imbricate, sheathing the shoot within (figs. 4.4, 4.5; figs. 6.1–6.3). The exact shape of most bud scales is difficult to distinguish because many buds are split adjacent to the shoot axis (figs. 4.4, 4.5), and other bud scales are packed together tightly (figs. 6.1–6.3). Those of the pollen cones show best (figs. 6.1–6.4). Each has a sharply pointed or apiculate tip (fig. 6.4). Due to imbrication and incomplete preservation, bud scales often appear to be narrower than they actually are (e.g., fig. 6.4). However, one bud scale with a frayed and missing apex (at the base of the specimen in fig. 6.4) reveals that they extend around nearly half the circumference of the cone at the point of attachment. Bud scales have a length : width ratio of ca. 1.5–2.0 : 1.

Pollen Cones

Pollen cones are borne in opposite/decussate pairs in the axils of virtually all leaves of specialized branches (figs. 6.1–6.3). Some consist of buds that occur in the axils of decussately arranged leaves with long internodes, but most have the fertile region of the cone extended distal to the basal bud scales (figs. 6.1–6.5). By comparison to pollen cones of *M. glyptostroboides*, where internodal elongation extends the sporophylls beyond the basal bud scales at maturity (Sterling 1949), these latter cones are interpreted to be relatively mature or senescent. Mature pollen cones of *M. foxii* measure 3–8 mm long and 2–5 mm in maximum diameter distal to the basal bud scales (figs. 6.1–6.4). Sporophylls appear opposite/decussate in arrangement (fig. 6.5), as they are in living specimens of *M. glyptostroboides* (Sterling 1949). The number of sporophylls is difficult to count from compression specimens, but if the number of sporophylls seen in an external view is approximately half the total, then the number can be estimated at 18–24.

Each microsporophyll consists of a basal shank that is attached at ca. 90° to the cone axis (fig. 6.5) and is terete in cross section (fig. 6.7, at *S*). Sporophylls bend distally at the cone margin (fig. 6.5) to form a spatulate distal lamina (figs. 6.6, 6.7). Also, as in the living species (Sterling 1949), three pollen sacs are attached abaxially and laterally to the sporophyll shank (figs. 6.6–6.8) just proximal to a spatulate distal lamina (figs 6.6, 6.7). Pollen sacs are oval to elliptical (figs. 6.6–6.8), measuring ca. 0.5–1 mm in maximum dimension.

Pollen

We have been able to recover only a small number of pollen grains from the pollen sacs, but as is characteristic of many taxodioid conifers, *M. foxii* pollen is nonsaccate and subspheroidal (figs. 6.9, 6.10). Grains are characteristically collapsed and folded (fig. 6.9), making identification of an apical papilla difficult. However, this feature appears to be present in at least one specimen. Only six grains could be measured, and these compare favorably with both *M. glyptostroboides* and *M. milleri*, being 17.5–24 μm in diameter. The *M. foxii* pollen has a verrucate surface and numerous orbicules (fig. 6.11), as do the other *Metasequoia* species (Rothwell and Basinger 1979). Slightly different sculpturing features on proximal and distal surfaces, like those of *M. milleri*, have not been detected in the small population of *M. foxii* pollen available for study.

Ovulate Cones

Ovulate cones are quite distinctive and clearly distinguish *M. foxii* from other species of *Metasequoia*. Cones range from globose (fig. 7.7) to cylindrical (figs. 7.2, 7.3), measuring 10–35 mm long and 11–22 mm in maximum diameter. They consist of cone scale complexes attached to a central axis (figs. 7.1–7.7). In agreement with other species of the genus (fig. 7.6), some cones are quadrangular in cross section (fig. 7.12) and show vertical rows of cone scale complexes in surface views (figs. 7.1, 7.3, 7.8). This led us to initially interpret cone scale arrangement as decussate (Falder et al. 1999), like other species of *Metasequoia*. However, the rows of cone scale complexes are typically angled to either the left (figs. 7.2, 7.8) or the right in *M. foxii*, rather than being vertical like the ovulate cones of *M. glyptostroboides* (fig. 7.6) and the other fossil species. Numerous cones are pentangular in cross section (fig.

