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Middle Eocene flora of Huadian, Jilin Province, Northeastern China*

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ABSTRACT. The fossil flora of Huadian, Jilin Province, China, is described based on leaves fruits, and one calyx. The megafossil plant remains occur in siltstones associated with oil shales that yield the Middle Eocene mammalian fauna. We provide a floristic inventory as a basis for comparison with floras of corresponding age in North America and Europe. Leaves of *Ginkgo*, *Metasequoia*, *Trochodendroides*, *Platanus*, *Castanea*, *Quercus*, *Carya*, and numerous undetermined dicotyledonous taxa, along with fruits of Menispermaceae (two genera), *Rhus*, *Koelreuteria*, and *Craigia,* and also calyx of *Chaneya* are included. The occurrence of Menispermaceae on the basis of fruits is a new record for the Eocene of Asia. The new combination, *Zizyphoides ezoensis* (Tanai) is presented for leaves of apparent trochodendraceous affinity. The Huadian flora also provides the first unequivocal fruits of *Koelreuteria* (Sapindaceae) from the Eocene of China. The taxonomic composition of the flora is consistent with an interpretation of temperate climate. The Huadian flora shares up to 37% of its megafossil genera with Middle Eocene floras of western North America, but only about 16% of its genera with Middle Eocene floras of Germany. These differences may reflect similar climate and land continuity between western North America and eastern Asia, as well as Eocene climatic differences and intervening barrier between eastern Asia and central Europe.

KEY WORDS: fossil, leaves, fruits, Eocene, Huadian, China

INTRODUCTION

The high diversity of the extant flora of eastern Asia (Qian & Ricklefs 1999) and the large number of genera endemic to the region (Qian 2001) have intrigued botanists for many years. Although the diversity is anomalous in comparison with other parts of the northern hemisphere today, we do not know how far back in the geologic past this condition existed (Thorne 1999). When did the eastern Asian flora achieve the high diversity which characterizes the region today? To address this question, we must examine Asian fossil assemblages of known age in comparison with those of other regions of the northern hemisphere.

In Northeast China, a relatively small number of sites have provided most of our data on early Tertiary megafossil plants (Fig. 1) reviewed by Tanai (1992) and Liu & Ferguson (1996). Those most intensively collected include the Wuyun coal mine of northern Heilongjiang Province, commonly treated as Palaeocene (Xiong 1986), the Eocene to perhaps Oligocene of Yilan coal mine flora of central Heilongjiang (He & Tao 1997), the Palaeocene to Eocene oil shales of Fushun coal mine in Liaoning (Endo 1926 a, b, 1934, 1942, WGCPC 1978), and the Eocene of Hunchun (Ablaev et al. 2003). In addtion, the flora from Sanhe, Jilin Province has been inter-

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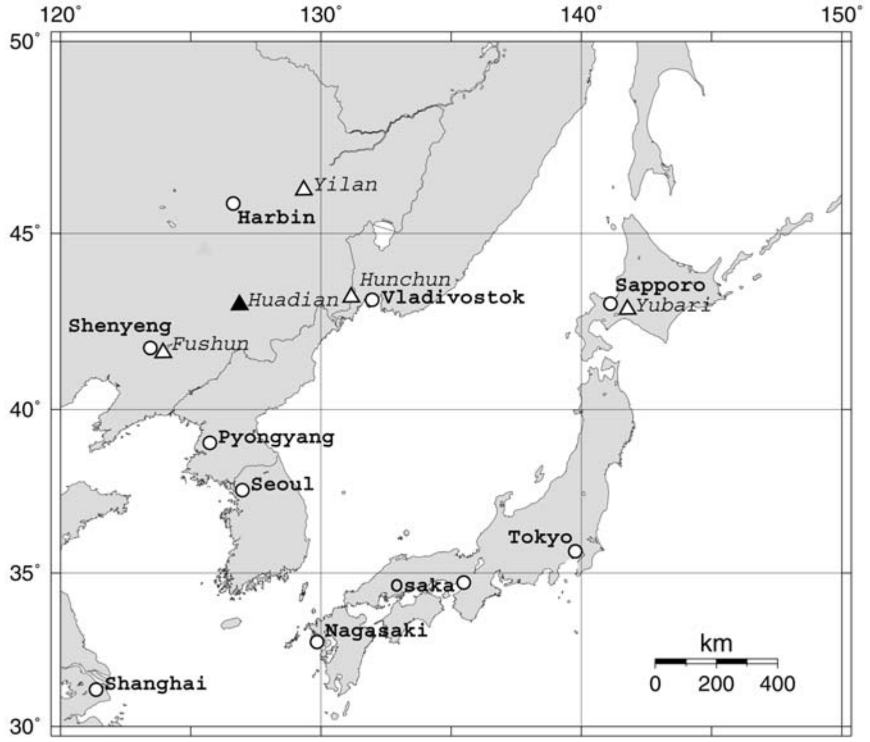

