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PLANTS PEOPLE
POSSIBILITIES

A MONOGRAPH OF CUPRESSACEAE AND SCIADOPITYS

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Chapter 6

THE FOSSIL RECORD OF CUPRESSACEAE *s. lat.*

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Early history

The fossil record of Cupressaceae (now including Taxodiaceae) is long and extensive. However, the origins of this group have remained obscure due to a paucity of well-characterised species of plants in the fossil record. One of the problems is the nature of the fossil record itself. Paleobotanists usually deal with isolated plant organs that are assigned to structural categories known as morphotaxa. Species of plants (i.e., whole plant concepts) based on fossil remains are far more helpful for assessing systematic relationships and recognising patterns of phylogeny, but these are much less common than morphotaxa. The most diagnostic remains for conifers are usually those of seed cones; but leafy shoots are among the most common types of cupressaceous fossils, and these are especially common in the Northern Hemisphere.

Most paleobotanists think that the ancestors of the Cupressaceae are represented in the fossil conifer family Voltziaceae that was widespread in the Upper Permian and Triassic (Florin, 1938–1945; Miller, 1977, 1982). Cones with lobed ovuliferous scales similar to those of extant *Cryptomeria* are common in Voltziaceae in genera such as *Aethophyllum* (Grauvogel-Stamm and Grauvogel, 1973), *Voltzia* Brongn., (Florin 1938–1945, 1951; Schweitzer, 1996), and *Conewagia* Axsmith, Taylor & Taylor (1998). However, the oldest plant remains that can probably be assigned to the Cupressaceae *s. lat.* are permineralised (petrified) seed cones from the lower Middle Triassic of Antarctica (Yao *et al.*, 1997). The genus *Parasciadopitys* Yao, Taylor & Taylor had helically arranged cone scale complexes with bracts and ovuliferous scales of approximately equal length that are fused at the base. Ovuliferous scales have five distal lobes and bear five inverted ovules. This fossil cone shows some similarities to those of *Sciadopitys* and the fossil genera *Pseudovoltzia* (Schweitzer, 1963), *Voltziopsis* Potonié (Townrow 1967), *Glyptolepis* Schimper (Axsmith & Taylor, 1997), and *Swedenborgia* Nathorst (Yao *et al.*, 1997). The fossil record, thus, agrees with molecular data that *Sciadopitys* and Cupressaceae *s .lat.* may have had a common origin.

The earliest fossil leaf remains thought by some authors to belong to the Cupressaceae are those reported by Lemoigne (1967) from the late Triassic of France. This material also includes pieces of wood and isolated ovulate cones. Leaves are decussate and scale-like with decurrent bases. Cones from these deposits show cone scale complexes like those of *Cryptomeria.* These remains are fragmentary, cuticular structure and wood anatomy are known and similarities to Cupressaceae were generally accepted by Miller (1977), although not universally accepted by other paleobotanists. Other twigs with opposite leaves from the Early to Middle Jurassic of Israel have been assigned by Chaloner & Lorch (1960) to Cupressaceae. These specimens have scale-like leaves with decurrent bases, but are now thought to belong to the Cheirolepidiaceae, an extinct family that is characterised by the production of *Classopollis* pollen and leaves with distinctive papillate epidermal cells.

The Jurassic genus *Elatides* Heer has been included by some authors in the taxodiaceous Cupressaceae. *Elatides* comprises a heterogeneous assemblage of species that are not necessarily closely related. The type species is too incompletely known to assign to a family, but several other species are apparently assignable to Cupressaceae. Particularly well known is *Elatides williamsonii* (Lindley & Hutton) Nathorst from the Yorkshire Jurassic Flora (reexamined by Harris, 1943, 1979) which is represented by leafy shoots, ovulate and pollen cones. Leaves are helically arranged and curve toward the shoot apex showing similarity in morphology to *Cunninghamia* with two adaxial bands of stomata. Pollen cones show three pollen sacs per microsporophyll (Harris 1979) and non-saccate pollen with a distal pore (Kurmann, 1991). Ovuliferous scales are three-lobed with one ovule per lobe. While *E. williamsonii* is the most completely known of the *Elatides* species, other taxa that have been put into this genus including the type specimen are not as complete. Therefore, using the name *Elatides* for *E. williamsonii* may not be an accurate reflection of affinity.

A similar problem exists with *Sewardiodendron laxum* (Phillips) Florin. A Jurassic whole plant has been described from Yima, Henan in central China (Yao *et al.*, 1998). While this nearly complete Chinese plant shows leafy branches with attached pollen and ovulate cones, and is probably a good example of taxodiaceous Cupressaceae, the type specimen of *Sewardiodendron* consists of sterile foliage from the Jurassic of Yorkshire. Because the type specimen is so fragmentary, the use of the name *S. laxum* for the Chinese material may be questioned. The Chinese plant shows helically arranged leaves with terminal ovulate cones and terminal clusters of pollen cones (Yao *et al.*, 1998). There are helically arranged cone scale complexes with partially fused bract and ovuliferous scale and six seeds per scale. Microsporophylls are helically arranged with

three abaxial pollen sacs and non-saccate pollen (Yao *et al.*, 1998). Despite potential nomenclatural problems, these Chinese fossils show the presence of Cupressaceae in Asia during the Jurassic.

Sphenolepis kurriana (Dunker) Schenk (Harris, 1953) is a species originally described from poorly preserved leaves from the Cretaceous Wealden Formation of Germany. Harris (1953) described new material from the Cretaceous Wealden Formation of Belgium including well-preserved ovulate cones. Leaves are rhomboidal, scale-like and had a photosynthetic leaf cushion. Harris (1953) compared these to *Athrotaxis* and *Glyptostrobus*. Cones are thought to be similar in form to *Sequoia* and *Athrotaxis*, with two rows of ovules like *Sequoia* and vascular anatomy like *Athrotaxis*, *Cunninghamia*, or *Taiwania* and contain small anatropous ovules.

Over the years, a number of other fossil taxa have been suggested to have cupressaceous (and taxodiaceous) affinities. Many of these, like cones of *Pararaucaria* Wieland from the Jurassic of Argentina (Stockey, 1977) or *Doliostrobus* Marion from the Eocene of Europe (Kvaček, 2002a), show a mixture of characters and are now classified in their own unique families. The extinct genera found in the Southern Hemisphere (e.g., *Monarophyllum*, *Otokauia*, *Paahake*, *Bungarbia)* were recently reviewed by Hill & Brodribb (1999). Many of these and other fragmentary remains are in need of reexamination with new specimens. For example, *Romeroites* Spegazzini (1924) is represented by a single cone and a few fragments from Argentina that have several orthotropous seeds per scale and a bract and scale that are fused for a greater part of their length (Stockey, 1977). It has been suggested that the *Cryptomeria* line seems to be the most ancient of the taxodiaceous Cupressaceae (Miller, 1977) and had evolved by the middle of the Mesozoic, as indicated by the Jurassic genus *Swedenborgia*. However, these remains are fragmentary and whole plants are needed to assess the level of character evolution.

Fossil record of modern Cupressaceae

While the earliest records for the Cupressaceae are poorly understood on the whole, a fossil record that allows the recognition of characters that distinguish extant taxa and closely related fossil taxa is present by the early Cretaceous. Characters of *Sciadopitys* and *Cunninghamia* are present in combinations not seen in the present day flora. These and other extant genera such as *Athrotaxis* are recognisable at the species level by the early to mid-Cretaceous (Ohsawa, 1994, 1997; Table 2 in Appendix).

Permineralised ovulate cones described as *Rhombostrobus cliffwoodensis* LaPasha & Miller (1981) from the Upper Cretaceous Magothy Formation, are oblong cones with helically arranged peltate cone scale complexes. There are at least 50 cone scale complexes that have a pronounced median ridge and a rhomboidal outline. The resin canal distribution in this cone is like that of *Cunninghamia*. The size and shape of the ovuliferous scale are similar to that seen in *Sequoia*, *Sequoiadendron* and *Metasequoia* (LaPasha & Miller 1981). Seeds are winged and anatropous. Cones of this type prompted LaPasha & Miller (1981) to suggest that modern taxodiaceous genera evolved from an ancestral complex in the Late Jurassic to Early Cretaceous. It is clear from the combinations of characters that are present in Early Cretaceous cones that this is an important time in the evolution of modern Cupressaceae.

Sciadopitys group

Sciadopitys is well known from permineralised ovulate cones from the Middle to Upper Cretaceous of Japan. Cones of *Sciadopitys yezo-koshizakae* (Ohsawa *et al.*, 1991) differ from those of *S. verticillata* in having a single vascular strand to the cone scale at its origin, rather than two or three strands and fewer resin canals in the bracts and ovuliferous scales. Cones show nine seeds per scale as in extant *Sciadopitys* and seem to fit well into this group. *Sciadopityostrobus* Saiki (1992) was also described from an ovulate cone from the Upper Cretaceous of Hokkaido, Japan. Cone scales of this taxon are not recurved like those in *Sciadopitys*. The ovuliferous scale is five-lobed rather than having numerous lobes and the bract and ovuliferous scale are fused at the base making it a unique extinct taxon (Saiki, 1992). Leaves of *Sciadopitys cretacea* were also described from the Upper Cretaceous of Hokkaido (Ogura, 1932). These leaves show the typical two vascular bundles and median stomatal groove (Plate 18, f. 1). They differ from those of extant *Sciadopitys* in lacking idioblasts in the spongy mesophyll and transfusion tissue in the bundle (Ohsawa *et al.*, 1991). These remains suggest that the *Sciadopitys* group, now monotypic, was more diverse in Asia in the past.