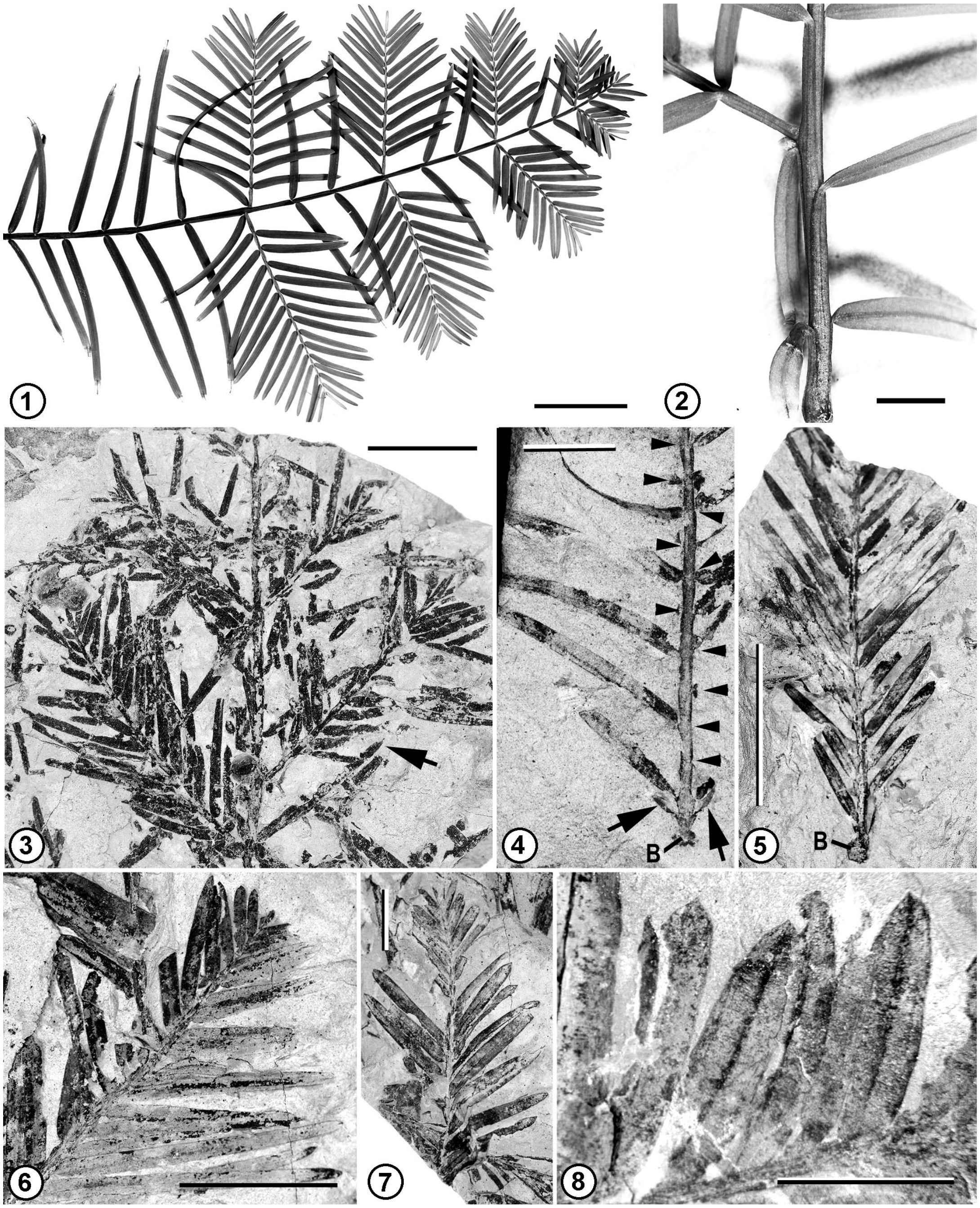

Fig. 4 *Metasequoia glyptostroboides* (fig. 4.1) and *M. foxii* sp. nov. (figs. 4.2–4.8). Fig. 4.1, Deciduous shoot of living plant with two orders of branching. First-order branch bears large leaves that diminish in size at apex. Second-order branches are borne oppositely in axils of leaves and bear smaller leaves. All leaves occur in decussate arrangement and twist at level of divergence from stem to produce a planar branch. Magnification ×0.75; bar = 2 cm. Fig. 4.2, Close-up of stem from living species showing a deciduous shoot with two orders of branching. Note dark vertical lines produced by margins of decurrent leaves and twisting of leaf bases at level of divergence. Note also that the base of secondary branch has no bud scales on these compound deciduous shoots. Magnification ×2.3; bar = 5 mm. Fig. 4.3, Shoot showing two orders of branching with larger leaves on penultimate branch and oppositely arranged ultimate branches with smaller leaves. One larger leaf shows attachment on right near base of shoot (arrow). S29,642 ×0.9; bar = 2 cm. Fig. 4.4, Simple deciduous shoot with large leaves that show decussate arrangement. Irregular basal swelling (at *B*) marks the position of bud scales. Positions of nodes marked by arrow points. Basal pair of bractlike leaves (at arrows) subtend larger foliar leaves. Leaves at every second node are preserved more or less on bedding plane, whereas those at alternating nodes are attached at right angles to bedding plane and either appear to be absent or are represented by only a fragment of leaf base. S19,996B ×0.78; bar = 2 cm. Fig. 4.5, Simple deciduous shoot with remnants of basal bud and shorter leaves than specimen in fig. 4.4. S28,086 ×1.35; bar = 2 cm. Fig. 4.6, Specimen with large leaves that shows characteristic reduction in leaf length toward apex of shoot. S19,944 ×1.5; bar = 2 cm. Fig. 4.7, Shoot with relatively small leaves with pointed apices. Note smaller, apparently immature leaves at apex. S19,671 ×0.5; bar = 2 cm. Fig. 4.8, Close-up of shoot with relatively short leaves showing midvein and characteristic leaf tips. S29,651 × 5.7; bar = 5 mm.