Fig. 1. Map showing position of Huadian (black triangle) and selected other Eocene localities in eastern Asia (white triangle), including Fushun, Yilan, Hunchun (China) and Yubari (Japan)

preted as Oligocene based on leaf correlations (Guo & Zhang 2002). In each of these cases, the geologic age has been estimated on the basis of floristic correlations (megafossil and/or palynological). The precision of these age estimates is uncertain because there is lack of corroborative evidence from other methods. It is not surprising, therefore, that different authors have proposed different ages for the same palaeobotanical assemblages. The same situation exists for early Tertiary leaf floras in other parts of eastern Asia, including Russia, Korea, and Japan.

To ascertain the age of fossil floral assemblages, it is desirable to obtain fossils directly from volcanically derived sediments that may be dated radiometrically. However, this has not been possible for these localities. Another means of independently dating the floras is by collecting fossil plants from localities in known proximity to marine invertebrate or mammalian fossil localities. Because mammals evolve at a faster rate than plants, we may expect greater precision of dating through correlations based on the former.

In this paper we give a preliminary account of a newly collected fossil flora associated with a well known Middle Eocene mammalian fauna at Gonglangtou near Huadian, in Jilin Province, northeastern China (Fig. 1). The flora is significant as the first Palaeogene plant assemblage from this part of Asia to be dated independently of the fossil plants themselves. The vertebrate fauna of the Gonglangtou oil shales includes a tarsiiform primate (*Asiomomys changbaicus*, Beard & Wang 1991), two galericine Erinaceids, a primitive soricid, and two possible sciuravid rodents, along with fish, reptiles and birds (Wang & Li 1990). The fauna is diagnostic of the Middle Eocene (Beard & Wang 1991, Beard, pers. comm. 2000) although its more precise position within this interval is unknown. The leaves and fruits treated in this article came from a siltstone lying between layers of oil shales that contain the Middle Eocene fauna. Hence, the mammalian fauna provides a good estimate for the age of the flora.

The occurrence of plant fossils at Huadian was observed by Minagawa (1943) during Japanese occupation of the region. Two genera were mentioned (*Quercus* and *Fagus*), but they were not illustrated or described and we have not relocated those collections. New leaf and fruit collections allow the recognition of 41 types of fossil plants.

Huadian is situated to the west of Chanbaishan Mountain, in hilly country with elevation below 500 m; relative elevation difference across the region is between 50 to 100 m. The modern climate is temperate with mild and continental monsoon. Mean annual temperature is 4 to 6°C and annual precipitation ranges from 625 to 800 mm. The natural vegetation apparently was mixed forest dominated by *Abies holophylla* and *Pinus koraiensis*. With the destruction of *Abies-Pinus* forest, secondary growth is dominated by *Betula platyphylla*, *Populus davidiana*, *Quercus mongolica*, *Fraxinus mandshurica*, and *Juglans mandshurica*. Other species such as *Betula costata*, *B. davurica*, *Acer mono*, *A. mandshurica*, *Phellodendron amurense, Tilia mandshurica*, *Ulmus propinqua*, *U. macrocarpa*, and *Fraxinus chinensis* var. *rhynchophylla* can be found in the deciduous broadleaved forest (Xing 1988). The Eocene fossil assemblage from Huadian differs significantly from the modern flora.