Sciadopitys-like leaves have been reported frequently in sediments from the Eocene to the Pliocene in Europe (Florin, 1963; Schneider, 1992a). *Sciadopitys tertiaria* Menzel is known from seed cones, isolated bracts and fragments of needles from the Lower Miocene to Upper Pliocene of Germany (Florin, 1963). This taxon is accepted by most workers as a valid species of *Sciadopitys* in Europe. However, leaves from the Upper Jurassic to Upper Cretaceous of Europe often referred to as *Sciadopitytes* Goeppert & Menge or *Sciadopityoides* Sveshnikova probably form a heterogeneous group that cannot be related to *Sciadopitys* with certainty (Manum, 1987). Other taxa of *Sciadopitys*-like leaves, such as *Tritaenia* Maegdefrau & Rudolf, are present in mass accumulations in the Late Jurassic to Early Cretaceous of Europe (Manum *et al.*, 2000). These leaves, although they appear similar in many respects to *Sciadopitys*, cannot be included in the genus (Manum, 1987; Manum *et al.*, 2000). *Sciadopitophyllum* Christophel from the Paleocene Smoky Tower locality of Alberta, first thought to be related to *Sciadopitys* (Christophel, 1973), does not show the characteristic bifurcate leaf (cladode) tip (Plate 18, f. 2). These leaves are now known to be borne on both long and short shoots (Plate 18, f. 3) and Christophel (1976) has suggested that they may not be closely related to *Sciadopitys*.

Subfamily Cunninghamioideae

The fossil record of Subfamily Cunninghamioideae extends back to the early Cretaceous in the Northern Hemisphere. Fossils in this group are known from permineralised ovulate cones and twigs with attached leaves. The name *Cunninghamiostrobus* Stopes & Fujii (1910) was originally proposed for ovulate cones similar to those of *Cunninghamia* that have large bracts and small tri-lobed ovuliferous scales bearing three anatropous ovules, but that differ from this genus in characters of the vascular trace to the cone scale complex. The earliest *Cunninghamiostrobus* is now *C. hueberi* Miller (1975) from the Cretaceous of California based on cones and needle-bearing twigs. The type species, *Cunninghamiostrobus yubariensis* Stopes & Fujii (1910), with several cones now known (Ogura, 1930; Ohana & Kimura 1995), comes from the Upper Cretaceous of Japan. The most complete of these specimens is a large cylindrical cone (6.5 cm long) with well-preserved seeds (Ohana & Kimura, 1995). *Cunninghamiostrobus goedertii* Miller & Crabtree (1989) from the Oligocene of Washington (Plate 18, f. 5) shows smaller spherical to elliptical cones (4 cm long), flattened seeds and upturned bracts with large numbers of resin canals. Leaves of this species (Miller, 1990), like those of *Cunninghamia*, show two broad, abaxial stomatal bands and minute serrations at the leaf margin (Plate 18, f. 5). Although the leaves associated with *Cunninghamiostrobus* are very similar to extant *Cunninghamia*, many of the cones show distinct differences in the number of resin canals in the bract and the shape of the vascular trace to the cone scale complex in transverse section.

Recently a new species based on cones, leaves, twigs and wood conforming to *Cunninghamia* has been described from the Upper Cretaceous of Alberta (Serbet, 1997). Leaves are helically arranged and show a centrally located resin canal with a single adaxial vascular bundle and two smaller lateral canals. Like those of *Cunninghamia konishii*, leaf tips are curved toward the shoot axis (Serbet, 1997). Bract margins in the cones are finely denticulate like those in *Cunninghamia konishii* and *C. lanceolata*.

Fossil *Cunninghamia* leaves have been described from Oligocene-Miocene compression fossils in western North America. These remains are usually described as *Cunninghamia chaneyi* Lakhanpal (1958). Recently, Kvaček & Rember (2000) compared the North American *Cunninghamia* to the European *C. miocenica*. The European species is known mainly from the Late Oligocene-Miocene and most of the records have been lumped into the single species (Palamarev *et al.*, 1978; Kovar, 1984; Walther, 1989; Kvaček & Rember, 2000). There are small compressed cones associated with this species that appear more similar in size to those of *C. konishii* than *C. lanceolata*. Cones of *Cunninghamia chaneyi* are more robust than those of *C. miocenica* and the North American species has broader adaxial stomatal bands (Kvaćek & Rember, 2000).

Cunninghamia-like leaves, which appear to conform to *Cunninghamia chaneyi*, have also been found at the Eocene McAbee locality of British Columbia. Recently, permineralised remains have been found in the Cretaceous of Hornby Island, British Columbia (Plate 18, f. 4, 7), but have so far not been studied in detail. These records show that members of this subfamily were widespread in the Northern Hemisphere during the Cretaceous and were still present in North America in the Oligocene (Meyer & Manchester, 1997).

Cunninghamites Presl ex Sternberg is a name given to several species of helically arranged *Cunninghamia*-like foliage attached to seed cones from the European Cretaceous (J. Kvaček, 1999; Kunzmann, 2001). Leaves that are attached by small deltoid leaf cushions have two bands of stomata on their adaxial surfaces and small marginal teeth. *Cunninghamites oxycedrus* Presl ex Sternberg and *C. lignitum* (Sternberg) Kvaček have recently been reexamined by Kunzmann (2001) and Kvaček (1999) respectively from cuticular remains. These may be conspecific (Kvaćek, 1999). Large seed cones (3.5 × 6.0 cm) have been found attached terminally to branches and have peltate cone scale complexes with hexagonal heads that bear four to five wingless seeds.

Harris (1953) described *Elatides bommeri* from the Wealden Formation of Belgium. This species is based on twigs with helically arranged leaves with a central resin canal and fibrous hypodermis. Terminal, ovoid, ovulate cones 1–2 cm long bore three-lobed ovuliferous scales and flattened seeds. It has been suggested by some authors that these cones are very similar in trace vasculature and general form to those of *Cunninghamia*, however, the leaves conform to the morphotaxon *Elatides* with a single band of adaxial stomata (Harris, 1953).

The species of *Elatides* with the most similarity to *Cunninghamia* is *E. harrisii* Zhou (1987) from the Lower Cretaceous of China. This taxon is based on foliage with well-preserved cuticle attached to both seed cones and pollen cones containing pollen. There are three seeds per scale, leaves have adaxial stomata and a toothed margin, and there are four to five pollen sacs per microsporophyll containing immature pollen (Zhou, 1987). Zhou (1987) presents an extensive table comparing the best preserved material in the genus *Elatides*.

Subfamily Taiwanioideae

Until relatively recently *Taiwania*-like seed cones were not known with certainty in the fossil record. Possible mummified *Taiwania* seed cones with leaves are described from the Paleocene/Eocene of Spitzbergen (Schloemer-Jäger, 1958) and the Miocene of Europe (Kilpper, 1968). Leaves known as *Taiwania japonica* Tanai & Onoe are known mostly from fragmentary leafy shoots from several floras in China and northern Japan (Tanai & Suzuki, 1963). Anatomical features of these specimens have not been investigated, and their precise affinities remain speculative.

The well-preserved Upper Cretaceous calcareous nodules from Hokkaido, Japan have revealed anatomical details of several different types of conifers attributable to subfamily Taiwanioideae. *Parataiwania nihongii* (Nishida *et al.*, 1992) was described from a single ellipsoidal cone with non-peltate cone scale complexes with tapered apices. Four anatropous, winged seeds are borne on a very small ovuliferous scale. The vascular trace to the cone scale complex is single and no vascular traces were seen to the ovuliferous scale. Although this cone also shows some similarities to *Cunninghamia*, the tissue zones of the cone lack the abundant thick-walled fibres and ovuliferous scale traces seen in this genus.

Mikasastrobus hokkaidoensis Saiki & Kimura (1993) was described from six cones from the Upper Cretaceous of Japan. Ovoid cones, 2–3.5 cm in diameter, with helically arranged cone scale complexes are borne terminally on shoots with needle-like leaves. There is a single, concentric vascular strand to the cone scale complex and a small ovuliferous scale tip like that seen in *Parataiwania*. The small ovuliferous scale tip is like *Cunninghamia*, but the vascular tissue arrangement is most like *Taiwania*.

Subfamily Athrotaxoideae

Although there have been several fossil taxa of the genus *Athrotaxis* described in the past, all of the Northern Hemisphere fossils were discounted by Florin (1960). Of these, *Athrotaxites berryi* Bell has been reexamined by Miller & LaPasha (1983). This taxon is known from leafy twigs, pollen cones and seed cones from the Early Cretaceous of North America. Extant *Athrotaxis selaginoides* and *A. laxifolia* have larger seed cones with more pointed cone scale complexes while *A. cupressoides* has smaller, more globose cones than those of *Athrotaxites berryi* (Miller & LaPasha, 1983). These fossils share a number of characters of leaves and pollen cones with *A. cupressoides*, but differ in a number of features. They cannot be included in the extant genus, but may show that conifers with many *Athrotaxis*-like characters existed in North America in the past.

The only good fossil record of the genus *Athrotaxis* comes from the Southern Hemisphere. Even here, many scattered fossil remains are not well-enough known to be assigned to this genus (Townrow, 1967). *Athrotaxis ungeri* (Halle) Florin is based on shoot and cone impressions from the Early Cretaceous near Lago San Martin in Patagonia. Foliage of these and other specimens from Ticó, Santa Cruz Province, Argentina were studied by Archangelsky (1963), but certain identification with *Athrotaxis* requires verification of cuticular studies with SEM (Hill & Brodribb, 1999). Leaf size, shape, and ultrastructure of the cuticle show that *A. ungeri* is a species similar to *A. cupressoides*. The unique stomatal morphology of *Athrotaxis* has allowed identification of these and other leaves by their cuticular remains (Hill & Brodribb, 1999).