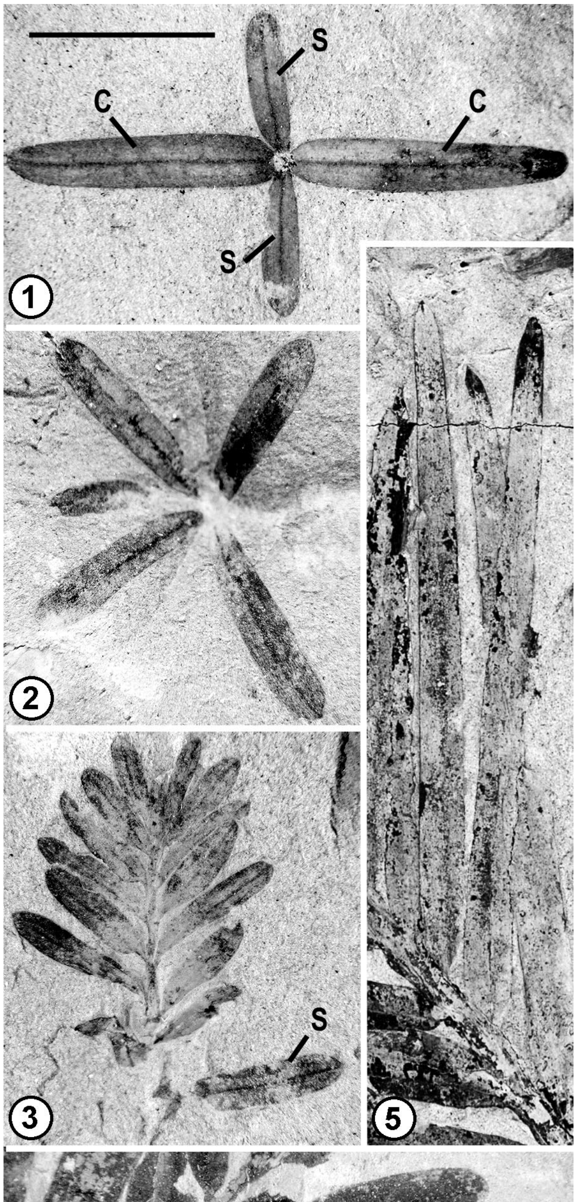

Fig. 5 *Metasequoia foxii* sp. nov. Leaf variation in seedlings and branches from more mature plants. All figs. × 4.0; scale = 1 cm. Fig. 5.1, *In situ* seedling near level of cotyledonary node, showing stem in cross section, with attached cotyledons (*C*) and basal pair of stem leaves (*S*). Note rounded and bluntly pointed apices. S51,651A. Fig. 5.2, *In situ* seedling showing leaves diverging from stem in decussate arrangement. Note bluntly pointed leaf apices. S28,160. Fig. 5.3, *In situ* seedling showing one leaf of stem (*S*) and lateral branch with decussate leaves bent into single plane. Note pointed leaf apices. S28,143. Fig. 5.4, Branch with relatively short leaves and short internodes. S19,853. Fig. 5.5, Branch with relatively long leaves with pointed apices. S19,944.

7.11) and display five rows of cone scale complexes (fig. 7.8), suggesting that cone scale arrangement is typically helical in *M. foxii*, an arrangement that is verified by apical cone views (figs. 7.9, 7.10). As in the other species of *Metasequoia* (e.g., fig. 7.6), cone scale complexes of *M. foxii* are peltate and horizontally elongated. Individual cone scale complexes range from 6 to 16 mm wide with pointed ends, and they show a prominent horizontally oriented central depression (figs. 7.1–7.4, 7.8). In section views the cone scales are 4–9 mm long, broadest at the cone margin, and they narrow conspicuously toward the axis (figs. 7.2, 7.5, 7.7, 7.11, 7.12).

Seeds

Seeds of *M. foxii* are extremely abundant and are generally similar to those of other *Metasequoia* species. They are oval to cordate, with a broad symmetrical wing in the major plane and a narrow elliptical body (figs. 7.13, 7.14; Falder et al. 1999). Individual seeds range from 3.5 to 9.0 mm long and from 2.75 to 7.0 mm wide. Most are widest in the midregion (figs. 7.13, 7.14), but a few broaden toward the chalaza (fig. 7.13, near bottom center). Cordate specimens display a chalazal notch that represents the point of attachment to the cone scale complex. The wing is narrowest at the micropylar end, where the seed body approaches the margin of the wing. A few specimens show evidence of germination (Falder et al. 1999), and in one seed a narrow curved radicle extends from the micropylar end (fig. 7.14, at arrow).