MATERIAL AND METHODS

The leaves, fruits, and calyx occur in a siltstone that was collected from the tailings of an underground oil shale mine at Gonglantou, Huadian County, Jilin Province. The Gonglantou oil shales are distributed over 15 km east to west with a dip of 10 to 30° to the SW and a strike of N 60 to 80°W (Nishida 1940). Vertebrate fossils, including fish (Zhou & Sun 1985), mammals and reptiles (Wang & Li 1990, Beard & Wang 1991) have been reported from these oil shales. Although we visited the several mines now active in the valley, plant megafossils were found only at Gonglangtou mine number 3, which is situated at N42°59′54″, E126°51′58″ (GPS; datum WGS84).

Collections were made from sediments brought to the surface and discarded by the miners. In addition, we confirmed the stratigraphic level of the fossiliferous stratum by touring the underground mine. The greenish grey, plant-bearing siltstone, which is about 8 meters thick, directly overlies oil shale number 6, and is in turn overlain by oil shale number 5. Although the vertebrate and invertebrate fossils are preserved directly in the oil shales, the leaves and fruits are confined to the siltstone. The oil shale is fissile and has a dark colour due to its organic-rich composition, and is interpreted to represent swampy lake deposition. The siltstone and sandstone sediments are light in colour, and are inferred to represent flooding from an adjacent stream. Both the oil shale and the siltstone contain abundant dispersed pollen, and studies are underway to compare the palynological assemblages (Chen 2002).

The specimens forming the basis of this paper were collected during one-day visits to the mine in 2000, 2001, and 2002. They are deposited in the Palaeobotanical Collection of the Botanical Institute, Academia Sinica, Beijing (PEPB), with some duplicates at the Florida Museum of Natural History, University of Florida (UF). Comparative work with other Middle Eocene floras was done at UF (West Branch Creek, Clarno flora), the Burke Memorial Washington State Museum, Seattle (Republic flora), and the Senckenberg Museum of Natural History, Frankfurt, Germany (Messel flora).

TAXONOMIC COMPOSITION OF THE MEGAFOSSIL FLORA

Currently, we recognize 41 types of fossil plants in the Huadian megafossil flora including 35 based on leaves, 5 based on fruits, and one calyx. No ferns were recovered, but three gymnosperms (*Ginkgo, Metasequoia*, and Cephalotaxaceae) are present. The majority of species are dicotyledonous angiosperms.

GINKGOACEAE

Ginkgo adiantoides (Unger) Heer

Pl. 1, fig. 1

Specimens. PEPB 054033, 053965, 054034.

Fan-shaped *Ginkgo* leaves ranging from small (1.7 cm long) to medium (3.5 cm long) are present. They show the typical radiating, subparallel, dichotomizing venation of the extant genus and have an undulating, but not dissected, distal margin. Cuticle is preserved but was not analyzed in this study.

Ginkgo leaves from the Tertiary that morphologically resemble the one living species are generally placed in the fossil species *Ginkgo adiantoides* (Tralau 1968). *Ginkgo* has an excellent fossil record in the Tertiary of the northern hemisphere, and in northeastern China, is also known from the Fushun (WGCPC 1978) and Yilan (He & Tao 1997) floras.

TAXODIACEAE

Metasequoia disticha (Heer) Miki

Pl. 1, fig. 2

Specimens. PEPB 054040, 053964, 054052.

The dawn redwood, *Metasequoia*, is recognized based on a few branchlets showing opposite needles diagnostic of that genus. The needles are 8–12 mm long and 1.5 mm wide, and have blunt, rounded apices.

Metasequoia is common at other Palaeogene sites in northeastern China (WGCPC 1978), as well as in Russia (Kodrul 1999). Although confined in its modern native distribution to China, *Metasequoia* is well-represented in the Tertiary of North America (for reviews, see Meyer & Manchester 1997, Stockey et al. 2001.

CEPHALOTAXACEAE

Cephalotaxus sp.

Pl. 1, fig. 3

Specimens. PEPB 054084, 054125.