Athrotaxis novae-zeelandiae (Ettingsh.) Florin is based on vegetative shoots from the Late Cretaceous of eastern Otago, New Zealand. Fossil leaves are extremely slender when compared to those of extant *Athrotaxis* but similar in size to an Oligocene species from Tasmania, *A. rhomboidea* (Hill *et al.*, 1993). Even though these leaves have been included in *Sequoiadendron* by Pole (1995), their subsidiary cell morphology places them in *Athrotaxis* (Villar de Seoane, 1998; Hill & Brodribb, 1999).

Athrotaxis fossils of leafy shoots and ovulate cones are relatively common in Tasmania from the Early Oligocene onwards (Hill *et al.*, 1993), and these fossils include forms that are similar in many respects to the extant species. Some, however, are well outside the morphological ranges of extant species. For example, *A. rhomboidea* Hill, Jordan & Carpenter (1993), as mentioned above, had very slender foliage compared to the extant species. Therefore, while there are isolated very old records of *Athrotaxis* from widespread localities around the Southern Hemisphere, the more recent record of this genus (Early Oligocene onwards) is concentrated in Tasmania where it is currently restricted.

Subfamily Sequoioideae

One of the most common groups of Cupressaceae in the fossil record is the sequoioids. Most of the records are from the Northern Hemisphere but *Austrosequoia wintonensis* Peters & Christophel (1978) was described from silicified cones and attached twigs with rhomboidal leaves from the Cenomanian of central Queensland, Australia. Cones show anatomical similarities to those of *Sequoia*, while leaves are more broadly rhomboidal and the authors compare these most closely with those of *Athrotaxis* (Peters & Christophel, 1978). Hill *et al.* (1993) described a second species of *Austrosequoia* from Early Oligocene sediments in Tasmania. This species was preserved as compressions of foliage and fragments of seed cones. The cuticular morphology of the Tasmanian species is clearly distinct from *Athrotaxis*, suggesting that the similarity of the Cretaceous fossil *Austrosequoia* foliage to that genus may be superficial.

Some of the earliest sequoioid fossils are permineralised cones of *Yezosequoia shimanukii* Nishida, Nishida and Ohsawa (1991) from the Turonian–Santonian of Hokkaido, Japan. These cones show peltate cone scale complexes with completely fused bract and ovuliferous scale. *Yezosequoia* is thought to be most similar in anatomy to *Sequoia*.

The genus *Metasequoia* has a very extensive fossil record and is one of the most common taxa in Northern Hemisphere Cretaceous and Paleocene Floras. This genus was originally described from fossil material (Miki, 1941) and later the living species *M. glyptostroboides* Hu & Cheng (1948) was described. Truly a "living fossil" *Metasequoia* is now known from the Cretaceous to the Recent (Stockey *et al.*, 2001b). More than 20 extinct species of this genus have been

described (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. Liu *et al.* (1999) placed most of these taxa into synonymy. The resulting changes have left three distinctive species of fossil *Metasequoia.*

Metasequoia occidentalis (Newberry) Chaney is a circumpolar species for compression/impression remains with an extremely long geological range (Table 2 in Appendix; Yang & Jin 2000). The great deal of overlap in size ranges for the plant organs of the three recognised fossil species of *Metasequoia* has caused much taxonomic confusion. Only with very large collections of plant organs from one locality can whole plants be identified (Stockey *et al.*, 2001b). It is very possible that there are several taxa included in *Metasequoia occidentalis*, but their description awaits extensive paleobotanical work on a locality-by-locality basis.

The best known taxon based on compression fossils is *Metasequoia foxii* Stockey, Rothwell & Falder (2001b) from the Paleocene of Alberta, Canada. These plants are known from trunks with silicified wood, leaves, branches, pollen cones with pollen, ovulate cones, seeds, and seedlings (Plate 18, f. 6, 9–13). Seeds have been found buried in the process of germination and remarkably well preserved layers of seedlings have been identified at two localities in central Alberta (Plate 18, f. 10, 11). This *Metasequoia* species was a large tree that inhabited the back swamps of fluvial systems in the Paleocene.

Metasequoia milleri Rothwell & Basinger (1979) was the first entire plant of *Metasequoia* reconstructed based on permineralised remains (Basinger, 1981; 1984). All plant organs are known including: pollen cones with pollen (Rothwell & Basinger, 1979), leaves, twigs, wood and roots (Basinger, 1981), seed cones and seeds (Basinger, 1984), and even the mycorrhizal fungi in the roots (Stockey *et al.*, 2001a). This *Metasequoia* species also inhabited wetlands (Cevallos-Ferriz *et al.*, 1991).

Drumhellera kurmanniae Serbet & Stockey (1991), a taxon first known for branches bearing permineralised pollen cones with non-saccate, slightly papillate pollen (Plate 19, f. 1–4) is now also represented by leafy shoots with helically arranged linear leaves (Plate 19, f. 7) and persistent bud scales, twigs with well-preserved wood, seed cones (Plate 19, f. 5) and seeds (Serbet, 1997). Vascular architecture in the seed cone is similar to *Metasequoia* and *Sequoiadendron*, but the cone scale vasculature has not so far been described at its point of origin. Leaves are most similar to *Sequoia* and *Metasequoia.*

Yubaristrobus nakajimae Ohsawa, Nishida & Nishida (1993) was described from a single permineralised seed cone from the Upper Cretaceous of Hokkaido (Table 2 in Appendix). Helically arranged, peltate cone scale complexes with completely united bract and scale have a unique vascular arrangement unlike any other known Cupressaceae. The vascular strand to the cone scale complex arises as a cylindrical vascular trace that divides into numerous bundles that encircle a few medullary bundles (Ohsawa *et al.*, 1993). Seeds are erect like the Cupressaceae *s. str.* and the taxodiaceous genera *Cryptomeria, Glyptostrobus* and *Taxodium* (Ohsawa *et al.*, 1993).

Quasisequoia florinii Srinivasan & Friis (1989) is known from compressed twigs with leaves and seed cones from the Upper Cretaceous of Sweden (Plate 19, f. 8). Leaves are helically arranged, scale-like, rhomboidal, and amphistomatic with well-preserved cuticle and are compared most closely with *Sequoiadendron* (Srinivasan & Friis, 1989). Seed cones were found in attachment to these leaves and are terminal and ovoid with helically arranged, four-sided cone scales. Srinivisan & Friis (1989) also described *Q. suecica, Q. scanica*, and *Q. aasenensis* from the Höganäs AB's kaolin quarry in Scania. In addition to these leaves, several isolated seeds (Plate 19, Fig. 6), seed cones and pollen cones with non-saccate pollen have been found at this site. Since this material is lignitic or charcoalified it is hoped that *Quasisequoia* cones and twigs may be sectioned in the future so that closer comparisons can be made to extant taxa and other permineralised remains, so that the diversity of taxa at this important locality is better understood. Since dimorphic leaves occur in extant *Sequoia*, this brings to question the possibility of dimorphic leaves in *Quasisequoia.*

Quasisequoia has also been recently described from the Oligocene–Miocene of Europe (Kunzmann, 1999). *Quasisequoia couttsiae* (Heer) Kunzmann is known from seed cones borne in clusters, seeds and foliage. Three to five seeds are borne per scale. These seeds are slightly curved and have marginal wings. Cuticle is similar to *Quasisequoia* from Sweden and these conifers are part of the European Tertiary coal forming vegetation (Kunzmann, 1999).

Boyd (1992) described three new genera of taxodiaceous Cupressaceae from the Pautøt Flora of west Greenland. *Peltaconus* Boyd (a taxon based on leaves and cone external features) is thought to be similar to *Sequoia* and *Sequoiadendron.* These may in fact be species of *Quasisequoia* but they are too poorly preserved to tell.

Haborosequoia nakajimae Ohsawa, M. Nishida & H. Nishida (1992) is represented by one small ovulate cone that is similar in appearance to Srinivasan & Friis's (1989, f. 11, 12) cone type four. Vascular strands to the bract and ovuliferous scale in *Haborosequoia* are similar to those in *Sequoia, Sequoiadendron* and *Metasequoia.* However, the resin canal placement and external morphology of the cone scale complex differ.

Ohsawa *et al.* (1992) described a second unnamed *Sequoia*-like cone from the Upper Cretaceous of Hokkaido (Table 2 in Appendix). This specimen is a small permineralised cone, 2.2 × 1.7 cm, with peltate,

helically arranged cone scales that have a distal groove and completely fused bract and ovuliferous scale. The cone most closely resembles *Sequoia* and *Sequoiadendron* but differs in having an abaxially concave reniform vascular cylinder rather than an elliptical cylinder as in these two taxa (Ohsawa *et al.*, 1992). The description of this *Sequoia*-like cone has pointed out the need for closer examination of *Austrosequoia* and *Drumhellera* in terms of trace vasculature and resin canal placement in the cones so that comparisons can be made to these and other fossils.