Seedlings

Specimens of *M. foxii* have been described earlier as the first evidence for fossilized taxodioid conifer seedlings (Falder et al. 1999), and their pattern of development will be the subject of another study. Therefore, only a summary of seedling structure is presented here. Some seedlings consist of a root, hypocotyl, and cotyledons, and virtually all are preserved upright in growth position. Of the 1850 seedlings with this structure, 1831 display two cotyledons, and the other 19 have three. Cotyledons measure 8–21 mm long (mean = 14.3 mm) and 1.2–3 mm wide (mean = 2.3 mm) and are consistently spread out onto the bedding plane (fig. 5.1). Most seedlings have stem leaves distal to the cotyledons (fig. 5.1) that diverge in a radial fashion (fig. 5.2). Stem leaves measure 3–13 mm long (mean = 7.3 mm) and have a maximum width of 0.6–2.0 mm (mean = 1.2 mm). Other seedlings show lateral branches that diverge either singly (fig. 5.3) or oppositely (Falder 1999; Falder et al. 1999). As with the deciduous shoots described above, leaves of the seedling branches twist at the level of divergence to conform to a single plane (fig. 5.3).

Discussion

Growth Form of *Metasequoia foxii*

Only one species of compressed taxodioid conifers is present at the Munce's Hill locality, and the *in situ* permineralized conifer trunk has characteristic taxodioid wood that is similar to that of living *Metasequoia* in most characters. However, as discussed below, wood rays of *M. foxii* are exceptionally tall,