Cephalotaxus is represented by a few incomplete needles. They are at least 3.7 cm long and 8.0 mm wide, and show two longitudinal dark stomatal bands only 0.8 mm apart, closely running to the midvein.

These needles closely resemble those from Yilan flora (He & Tao 1997), for which the generic identification has been confirmed by cuticular analysis.

MENISPERMACEAE

Two kinds of fruits from Huadian are significant in providing the earliest confirmed records for Menispermaceae in the Tertiary of eastern Asia.

Diploclisia sp.

Pl. 4, figs 1, 2

Specimen. PEPB 054019a, b.

Endocarp 4.0 mm long and 3.5 mm wide, obliquely obovate with broadly rounded dorsal surface and truncate base, with a keel along the dorsal surface in plane of symmetry; lateral face bearing a horseshoe-shaped ridge separating dorsal and ventral ornamentation; dorsal surface with 26 radially aligned ribs alternating with rounded grooves, ventral flank smooth, concave.

Horseshoe-shaped endocarps with fluted sculpture are diagnostic of the Menispermeae tribe of the Menispermaceae. This species, represented by a single specimen, is similar to *Diploclisia auriformis* (Hollick) Manchester from the Eocene of Alaska, England, and Oregon (Manchester 1994), but is about 2 mm shorter and 0.5–1.5 mm narrower.

Palaeosinomenium venablesii Chandler

Pl. 4, fig. 3

Specimen. PEPB 054014.

Endocarp 3.0 mm long and 3.5 mm wide, obliquely C-shaped with a broadly rounded dorsal margin and truncate ventral margin, with a keel along the dorsal surface in plane of symmetry; lateral face bearing a c-shaped ridge separating dorsal and ventral ornamentation, with about 20 radially aligned ridges alternating with rounded grooves, fluted both dorsally and ventrally.

This specimen corresponds precisely to the species *Palaeosinomenium venablesii*, previously recognized from the early Eocene of England (Chandler 1961) and Middle Eocene of Oregon (Manchester 1994). It differs from *Diploclisia* described above, by being wider than high, and by having sculpture on the ventral as well as dorsal flanks. Extant genera with similar endocarps occur only in the tribe Menispermeae. The living genera most similar in endocarp morphology are *Sinomenium* and *Menispermum* (Chandler 1961).

cf. **Menispermaceae**

Pl. 3, fig. 9

Specimen. PEPB 054057.

One leaf 5.6 cm long and 4.2 cm wide shows an entire margined lamina with a cordate base and acute apex. Venation actinodromous, with 5 primary veins radiating from the base. A thin vein runs along the margin of the lamina.

This syndrome of architectural features (entire margin, cordate base, actinodromous venation and fimbrial vein) characterizes at least 18 genera of the Menispermaceae family (Thanikaimoni 1984). Fossil leaves attributed to Menispermaceae as *Cocculus* and *Menispermites* in earlier literature have turned out to be *Zizyphoides*, an extinct genus unrelated to Menispermaceae (see below).

CERCIDIPHYLLACEAE

Trochodendroides arctica (Heer) Berry

Pl. 1, fig. 4

Specimens. PEPB 053901, 053992, 053090.

The lamina size ranges from 3.0–7.0 cm long, 3.2–6.0 cm wide. The leaves are recognized by actinodromous primary venation with 3–5 major veins arising from the base and closely spaced, rounded marginal, glandular teeth, with a principal vein and two accessory veins entering each tooth.

This leaf type, considered to represent Cercidiphyllaceae (Crane 1984), has been found at numerous localities throughout early Tertiary of northern hemisphere, usually in association with fruits of the extinct genus *Nyssidium* (Crane 1984). In Northeast China, they were previously recognized from the Wuyun (Tao & Xiong 1986), and are also observed in the Yilan (identified as *Cercidiphyllum arcticum* (Heer) Brown, He & Tao 1997) and Fushun (WGCPC 1978) floras.

Nyssidium sp.

Pl. 4, fig. 4

Specimens. PEPB 054008, 054011, 054022, 054111.