Another genus based on permineralised, sequoioid cones, *Nephrostrobus* LaPasha & Miller (1981) was described from the Upper Cretaceous Magothy Formation of New Jersey. These authors described the genus *Nephrostrobus* with two species, *N. cliffwoodensis* and *N. bifurcatus*. *Nephrostrobus* has oblong seed cones with helically arranged, peltate cone scale complexes with bracts and ovuliferous scales that are completely fused. The trace to the complex is oval in cross section dividing distally to 20 or more strands that are arranged in a reniform pattern. There is at least one winged seed per scale. The two species differ in the branching of the complex trace and resin canals and in some characters of the cone axis. *Nephrostrobus* cones have scale and bract of about equal size as in *Sequoia*, *Sequoiadendron* and *Metasequoia* (LaPasha & Miller, 1981). The reniform pattern of the vascular traces as they depart from the axis stele is similar to the pattern in *Metasequoia* (LaPasha & Miller, 1981).

Sequoia-like foliage has been reported many times in the fossil record (Miller, 1977). However, these records were reviewed by Penny (1947) and Miller (1977) who concluded that many of the taxa are based on superficial resemblance. Penny (1947, p. 293) states that, "No genus among all the Cretaceous conifers contains so many species of doubtful affinities as *Sequoia*". Nomenclature in this group has been particularly complex. Leaves referred to as *Sequoia reichenbachii* (Geinitz) Heer (= *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey, = *Araucarites reichenbachii* Geinitz) were widespread in the Northern Hemisphere during the Cretaceous (Hollick & Jeffrey, 1909). These falcate leaves, which are tetragonal in cross section with three resin canals, were studied using anatomical sections by Hollick & Jeffrey (1909) and later by Penny (1947) from the Magothy Flora of eastern North America. The leaves in the North American Cretaceous are associated with cones of *Sequoia ambigua* Heer (Penny, 1947) but complete anatomy has not been described and attachments were not found.

Probably the best records of *Sequoia*-like plants are those of *S. abietina* (Brongniart) Knobloch from the Neogene of Europe (Kilpper, 1968). This species is represented by compressed specimens of leafy shoots and seed cones with preserved cuticles, and is similar to the living *S. sempervirens*. *Sequoia abietina* trees were apparently a common component of late successional forests within Miocene lignite mires (Schneider, 1992b).

The genus *Geinitzia* Endlicher is a morphotaxon for leaves that have been included at one time or another in both the Araucariaceae and the taxodiaceous Cupressaceae. The first described species was *Araucarites reichenbachii* (Geinitz, 1842); however, many authors both recently and in the past (Harris, 1979; Kunzmann, 1999) have used the name *Geinitzia* for leaves that have been formerly included in many genera including *Araucaria*, *Araucarites*, *Pagiophyllum*, *Cryptomeria*, *Sequoia*, *Sequoiadendron*, *Sequoiites*, and *Elatides*. Although Harris (1979) tried to clear up the taxonomy, it is clear that several different types of foliage may be included. *Geinitzia* should probably be regarded as a morphotaxon of leaves that are helically arranged on branches, falcate, needle-like, rhomboidal in outline and merging into a basal cushion on the stem without a contraction. Because many fossils representing several taxa may look like the original type (Seward, 1919), the type species, *G. reichenbachii*, should probably be reserved for specimens that come from the original locality.

Using this approach, other Mesozoic foliage that fits this general description could be treated as *Geinitzia*. As more plants are known and reconstructed, a better understanding of juvenile vs. adult foliage and type of attached cones will enable paleobotanists to recognise what is a whole plant. Only then can the affinities be assessed. It is clear that conifers in the "*Geinitzia* group" were important elements of the European flora in the Upper Cretaceous (Kunzmann & Friis, 1999; Kunzmann, 1999).

Associated with *Geinitzia* foliage in the European fossil record are seed cones (Plate 19, f. 12) containing numerous curved seeds with two lateral wings (Kunzmann & Friis, 1999; Kunzmann, 2003). If found isolated, these seeds form a group of genera distinguished by their shape and size, the most common of which are *Cupressospermum* Mai (1960), *Alapaya* Dorofeev, and *Seletya* Dorofeev (1978). Kunzmann (1999) later found *Alapaya* seeds in sequoioid cones with helically arranged peltate cone scale complexes each bearing up to 13 seeds. *Cupressospermum* seeds (Plate 19, f. 9, 10) were found in ovulate cones (Plate 19, f. 8) attached to foliage assigned to *Chamaecyparites* Endlicher (Kunzmann, 1999). Each seed cone consists of helically arranged scales bearing three seeds on each cone scale complex. Kunzmann (1999) considers all of this material to be a separate family, the Geinitziaceae. The curved ovule seems to be the only unique character of these conifers. The oldest ovules of this type are from the Cenomanian of Bohemia (J. Kvaček, in prep.) and Kazakhstan (Frumina & Zhilin, 1995) and *Cupressospermum* extends up to the Miocene (Mai, 1960; 1995). Whatever taxonomy one uses, it is clear that a unique group of conifers related to the sequoioid Cupressaceae were present in Europe during this time.

Subfamily Taxodioideae

The fossil record of this subfamily is represented primarily by shoots with linear leaves that are alternate, rather than opposite as they are in *Metasequoia.* These remains have been reviewed recently by Aulenback & LePage (1981). *Taxodium*-like specimens range from the early Mesozoic to the Recent in the Northern Hemisphere (Chaney, 1951; Aulenback & LePage, 1998). *Glyptostrobus* foliage is known from the Cretaceous and Tertiary (Aulenback & LePage, 1998) and forests of *Glyptostrobus* were common throughout Europe, North America, Asia and Japan from the Early Tertiary to the Late Pleistocene (Matsumoto *et al.*, 1997).

Glyptostrobus comoxensis Bell (1957) was described from branches with leaves, seed cones and seeds from the Comox Formation on Vancouver Island. Cones are borne on long peduncles bearing leaves of the cryptomerioid type. However, the cone scales are wedge-shaped with flattened abaxial surfaces and bear a short apical mucro. Boyd (1992) and Aulenback & LePage (1998) feel that this fossil material should not be classified with *Glyptostrobus.*

Glyptostrobus nordenskioeldii (Heer) Brown (1962) is among the most abundant fossils at a number of Paleocene sites in North America (Chandrasekharam, 1974; Christophel, 1976; Aulenback & LePage, 1998). Christophel (1976) points out the presence of cupressoid, cryptomeroid and taxodioid foliage on the same *Glyptostrobus* specimens at the Smoky Tower locality in Alberta underscoring the difficulty of identification of small isolated foliage fragments within this genus (Plate 20, f. 3). Some of the twigs also bear seed and pollen cones (Christophel, 1976). Cones from the Alberta specimens (Plate 20, f. 1) are very similar to those of extant *Glyptostrobus pensilis* Endlicher but internal anatomy is not known.

While Schweitzer (1974) reviewed the fossil record of *Glyptostrobus* from the Spitzbergen localities and concluded that two taxa were present, Christophel (1976) on the basis of the amount of variation seen in the Alberta material, suggested that there is probably less variability in the European species. Indeed some of the commonly used taxa for *Glyptostrobus* in the Northern Hemisphere were recently synonymised by Boulter & Kvaček (1989). Cuticular morphology of *Glyptostrobus dunoyeri* (Baily) Boulter & Z. Kvaček is similar to extant *Glyptostrobus. Glyptostrobus* was an important coal-forming conifer in Eurasia (Boulter & Kvaček, 1989) and was a common element in Miocene swamps in Europe (Schneider, 1992a, b). The extent of the similarity of *Glyptostrobus* species in North America and Europe, however, is not known as the seed and pollen cones are unknown for much of this material and anatomical details are not available.

The best preserved and most well-known species of *Glyptostrobus* is from the Miocene of Hokkaido, Japan (Matsumoto *et al.*, 1997). *Glyptostrobus rubenosawaensis* Matsumoto, Ohsawa, Nishida & Nishida was described from permineralised cryptomeroid, taxodioid and cupressoid leaves attached to shoots with attached ovulate and pollen cones (Plate 20, f. 2). This species differs from *G. pensilis* in having larger seed cones and a more prominent bract (Matsumoto *et al.*, 1997). All of the anatomical details are known for *G. rubenosawaensis* including leaves, seeds, seed cones and pollen cones and preservation is excellent.

Of the taxa that show potential affinities to *Taxodium,* the best known is *T. wallisii* Aulenback & LePage (1998). These exceptionally well-preserved silicified remains come from the Late Cretaceous Horseshoe Canyon Formation near Drumheller, Alberta, Canada. Branches bearing dimorphic leaves, pollen cones, pollen, seed cones and seeds are known in abundance. Vegetative axes bear taxodioid and rarely cupressoid leaves while those that bear cones have cupressoid foliage (Aulenback & LePage, 1998). Ovulate cones are globose with up to 15 helically arranged cone scale complexes each of which bears two triangular seeds. Pollen cones bear five to nine abaxial pollen sacs in two rows that contain non-saccate pollen with a minute papilla. The arrangement of cones on branches and the subtending leaves resemble those of *Taxodium* (Aulenback & LePage, 1998). The cone scales were probably deciduous like those of *Taxodium,* but cone size is small (13 mm diam). *Taxodium dubium* (Sternberg) Heer from the Neogene of Europe (Plate 20, f. 4) is quite similar to *T. wallisii,* whereas the Paleogene *T. balticum* Sveshnikova & Budantsev differs by having more pronounced appendages on the cone scale complexes (Mai & Walther, 1978).

Cryptomeria rhenana Kilpper (1968) was described from compressed leafy shoots and seed cones from the Miocene of Europe. Based on external morphology and cuticular features these specimens differ from the extant *C. japonica* by several characters. Seed cones of the extinct species appear to be more woody than the living species, and the bract and ovuliferous scale are united to differing degrees in different parts of the cone. The bract and ovuliferous scale are less completely united in basal regions of the cone. In addition, the free tips arise from the outer surface of the ovuliferous scale in the fossil, whereas they extend from the distal margin of the scale in the living species.