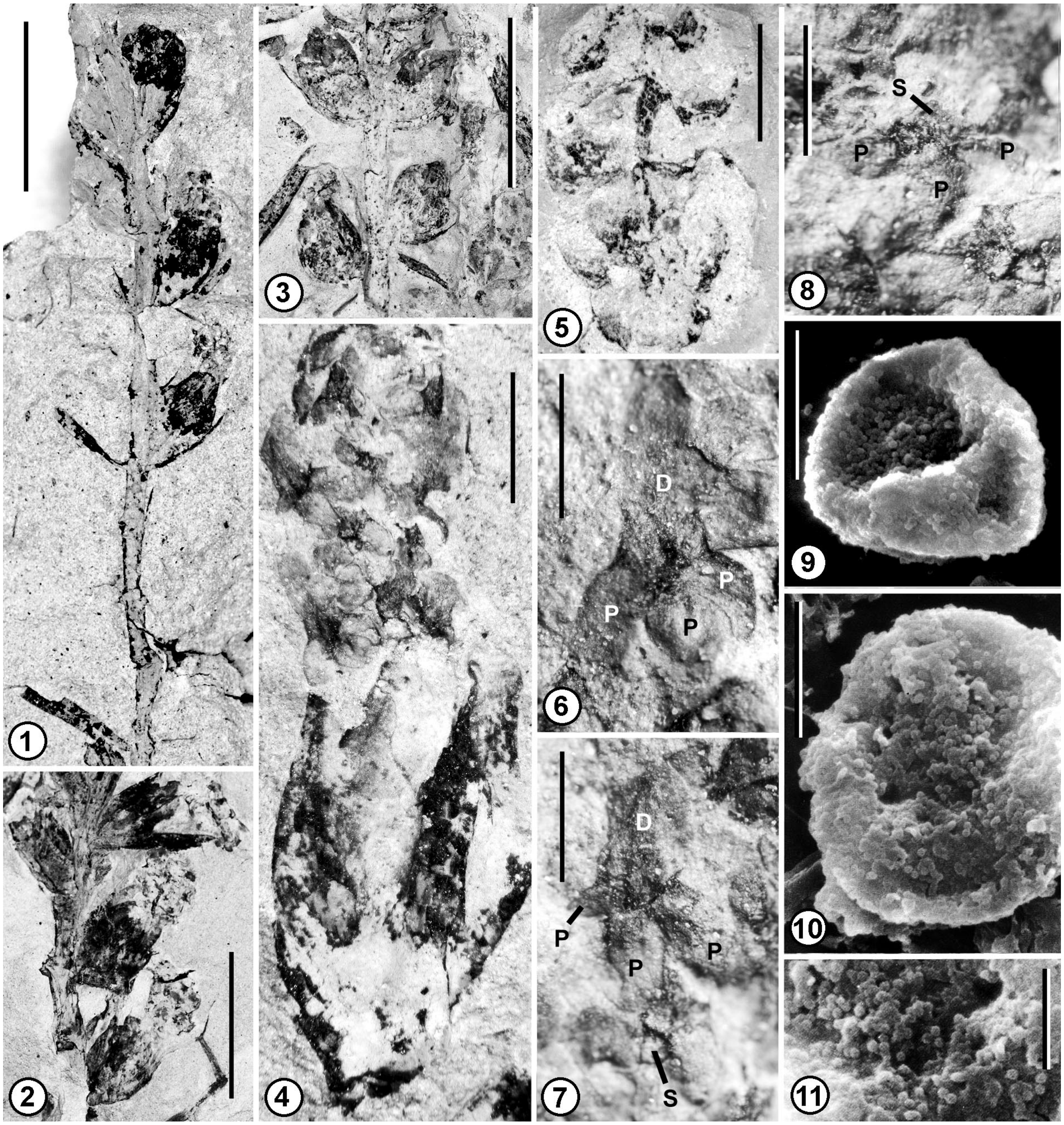

Fig. 6 *Metasequoia foxii* sp. nov. Pollen cones and pollen. Fig. 6.1, Shoot with pollen cones in axils of opposite/decussate leaves. S36,516 ×2.5; bar = 1 cm. Fig. 6.2, Shoot with several attached pollen cones with fertile zones extended out of basal bud scales. S28,082 ×2.4; bar = 1 cm. Fig. 6.3, Shoot bearing relatively mature pollen cones in axils of opposite/decussate leaves. Some cones have extended fertile regions, while others apparently do not. S19,955 ×2.5; bar = 1 cm. Fig. 6.4, Pollen cone with fertile zone extended beyond pointed bud scales. Imbricating makes scales appear narrower than they actually are. Note dark sporophyll shanks and distal laminae in apical fertile region. S28,081B ×10; bar = 0.2 mm. Fig. 6.5, Isolated fertile zone of pollen cone showing opposite attachment of sporophylls to central axis. S36,520 ×9; bar = 2 mm. Fig. 6.6, Microsporophyll from lower left in fertile zone of fig. 6.5 showing three pollen sacs (*P*) adaxially attached below distal lamina (*D*). S36,520 ×22; bar = 0.5 mm. Fig. 6.7, Enlargement of specimen in fig. 6.5 showing distal lamina (*D*) and three pollen sacs (*P*) of upper sporophyll and angular shank (*S*) of second sporophyll below. S36,520 ×20; bar = 0.5 mm. Fig. 6.8, Enlargement of specimen in fig. 6.5 showing cross section of microsporophyll with three pollen sacs (*P*) attached to sporophyll shank (*S*). S36,520 ×20; bar = 0.5 mm. Fig. 6.9, SEM of collapsed subspheroidal pollen grain; ×2230; bar = 10 μm. Fig. 6.10, Pollen grain with possible papilla; ×2100; bar = 10 μm. Fig. 6.11, Enlargement of pollen grain in fig. 6.10 showing orbicules on verrucate surface; ×3,000; bar = 5 μm.