Follicles elliptical, 5.0–7.0 mm long, and 2.4–3.3 mm wide, with striations that are oblique to the long axis.

Only a few isolated fruits or carpels were found at Huadian, although complete inflorescences or infructescences occur at Fushun and Yilan (Manchester, own observation).

TROCHODENDRACEAE

Zizyphoides ezoensis (Tanai) **comb. nov.**

Pl. 1, fig. 5

Specimen. PEPB 054061.

Basionym. *Cocculus ezoensis* Tanai. Tanai 1970. J. Fac. Sci. Hokkaido Univ., ser. 4, Geol. Mineralogy, 14 (4): 478, pl. 11, figs 1, 5, pl. 12, fig. 2.

Leaf probably almost orbicular, preserved length of 5.0 cm, width of 5.7 cm, base obtusely rounded. Margin in the lower part of the leaf entire, crenate in the upper part. Venation actinodromous, the two lateral primaries curving upwards an acute angle. Visible length of petoliole 2.2 cm.

The above description is based on the single specimen known from Huadian, however the species is common at many other sites in the Paleogene of Asia. This leaf type is similar to *Trochodendroides* in the overall shape and palmate venation, but differs by having more gentle dentations; the lower part of the lamina is entire-margined. *Zizyphoides* foliage is associated with fruits of the extinct trochodendraceous genus *Nordenskioldia* at numerous Palaeogene sites around the northern hemisphere (Crane et al. 1991), including the type area for the species *Cocculus ezoensis* (Tanai 1970). The genus persisted with the same kind of fruits into the Middle Miocene of western North America (Manchester et al. 1991). We have not recovered *Nordenskioldia* fruits from Huadian, although isolated fruitlets are present in low abundance in the Fushun flora (Manchester, own observation).

PLATANACEAE

cf. ***Platanus*** sp.

Pl. 2, fig. 3

Specimen. PEPB 054115.

This trilobate leaf has regularly spaced teeth with rounded sinuses. The base is broken so it is not possible to determine if the basal venation was really like that of *Platanus*. In the characters preserved, the lamina is comparable to that of leaves of extant *Platanus*.

Platimeliphyllum sp.

Pl. 2, fig. 4, 5

Specimen. PEPB 053987.

One leaf specimen appears to correspond to a species that is very common at Fushun (WGCPC 1978). Although this species was formerly assigned to *Betula fushunensis* Chen (WGCPC 1978), its architectural and epidermal characters are diagnostic of Platanaceae, and it commonly co-occurs with platanaceous reproductive structures in Palaeocene and Eocene sediments of the northern hemisphere (Maslova 2002). The genus *Platimeliphyllum* Maslova (2002) accommodates leaves of this kind, which resemble some Hamamelidaceae in general form but have cuticle and associated reproductive structures diagnostic of Platanaceae. *Platimeliphyllum* is recognized by the combination of sharp teeth that have prominently concave apical sinuses, spaced one per secondary vein as well as at the extremities of main branches of the secondary veins, percurrent, widely spaced tertiary veins, the basal two pairs of secondaries each giving off several successive branches to the margin, and by the presence of thick, well preserved cuticle.

HAMAMELIDACEAE

Liquidambar sp.

Pl. 3, figs 6–8

Specimens. PEPB 054058, 054064, 054065.

Fragmentary trilobate leaves est. 6 cm long and 7 cm wide, with actinodromous venation and closely spaced glandular teeth on the leaf margin. The primary veins spread 45 degrees apart. The lobes are gradually narrowed and apically attenuate.

The three specimens from Huadian are very similar to *Liquidambar miosinica* Hu & Chaney from the Miocene Shanwang flora. Horiuchi (1996) processed cuticle of comparable leaves from the Miocene Yagii flora of Japan. The paracytic stomatal complexes confirmed affinity to *Liquidambar* and distinguished the leaves from those of morphologically similar *Acer* and *Kalopanax* species. The genus is also known from leaves at the Yilan flora (He & Tao 1997).

cf. ***Parrotia*** sp.

Pl. 2, fig. 6, Pl. 3, fig. 11

Specimens. PEPB 054036, PEPB s.n.