Glyptodium Boyd (1992) was described from stems with attached, globose ovulate cones and cupressoid leaves from the Pautøt Flora of west Greenland. Based on the terminal attachment of cones, number of apical lobes on the ovuliferous scale and the bract shape Boyd (1992) viewed these as intermediate between *Glyptostrobus* and *Taxodium.* Preservation however precludes detailed study of the internal anatomy or cuticle of these remains and their taxonomic affinities remain speculative.

Parataxodium wigginsii Arnold & Lowther (1955) is represented by leafy shoots with associated seed cones, seeds and pollen cones from the Upper Cretaceous of Alaska. Abundant linear to oblong leaves that are alternate or sometimes opposite are present at the site on the Colville River, and shoots were shed at the end

of the growing season. Cones are small, 10 × 13 mm, each borne on a naked peduncle with persistent cone scales. Leaf arrangement and deciduous habit are like that seen in *Taxodium*. The individual leaf shape and angle of divergence is most like *Metasequoia*. Because they are compressions and sample size was not great, the arrangement of cone scale complexes is difficult to determine. Without internal anatomy it is difficult to assess the closest affinities of *Parataxodium* but the genus does show characters of both subfamilies: Sequoioideae and Taxodioideae.

The extinct genus *Ceratostrobus* Velenovský (1885) from the Upper Cretaceous (Cenomanian) of Bohemia displays *Cryptomeria*-like leafy shoots that bear terminal seed cones that are spherical to elliposidal in shape. The cone scale complexes are similar to extant *Cryptomeria*, consisting of a three-lobed ovuliferous scale and a massive bract that are free from each other at the tip (J. Kvaček, in prep.).

Subfamily Cupressoideae

McIver (2001) described *Widdringtonia americana* from 95 million year old Cretaceous sediments in North America based on alternate, rarely opposite, branches, twigs bearing leaves on both long and short shoots, globose, quadrivalvate seed cones and terminal pollen cones. These remains are very similar to extant *Widdringtonia*, but in the extant genus the leaves are consistently decussate. Seed cones are most similar to extant *W. nodiflora* and *W. whytei*, lacking the warty margins and resin tubercles as are reported in the two other extant species (McIver, 2001).

Several types of *Widdringtonia*-like leaves from the Eurasian Cretaceous and Tertiary were reviewed by McIver (2001). These often have been confused with *Tetraclinis* with which some probably are allied (Kvaćek *et al.*, 2000; McIver, 2001). The affinities of others are ambiguous.

Callitris, the dominant member of the Cupressaceae in Australia today, is very rare in the fossil record, with the oldest record being stem fragments and dispersed cuticle in the mid-Cenozoic Latrobe Valley coal (Blackburn, 1985). Jordan (1995) described an extinct species, *Callitris strahanensis*, from the Pleistocene on Tasmania's west coast and there are undescribed fossils known from the Oligocene Lea River sediments in northwest Tasmania (B. Hill, pers. obs.)

Hill & Whang (1996) described a fossil species of *Fitzroya* from the Oligocene of Tasmania that is similar to the South American endemic, *F. cupressoides*, the only extant species of this genus. Hill & Paull (2003) re-examined these specimens, along with other undescribed macrofossils from Tasmania as well as specimens of *Dacrycarpus acutifolius*. They concluded that all of these specimens are probably the remains of a single variable species of *Fitzroya*, *F. acutifolius* (R. S. Hill & Whang) R. S. Hill & Paull (Hill & Paull, 2003; see Plate 20, f. 5, 6).

The oldest records of *Libocedrus*, *L. acutifolius* Whang & Hill and *L. obtusifolius* Whang & Hill (1999) are two species from the late Paleocene of New South Wales (Plate 20, f. 7, 8). These leaves are well known from cuticular morphology and show some characters in common with *Austrocedrus*. Whang & Hill (1999) suggest that they actually may be a part of an ancestral complex that gave rise to *Austrocedrus*, *Libocedrus*, and *Papuacedrus*. *Libocedrus* is also known from the early Eocene of the west coast of Tasmania (Hill & Brodribb, 1999, Table 2 in Appendix). By the early Oligocene in Tasmania, *Libocedrus* was relatively common, with both foliage and ovuliferous cones being recorded (Hill & Carpenter, 1989, Table 2 in Appendix). The only other published record of *Libocedrus* from the Southern Hemisphere is foliage of the extant *L. plumosa* from the Late Miocene–Pliocene of Great Barrier Island in New Zealand (Couper & McQueen, 1954).

Austrocedrus tasmanica Hill & Carpenter (1989) has been reported from compressed ovuliferous cones from the Late Oligocene-Early Miocene sediments in central Tasmania. These authors also consider *Libocedrus chilensis* Berry (1938) most likely to be a species of *Austrocedrus*, but preservation is poor, making comparisons difficult. *Austrocedrus tasmanica* has four valvate scales in two pairs of differing size, each bearing an abaxial tubercle just below the apex (Hill & Carpenter, 1989).

Zhou & Li (1994) described *Papuacedrus shenii* from the Eocene of the Antarctic Peninsula. However, these remains are fragmentary and no organic material is present making it difficult to determine whether they are in fact *Papuacedrus* or more closely related to *Austrocedrus* or *Libocedrus*. *Papuacedrus australis* Hill & Carpenter (1989) was described based on leaves with cuticular remains in whorls of four (Plate 20, f. 9) that show pronounced Florin rings around the stomata. *Papuacedrus* foliage persisted in Tasmania from the Early Oligocene to the Early Miocene (Hill & Carpenter, 1989).

The name *Cupressinocladus interruptus* (Newberry) Schweitzer (1974) has been used for cupressoid foliage (Plate 21, f. 1) of unknown affinities that occurs throughout the Northern Hemisphere in the Late Cretaceous and early Tertiary (Florin, 1963). Fertile material was unknown until the study of the Ravenscrag Flora by McIver & Basinger (1987, 1993). This morphotaxon for leaves spans so much time and space that authors have suggested that more than one natural species may have borne this foliage type. Since its original description there are, in fact, at least three separate taxa described in two different genera with attached cones that are now known to bear this foliage type. Leaves have been thought by many workers to be similar to those of *Thuja*. In Europe, *Cupressinocladus* has been associated with cones described as *Cupressoconus* Kilpper (1968) some of which show similarities to extant *Cupressus* and may, in fact, represent this genus (Boulter & Kvaček, 1989).

The oldest of the cupressoids (Tribe Cupresseae) is *Chamaecyparis corpulenta* (Bell) McIver (1994) known from the Upper Cretaceous Comox Formation of Vancouver Island. Foliage is flattened in a single plane and twigs are highly branched, alternately as in *Thuja*. Oppositely arranged leaves of the *Cupressinocladus interruptus* type are scale-like, decussate and persistent (McIver, 1994). Lateral leaves are closely appressed to the facial leaves and only the mucronate tip is free. Seed cones are woody and four-scaled and terminate leafy branches with a morphology like that seen in *Chamaecyparis*. They compare most closely to those of *C. nootkatensis* (= *Xanthocyparis nootkatensis*), but are much smaller in size, only up to 3 mm in diameter (McIver, 1994). The presence of four-scaled cones in *Chamaecyparis corpulenta*, along with those of *Mesocyparis* (see below), suggests that this cone type was more primitive than those with eight scales that were originally thought to be ancestral (Li, 1953).

Compressed leaves and associated seed cones of *Chamaecyparis* have been reported from North America in the Miocene Clarkia flora (Kvaćek & Rember, 2000). These leaves with well-preserved cuticle are similar to extant *C. lawsoniana* and perhaps represent a new species. The fossil record of *Chamaecyparis* in Europe, on the other hand, is very fragmentary (Kvaćek & Rember, 2000).

The genus *Mesocyparis* was first described by McIver & Basinger (1987) from the Paleocene Ravenscrag Formation of southwestern Saskatchewan, Canada. *Mesocyparis borealis* McIver & Basinger was based on twigs with opposite branching, and scale-like decussate acute-tipped persistent leaves that are linear on leading shoots and short and broad on short shoots, sometimes appearing slightly ridged as in *Thuja*. Seed cones that are globose and woody with four equal descussate scales with prominent umbos are most similar to *Chamaecyparis*. Pollen cones have two to three pollen sacs per microsporophyll. McIver & Basinger (1987) suggested that these fossil remains may show an intermediate relationship between *Thuja*, *Chamaecyparis*, *Calocedrus* and *Thujopsis* and Southern Hemisphere taxa such as *Libocedrus*, *Austrocedrus* and *Papuacedrus*.

Mesocyparis umbonata McIver & Aulenback (1994) is known from silicified, three-dimensional leafy twigs of the *Cupressinocladus interruptus* type with attached seed cones, seeds, pollen cones, pollen and woody stems. The large number of specimens and excellent preservation have allowed for a description of most of the plant (McIver & Aulenback, 1994). Leaves are borne on flattened axes with an opposite, sometimes alternate, branching pattern. Globose, woody seed cones (4 mm in diameter) with four equal-sized cone scales with small umbos are borne in decussate pairs. There are two orthotropous seeds per scale that have micropylar beaks and lateral wings. Pollen cones bear two abaxial sporangia per microsporophyll and elliptical, psilate pollen with small orbicules. This species differs from *M. borealis* in the position of seed cone attachment, cone size and features of the umbo. It is clear from these recent studies that *Mesocyparis* was a significant part of the mid- to high-latitude circumboreal vegetation (McIver & Aulenback, 1994).