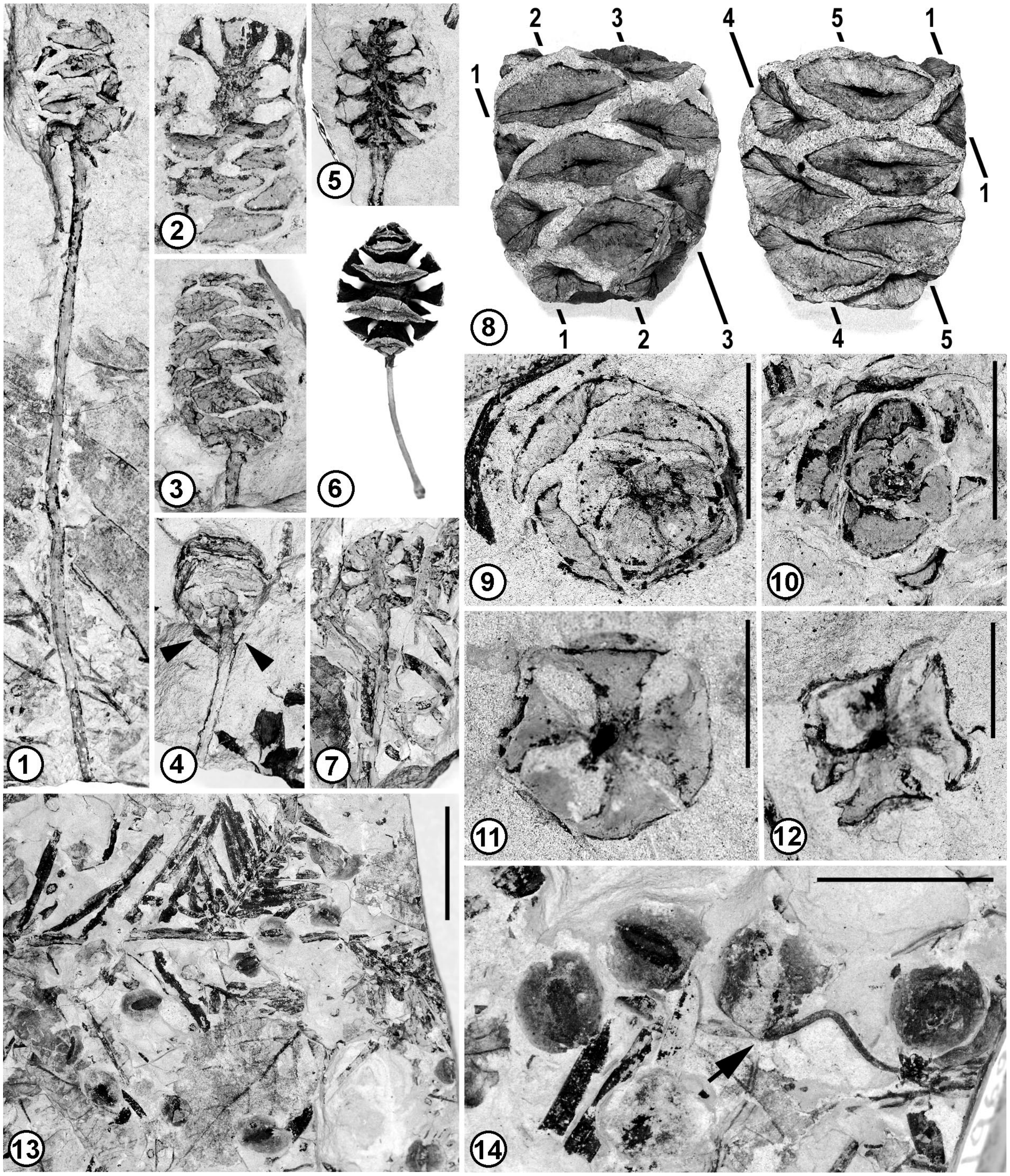

Fig. 7 Ovulate cones of *M. foxii* gen. et sp. nov. (figs. 7.1–7.5, 7.7–7.12) and *M. glyptostroboides* (fig. 7.6) and ovules dispersed among other *M. foxii* remains on rock surfaces (figs. 7.13, 7.14). Figs. 7.1–7.7 ×1.0. Fig. 7.1, Holotype, cone attached to long stem with no visible leaves. Note obliquely vertical row of cone scale complexes. S28,476. Fig. 7.2, Large cone exposed in radial section in apical region and at surface in basal region. S36,266. Fig. 7.3, Surface view of large cone with obliquely vertical row of cone scale complexes. S20,197. Fig. 7.4, Oblique basal view of attached cone showing opposite pair of subtending leaves (arrow points). S28,586. Fig. 7.5, Radial section of cone showing shape of cone scale complexes in this view. S29,040. Fig. 7.6, Longitudinal view of attached *M. glyptostroboides* ovulate cone for comparison to fossils. Fig. 7.7, Longitudinal section of small attached cone. S36,409. Fig. 7.8, Front and back views of ovulate cone cast showing five obliquely vertical rows of ovuliferous cone scale complexes. Each row is identified by a diagonal line that is numbered at top and bottom. Part of row 1 is seen at left of front, and the rest is present on back (at right). S57,274 ×2.0. Fig. 7.9, Oblique view of cone apex showing helical arrangement of cone scale complexes. S36,322A ×2.5; bar = 1 cm. Fig. 7.10, Apical view showing helical arrangement of cone scale complexes. S36,409 ×2.4; bar = 1 cm. Fig. 7.11, Cross section through cone with helical arrangement, showing five rows of cone scale complexes. S28,548 ×2.5; bar = 1 cm. Fig. 7.12, Cross section of cone with decussate arrangement, showing four rows of cone scale complexes. S20,227 ×18; bar = 1 cm. Fig. 7.13, Rock surface showing plant debris including shoot and several dispersed seeds of *M. foxii*. Because of the prominent wing, seeds are elliptical or cordate and nearly as broad as they are long. S19,714 ×0.9; bar = 2 cm. Fig. 7.14, Four dispersed seeds of *M. foxii*. Specimen at right center was germinating, showing flexuous root (arrow) extending from the micropyle. Seed at left shows basal cleft. S19,690 ×2.8; bar = 2 cm.

Table 1

Characters of Species of *Metasequoia*

	M. glyptostroboides	*M. foxii*	*M. occidentalis*	*M. milleri*
Wood:				
Ray height (number of cells)	≤20+	**≤113**	?	≤80
Leaf:				
Attachment (O = opposite, S = subopposite)	O, S	O, S	O, S	O
Arrangement (D = decussate)	D	D	D	D
Shape (O = ovate, L = linear)	L	O, L	O, L	O, L
Tip shape (R = rounded, B = bluntly pointed, M = mucronate)	B	R, B, M	R, M	B
Length (mm)	8–50	2–43	6–25	?
Width (mm)	1.0–3.0	0.5–**4.5**	1.0–2.0	0.7–1.5
Pollen cone:				
Shape (G = globose, O = ovate)	G	G, O	G, O	O
Sporophyll arrangement (D = decussate, H = helical [at inception])	D	D	D	H
Length (mm)	2.0–4.3	3–**8**	1–5	1–3
Width (mm)	1.9–3.5	**2–5**	0.5–4	1.2–2.9
Number of sporophylls	30–40	**18–24**	?	30
Number of sporangia/sporophylls	2–3	3	?	3
Mature pollen sacs exposed by relaxing of bud scales (R) and elongation of axis (E)	E	E	E	R
Pollen:				
Papilla (P = present)	P	?	P	P
Pollen diameter (μm)	19.0–32.3	17.5–24.0	18–38	19–27
Ovulate cone:				
Shape (G = globose, O = ovoid, C = cylindrical)	G, O	G, C, O	G, O	G, C
Length (mm)	6–25	10–35	11–40	≤25
Width (mm)	6–25	11–22	6–34	≤17
Scale arrangement (D = decussate, H = helical)	D	(D), **H**	D	D
Scale length (mm)	5–17	4–9	6–12	5–6
Scale width (mm)	2–15	6–16	7–15	3–12
Seed:				
Length (mm)	4–7	3.5–**9.0**	≤5	5
Width (mm)	3–6	2.75–7.0	≤4	3–4
Shape (C = cordate, O = ovoid)	C, O	C, O	C, O	?
Widest point (C = at center, B = toward base)	C	C, (B)	C, B	?
Seedling:				
Number of cotyledons	2, (3, 4)	2, (3)	?	?
Cotyledon length (mm)	8–19	8–21	?	?
Cotyledon width (mm)	1.1–2.5	1.2–3.0	?	?
Length of branches (mm)	32–87	**3–21**	?	?
Length of stem leaves (mm)	8–20	**3–13**	?	?

Note. Characters that, in combination, are diagnostic of *M. foxii* are in boldface type. All characters within parentheses occur at low frequencies.

ranging to more than 110 cells high. While the wood of the trunk appears to be distinctive at the species level, it is quite similar to that of *M. occidentalis*, *M. milleri*, and specimens described as *M. siberica* Shilkina (Gorbunov and Shilkina 1972) in other features. For this reason, and because *M. foxii* is virtually the only species of compressed conifers at the Munce's Hill locality, we interpret the permineralized trunk to be the base of the stem of *M. foxii*. If this interpretation is correct, then *M. foxii* was a large tree like the living species *M. glyptostroboides*.

Tangential diameter of the tracheids of *M. foxii* further supports this interpretation. Carlquist (1975) has documented that in living conifers tracheid length is directly related to stem height or branch size. We also know that tangential diameter of conifer tracheids increases with increase in tracheid length, the tangential diameters of tracheids increasing outward in the wood (Bannan 1965). Therefore, maximum tangential diameter of tracheids in a stem is a rough indicator of stem height. Tracheids of *M. glyptostroboides* measure 30–40 μm in tangential diameter, whereas those of *M. foxii* are up to 55 μm. While we cannot determine the maximum growth potential for M. *foxii* from the information available, these data suggest that the plant grew taller than the living *M. glyptostroboides*.

All well-known species of *Metasequoia* are deciduous plants that abscise individual leaves, simple leafy shoots, and compound leafy shoots. Senescent pollen and ovulate cones are abscised from *M. glyptostroboides*, and occasionally larger branches are shed as well. In *M. glyptostroboides*, immature branches are enclosed in buds that remain dormant until the next growing season. Vegetative shoots grow from these buds and are abscised at the end of the growing season, with the bud scales remaining attached to the base of the abscised branch. The presence of bud scales at the base of nearly all dispersed shoots at Munce's Hill and Gao Mine and the occurrence of vegetative shoots in dense mats at both localities strongly suggest that *M. foxii* was deciduous also.

Comparison to Currently Recognized Species of Metasequoia

An examination of the characters for *M. glyptostroboides*, *M. occidentalis*, and *M. milleri* that are available to be compared with those of *M. foxii* emphasizes that there is a great degree of similarity among each of the organs of *Metasequoia* species (table 1). All are apparently highly branched, woody trees with deciduous shoots, decussate phyllotaxis, opposite branching, pollen cones borne on specialized shoots, and ovulate cones that terminate stems with long internodes and that appear to be "naked" stalks. In all species the leaves of lateral shoots twist at the level of divergence from the stem to form a planar branch. The sizes and shapes of most organs also have overlapping ranges of variation for most characters (table 1). Only because *M. foxii* is represented by large numbers of specimens for virtually all of the organs of the sporophyte have we been able to document that it represents a separate species.

Ovulate cones are the most distinctive organs of the new species. Whereas most or all of the ovulate cones of other species display four ranks of decussately arranged cone scale complexes (Liu et al. 1999), a majority of *M. foxii* cones have helically arranged cone scale complexes in five ranks (fig. 7). The pollen cones of *M. foxii*, *M. glyptostroboides*, and *M. occidentalis* have decussately arranged microsporophylls that are extended above the basal bud scales and are separated by internodal elongation at maturity. In contrast, those of *M. milleri* are exposed at maturity by spreading of the surrounding bud scales, and the sporophylls are initiated in a helical arrangement, becoming randomly arranged at maturity (Rothwell and Basinger 1979). Pollen cones of *M. foxii* range to longer than the other species (i.e., 8 mm), whereas those of *M. glyptostroboides*, *M. occidentalis*, and *M. milleri* reach a maximum of only 4.3, 5, and 3 mm, respectively (table 1).