Archicupressus Ohsawa, H. Nishida & M. Nishida (1992) is a genus used for permineralised ovulate cones from the Upper Cretaceous of Hokkaido. *Archicupressus nihongii* has peltate cone scale complexes in whorls of three on the cone axis. Each cone scale has a bristle-like projection of the bract and orthotropous seeds. The vascular trace to the cone scale complex arises as a cylindrical strand that divides into several bundles distally and becomes arranged in a reniform pattern with an abaxial invagination. Cone characters are similar to those in *Chamaecyparis* or *Cupressus*.

The early Paleocene Ravenscrag Formation in southwestern Saskatchewan has also yielded leafy twigs bearing cones similar to *Fokienia* (McIver & Basinger, 1990). *Fokienia ravenscragensis* McIver & Basinger (1990) cones are woody and decussate with peltate scales and borne in opposite pairs on foliage that bears thin flattened leaves in whorls of four. Although branching pattern and leaf morphology differ from *Fokienia* and are more like *Thujopsis* or *Calocedrus*, McIver & Basinger put this species in the genus based on the structure of the seed cones. In 1992, McIver emended the diagnosis of *F. ravenscragensis* based on more complete specimens from High River, Alberta. Pollen cones were described with spheroidal inaperturate grains (McIver, 1992).

Fossil foliage and seed cones of *Thuja* are now known from the Paleocene of Ellesmere Island in the Canadian Arctic. *Thuja polaris* McIver & Basinger (1989) bore alternately branched twigs with scale-like, decussate leaves. Seed cones are oblong with eight to nine pairs of thin cone scales with reflexed umbos. Cones and foliage are similar to extant *Thuja plicata*, but the fossil cones have twice as many cone scale complexes per cone. McIver & Basinger (1993) also reviewed the fossil record of *Thuja*-like foliage and concluded that many of these morphotaxa should not be included in extant genera.

Four other taxa have been included in the genus *Thuja* that are known from both fertile and vegetative remains (Akhmetiev, 1973; Huzioka & Uemura, 1973; Schweitzer 1974, Bennike, 1990; LePage, 2003). *Thuja ehrenswaerdii* (Heer) Heer from the Tertiary of Spitzbergen has small cones with up to four pairs of closely overlapping, imbricate scales that lack umbos. Schweitzer (1974) described the cones as similar to those of extant *T. sutchuenensis*, while the leaves are more similar to *T. plicata*. There are no resin glands in this species and the leaves are more spreading than those of *T. plicata*. The cones of *T. nipponica* Tanai & Onoe were described from the Late Miocene of Akita Prefecture in Japan by Huzioka & Uemura (1973) and the Miocene of Sikhote Alin, Russia (Akhmetiev, 1973). Cones are elliptical with three to four pairs of cone scales. *Thuja*-like remains have been reported from a number of Miocene localities in Japan and

these conifers were probably widespread there in the past. *Thuja occidentalis* (Bennike, 1990) was identified on leaves, twigs, seeds and cones, thought to belong to *Thuja*; however, LePage (2003) believes that there is no justification for such an assignment. A new species of *Thuja*, *T. smileyi* LePage (2003) was recently described from the Late Cretaceous (Turonian) of Alaska. This material is represented by one decorticated branch bearing helically arranged structures that are interpreted as seed cones. These compressed remains are described as having five to six pairs of oppositely arranged cone scale complexes with triangular reflexed umbos (LePage, 2003). Preservation is poor and not many diagnostic characters are present leaving the identity of this fossil as a species of *Thuja* (or even Cupressaceae) in doubt. Only larger collections of material from the same locality will allow us to interpret these remains.

Well-preserved *Calocedrus* is known from the Miocene Clarkia flora based on twigs with leaves, cones and seeds (Kvaček & Rember, 2000). Leaves are similar to extant *C. formosana* Florin but cones and leaves are larger. The fossil record of *Calocedrus* in Europe is represented by *C. suleticensis* (Brabenec) Z. Kvaček from the Oligocene-Early Miocene (Kvaček, 1999). Other European remains are fragmentary.

The fossil record of *Tetraclinis* has recently been reviewed by Kvaček *et al.* (2000). *Tetraclinis* has an excellent fossil record in Europe during the Tertiary based on seed cones, seeds and foliage (Kvaček, 1989; Kovar-Eder & Kvaček, 1995; Mai, 1996). Two fossil species are known: *T. brachyodon* (Brongniart) Mai & Walther (Plate 21, f. 2), from the Early Eocene to the Early Pliocene, and *T. salicornioides* (Unger) Kvaček, from the Middle Eocene to Early Pliocene (Kvaček *et al.*, 2000). Kvaček *et al.* (2000) reexamined the North American fossil record (Oligocene and Miocene) and have placed the material described by Meyer & Manchester (1997) into *T. salicornioides* as a new variety *T. salicornioides* (Unger) Kvaček var. *praedecurrens* (Knowlton) Kvaček & Manchester. Cones and seeds of the fossil taxon are similar to those of extant *T. articulata* (Vahl) Masters but leaves are more spreading. Kvaček *et al.* (2000) suggest that the presence of *Tetraclinis* in North America and its absence in the fossil floras of Asia indicates that it probably spread across the North Atlantic during the early or middle Tertiary.

Juniperus is known from compression fossils in the Late Oligocene of western North America from leafy shoots bearing closely appressed leaves with awl-like tips (Axelrod, 1987; Wolfe & Schorn, 1990). Large (9–14 mm) cones have been found associated with these branches. Fertile branches of *Juniperus* have been reported recently from the Eocene/Oligocene boundary of Europe (Kvaček, 2002b). *Juniperus pauli* Kvaček is based on anatomically preserved leafy shoots, pollen cones, seed cones and seeds (Plate 21, f. 3–7). This species appears to be closely related to *Juniperus* section *Sabina* [a classification not supported in this monograph, AF] in having multi-seeded cones, and scale-like leaves with entire margins (Kvaček, 2002b).

Conclusions

Earlier workers stated that the *Cryptomeria* line seems to be the most ancient of the taxodiaceous Cupressaceae (Miller, 1977), and most paleobotanists look to the Voltziales for probable ancestors. However, the fossil record of Cupressaceae *s. lat.* shows that characters of *Sciadopitys* and *Cunninghamia* are present in the Triassic *Parasciadopitys* from Antarctica. This questions results that separate *Sciadopitys* from the Cupressaceae (e.g., Chase *et al.*, 1993; Chaw *et al.*, 1997), but supports the results of other recent molecular studies implying that *Cunninghamia* may be basal among living cupressaceous genera (Gadek *et al.*, 2000; Kusumi *et al.*, 2000). It is clear that more work is needed on Permian Voltziales to help establish the origins of Cupressaceae, and on Triassic and Jurassic conifers to better understand character evolution within Cupressaceae *s. lat.* The fossil record of *Cryptomeria* itself is not well understood due to the often fragmentary nature of fossil plants, since "cryptomerioid" foliage also is present in genera such as *Sequoia* and *Glyptostrobus*.

Permineralised remains of Cupressaceae are especially abundant in the Upper Cretaceous calcareous nodules from Japan, where *Sciadopitys*, Cunninghamioideae, Taiwanioideae, Sequoioideae and Cupressoideae are all present. The fossil record of Taiwanioideae is especially important here. In North America Cunninghamioideae, Sequoioideae, Taxodioideae and Cupressoideae are well known from the Upper Cretaceous and Paleocene. In Europe *Sciadopitys*, Cunninghamioideae, Sequoioideae, Taxodioideae and Cupressoideae are all well represented. Subfamily Athrotaxoideae seems to have been centered in the Southern Hemisphere since the early Cretaceous, although some conifer remains from North America show several *Athrotaxis*-like characters. Understanding the evolution of this cupressaceous group will require more and better preserved fossil material from both hemispheres.

Our current understanding of the fossil record of Cupressaceae *s. lat.* is based on a very extensive and world-wide fossil record. Characters that are used to delineate the Recent taxa of Cupressaceae, at least at the subfamily level, were present by the Cretaceous. While several extant genera are present by the end of the Cretaceous, there are many more fossil genera. It is clear that the Cretaceous period, while it is currently recognised as a very important time for the evolution of flowering plants, was also a time of great diversity and evolutionary change for Cupressaceae.

Plate 18. **1.** *Sciadopitys cretacea* leaf x.s., Upper Cretaceous, Hokkaido, Japan. × 34. **2.** *Sciadopitophyllum canadense* leaf tips, Paleocene, Alberta, Canada. × 4. **3.** *Sciadopitophyllum canadense* leafy shoot, Paleocene, Alberta, Canada. × 0.6. **4.** *Cunninghamia* sp. Upper Cretaceous, Hornby Island, British Columbia, Canada. × 10. **5.** *Cunninghamiostrobus goedertii* leaf showing adaxial stomatal bands and serrate margin, Oligocene, Washington State, USA. × 4. **6.** *Metasequoia foxii* seed cone, Paleocene, Alberta, Canada. × 2. **7.** *Cunninghamia* sp., Upper Cretaceous, Hornby Island, British Columbia, Canada. × 1. **8.** *Cunninghamiostrobus goedertii* cone x.s., Oligocene, Washington State, USA. × 1.3. **9.** *Metasequoia foxii* seed cone and foliage, Paleocene, Alberta, Canada. × 1.3. **10.** *Metasequoia foxii* seedling showing cotyledons and first leaves, Paleocene, Alberta, Canada. × 1.7. **11.** *Metasequoia foxii* seedlings, Paleocene, Alberta, Canada. × 1. **12.** *Metasequoia foxii* seed cone, seeds and leaves, Paleocene, Alberta, Canada. × 1. **13.** *Metasequoia foxii* foliage and seeds, Paleocene, Alberta, Canada. × 0.8.

Plate 19. **1.** *Drumhellera kurmanniae* pollen cone l.s., Upper Cretaceous, Alberta, Canada. × 40. **2.** *Drumhellera kurmanniae* pollen cone showing pollen in situ, Upper Cretaceous, Alberta, Canada. × 270. **3.** *Drumhellera kurmanniae* pollen, Upper Cretaceous, Alberta, Canada. × 950. **4.** *Drumhellera kurmanniae* pollen cones attached to twig, Upper Cretaceous, Alberta, Canada. × 3. **5.** *Drumhellera kurmanniae* seed cone macerated from ironstone matrix, Upper Cretaceous, Alberta, Canada. × 2. **6.** Seed assignable to *Quasisequoia florinii*, Upper Cretaceous, Scania, Sweden. × 4. **7.** *Drumhellera kurmanniae* leaf x.s., Upper Cretaceous, Alberta, Canada. Arrow indicates resin canal. × 35. **8.** *Quasisequoia florinii* seed cone, Upper Cretaceous, Scania, Sweden. × 4. **9.** *Cupressospermum saxonicum* seed, Upper Miocene, Germany. × 9. **10.** *Cupressospermum saxonicum* seed, Upper Miocene, Germany. × 9. **11.** *Cupressospermum saxonicum* seed cone, Upper Miocene, Germany. × 3. **12.** *Geinitzia formosa* seed cones, Upper Cretaceous, Quedlinburg, Germany. × 1.

Plate 20. **1.** *Glyptostrobus nordenskioeldii* leafy twigs with terminal seed cones, Paleocene, Joffre Bridge, Alberta, Canada. × 1. **2.** *Glyptostrobus rubenosawaensis* seed cones in chert matrix, Miocene, Hokkaido, Japan. × 1. **3.** *Glyptostrobus nordenskioeldii* leafy shoot system, Paleocene, Smoky Tower, Alberta, Canada. × 0.8. **4.** *Taxodium dubium* leafy shoot system, Miocene, Bilina Mine, Czech Republic. × 1. **5.** *Fitzroya acutifolius*, two leafy shoots, Oligocene, Lea River, Tasmania, Australia. × 9. **6.** *Fitzroya acutifolius*, three leafy shoots, Oligocene/Miocene, Monpeelyata, Tasmania, Australia. Arrow indicates where one leaf of whorl of three has been removed. × 8. **7.** *Libocedrus jacksonii* leafy shoot, Oligocene, Little Rapid River, Tasmania, Australia. × 19. **8.** *Libocedrus mesibovii* leafy shoot, Oligocene, Little Rapid River, Tasmania, Australia. × 17. **9.** *Papuacedrus australis* leafy shoot, Oligocene/Miocene, Pioneer, Tasmania, Australia. × 11.

Plate 21. **1.** *Cupressinocladus interruptus* leafy shoot system, Cretaceous, Alexo, Alberta, Canada. × 4. **2.** *Tetraclinis brachyodon* leafy fertile shoot system, Miocene, Radoboj, Croatia. × 1.3. **3.** *Juniperus pauli* leafy shoot system, Eocene/Oligocene, Roudníky, North Bohemia, Czech Republic. × 1.8. **4.** *Juniperus pauli* leafy fertile shoot with attached seed cone, Eocene/Oligocene, Roudníky, North Bohemia, Czech Republic. × 3.5. **5.** *Juniperus pauli* detail of seed cone, Eocene/Oligocene, Roudníky, North Bohemia, Czech Republic. × 7.4. **6.** *Juniperus pauli* detail of seed, Eocene/Oligocene, Roudníky, North Bohemia, Czech Republic. × 9. **7.** *Juniperus pauli* pollen cone, Eocene/Oligocene, Roudníky, North Bohemia, Czech Republic. × 9.

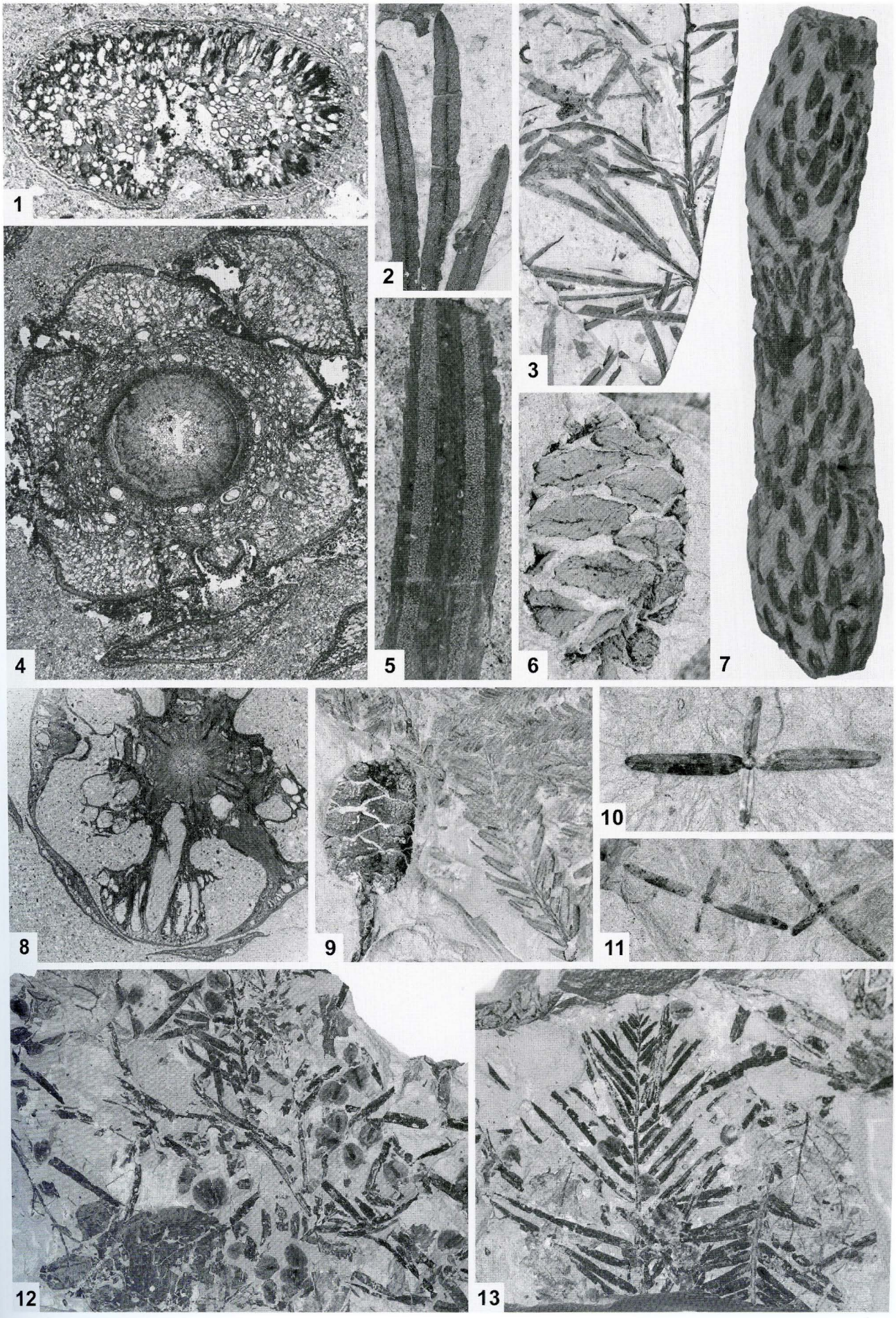
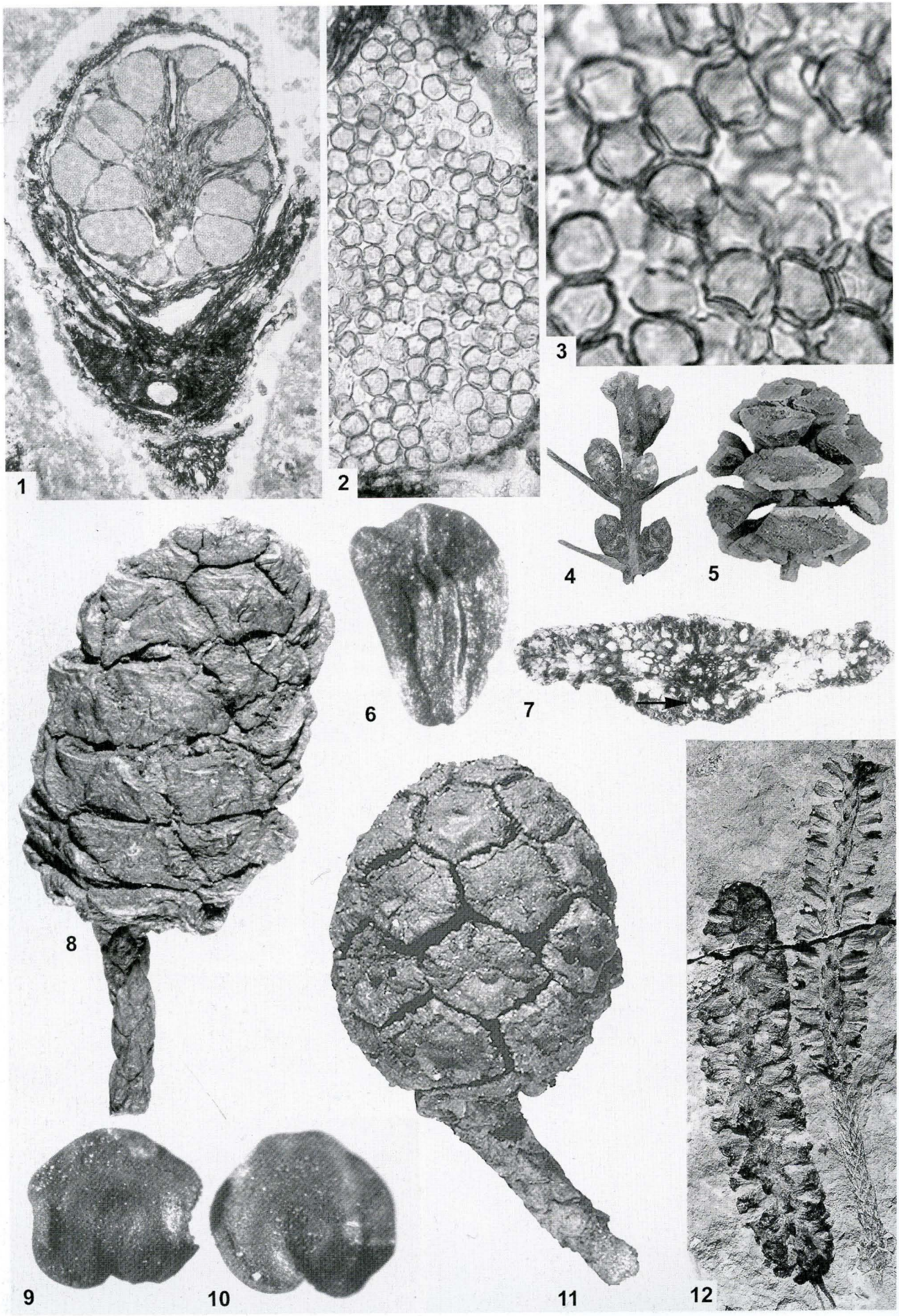