Foliage leaves of *M. foxii* are similar to those of the other *Metasequoia* species in most respects, but they may range to much wider (i.e., 4.5 mm, where none of the other species are described as having leaves wider than 3 mm; Liu et al. 1999; table 1). Seeds of *M. foxii* range to considerably larger than the other species, measuring 3.5–9.0 mm long and 2.75–7.0 mm wide, whereas those of *M. glyptostroboides* are only 4.0–7.0 mm long and 3.0–6.0 mm wide (Liu et al. 1999; table 1). Seeds of the other fossil species are described as being even smaller (table 1). In contrast, seedling branches and branch leaves of *M. foxii* are shorter and smaller than those of *M. glyptostroboides* (Falder 1999; table 1). Seedling branches measure 3–21 mm long for *M. foxii* and 32–87 mm long for *M. glyptostroboides*, while branch leaves are 3–13 mm long and 8–20 mm long, respectively. Seedlings are not known for the other two species.

Taxodioid wood is common in the fossil record, often under the genus *Taxodioxylon* Hartig, some of which may represent that of *Metasequoia*. A few specimens have been assigned to species of *Megasequoia*, but these are of equivocal identity and are usually associated with compressed remains of genera other than *Metasequoia* (e.g., *M. siberica* Gorbunov and Shilkina 1972). Up to the present, the wood type belonging to *M. occidentalis* has not been demonstrated. The wood of *M. foxii*, *M. glyptostroboides*, and *M. milleri* is similar in most respects, but ray heights vary considerably among the species. Rays of *M. glyptostroboides* are reported to be up to 20+ cells high, while those of *M. milleri* are up to 80 cells high (Basinger 1981). In contrast, rays in the Munce's Hill wood of *M. foxii* are up to 113 cells high, the highest rays produced by any taxon of the taxodiaceous/cupressaceous clade that is known as a whole plant.

Evolutionary Diversification within the Genus Metasequoia

By the careful and comprehensive evaluation of all *Metasequoia* species, Liu et al. (1999) have demonstrated convincingly that the fossils on which most extinct species of the genus are based conform to the range of variation for organs of *M. occidentalis*. This realization has prompted a reduction in the number of recognized compression species of *Metasequoia* from as many as 21 to three. The dramatic fluctuation in number of *Metasequoia* species emphasizes the structural simplicity of taxodioid conifer organs and the cryptic nature of specifically diagnostic characters.

Similarities between the extinct *M. occidentalis* and the extant species *M. glyptostroboides* are striking (e.g., table 1; Liu et al. 1999). Indeed, if specimens of *M. glyptostroboides* were fossils showing only the features known for *M. occidentalis* (table 1), it is doubtful that there would be sufficient distinctive characters for *M. glyptostroboides* to be retained as a separate species. *Metasequoia milleri* is a bit more distinct from *M. occidentalis*. In part, this is because differences in preservational mode preserve quite different suites of characters for each. However, at least two characters of the pollen cones are also different for the two species (table 1; Rothwell and Basinger 1979; Liu et al. 1999).

Metasequoia foxii has a larger number of specifically distinctive characters than do any of the other species of the genus (table 1). Moreover, the distinctive characters of this species are distributed among most of the organs of the plant, including the stem (i.e., wood), vegetative leaf, pollen cone, ovulate cone, seed, and seedling. This distribution emphasizes the distinctiveness of the overall *M. foxii* plant, but it also prompts us to ponder whether we would have been able to clearly distinguish our material as a new species if we had (1) fewer of the organs to examine for characters, (2) fewer specimens of each organ from which to determine ranges of variation, (3) fewer growth stages from which to interpret ontogenetic differences (Falder 1999), and/or (4) only one mode of preservation from which to recognize taxonomically informative characters.

If *M. foxii* were represented by far fewer compression specimens that included only a small number of plant organs, we suspect that we would have been unable to recognize that they fall outside the ranges of variation documented by Liu et al.

(1999) for *M. occidentalis*. If so, the new species would have gone unrecognized. In this situation, we are prompted to wonder if there could be one or more undocumented distinct species of *Metasequoia* among the specimens and organs on which many of the recently synonymized species were originally described (Yang and Jin 2000). We consider it unlikely that all of the *Metasequoia* plants that grew in the Northern Hemisphere from the Upper Cretaceous through the Pleistocene belong to the same species except those at one Middle Eocene locality in British Columbia (i.e., *M. milleri*) and those at two Paleocene localities in Alberta (i.e., *M. foxii*). It seems more reasonable to hypothesize that speciation in the genus *Metasequoia* was more widespread in both time and space, but description of other fossil *Metasequoia* collections that are comparable to those of *M. foxii* will be required to recognize and document the additional species.

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