Plate 18.



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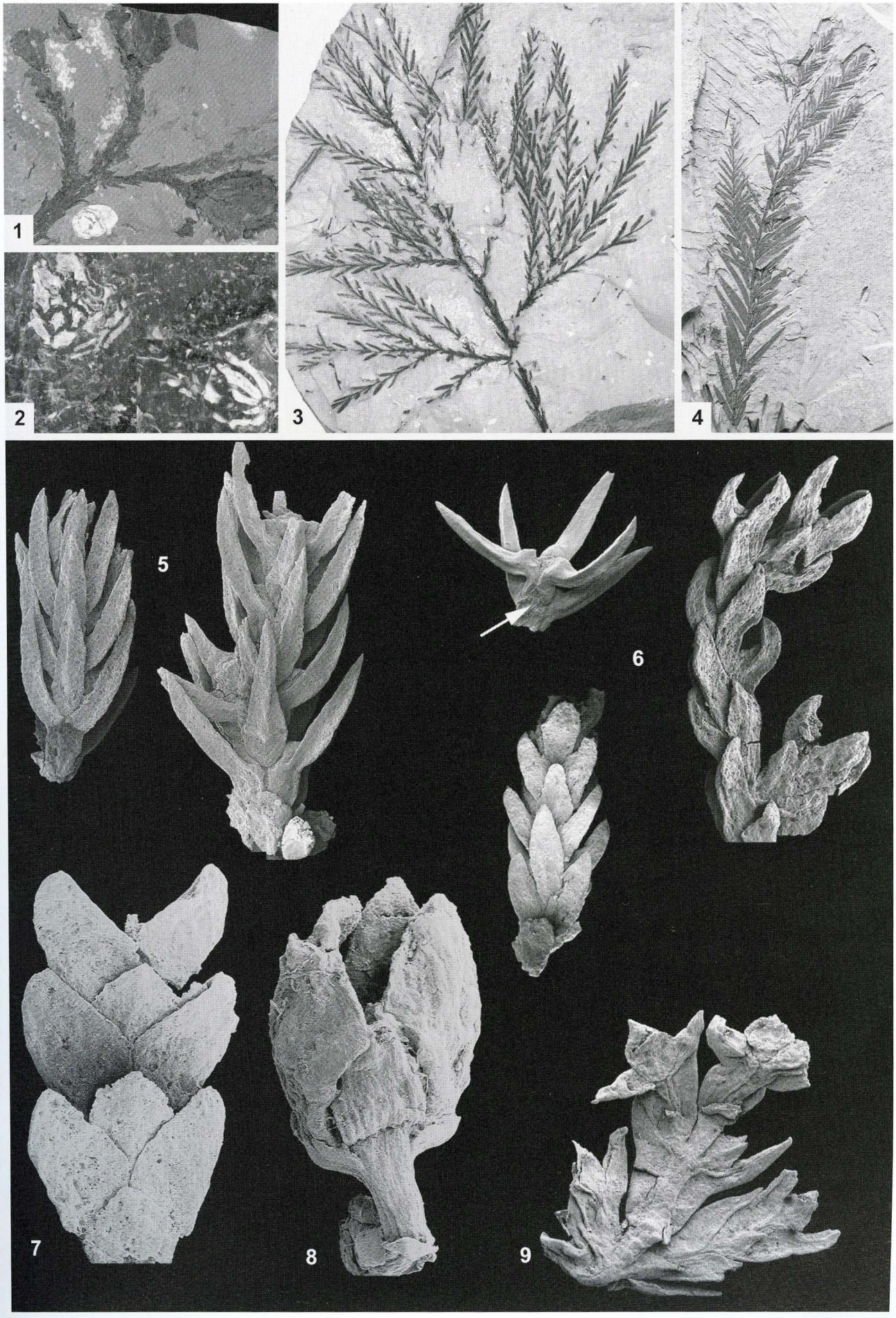

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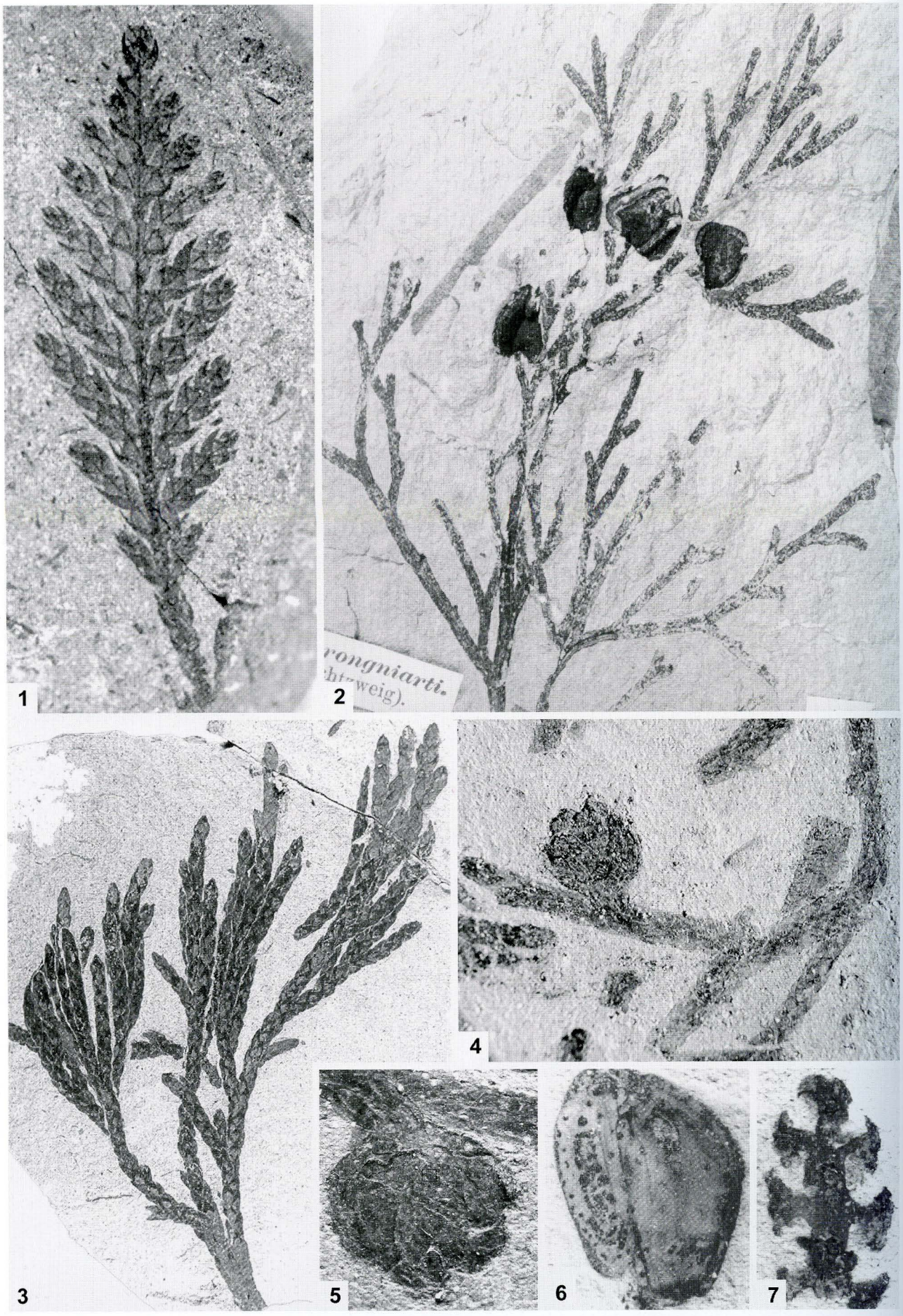

Plate 21.