The lamina is elliptical, 5.9 cm long, 2.8 cm wide, with a cuneate-rounded base and acute apex, with teeth distributed only in the apical half of the leaf, arranged one per secondary vein. The teeth have straight or convex lower sides, and concave apical sides. Petiole about 0.9 mm long, thin (0.3 mm).

This leaf resembles those of extant *Parrotia*, although similar in lamina form to *Platimeliphyllum.*

FAGACEAE

cf. ***Quercus berryi*** Trelease

Pl. 1, figs 7, 8

Specimens. PEPB 053852, 053920, 053970, 053979.

These narrow elliptical laminae are characterized by a cuneate base, acute apex, and range from about 3.5 to 10.0 cm long and 1.3 to 2.0 cm wide. They have pinnate venation with up to 13 pairs of secondary veins and are serrate with teeth in the upper 2/3 of lamina, arranged one tooth per secondary vein.

This species shows features found in some species of *Quercus*, *Castanopsis* and *Lithocarpus*. It compares favorably with *Quercus berryi* of the lower Oligocene Bridge Creek flora of Oregon in western North America (Meyer & Manchester 1997).

Castanea fujiyamae Tanai

Pl. 1, figs 6, 9

Specimens. PEPB 054085, 053966, 054102, 054114.

Leaves with a relatively stout midvein whose course slightly deflected by the departure of secondary veins; venation pinnate, straight and parallel secondary veins (ca. 13 pairs) and prominent spinose teeth (one per secondary vein) with concave apical sides and convex to straight basal sides; tertiary veins percurrent.

The syndrome of straight pinnate secondary veins and one spinose tooth per secondary vein characterizes several genera of Fagaceae. These leaves compare favorably with those described as *Castanea fujiyamae* from the Early Oligocene of the Kitami region of northeastern Hokkaido, Japan (Tanai 1970, 1995).

cf. ***Fagus*** sp.

Pl. 2, fig. 2

Specimen. PEPB 054083.

Leaf narrow elliptic, est. 7.5 cm long, 2.2 cm wide, base rounded, asymmetrical. Venation pinnate, craspedodromous, primary vein slightly curved, with ca.16 pairs of secondary veins. Teeth small, arranged one per secondary vein.

This specimen conforms in many of its characters to *Castanea fujiyamae*, but has less pronounced teeth and an asymmetrical base. In these features, it is more similar to extant *Fagus*. The presence of this genus during the Eocene is confirmed by both leaves and fruits from western North America (Manchester & Dillhoff, 2004).

BETULACEAE

Alnus sp.

Pl. 6, fig. 9

Specimen. PEPB 053980.

Only a small part of one leaf preserved, with serrate margin. Venation pinnate, with craspedodromous secondary veins that are slightly curved. Tertiary veins percurrent, alternate. Two or more nonglandular teeth per secondary vein.

This leaf type corresponds to *Alnus* in the shape and distribution of teeth and the spacing and course of the secondary and tertiary veins. Dispersed pollen diagnostic of the genus is also present in the siltstone (Chen 2002). Leaves of *Alnus* are more common at the Yilan (He & Tao 1997) and Fushun (WGCPC 1978) localities.

JUGLANDACEAE

Carya sp.

Pl. 3, figs 1, 4, 5

Specimens. PEPB 053976, 054060, 054089, 054041.

Leaflets oblong with cuneate, asymmetrical base, estimated length 4.3–10.0 cm, width 1.5–3.0 cm. Margin finely serrate, non-glandular. Venation pinnate, semicraspedodromous, with 8–14 pairs of secondaries that form smooth marginal loops. Intersecondaries rare or absent. Tertiary veins percurrent, opposite. Petiolules up to at least 4.5 mm in length.

This taxon, represented at Huadian by four incomplete leaflets, is similar to the species initially described as *Carya ezoensis* Tanai from the Kushiro Coal field of Hokkaido, Japan (Tanai 1970). Although the species was formally transferred to *Pterocarya* (see Tanai 1992), the correct assignment to *Carya* still seems probable. Pollen diagnostic of *Carya* is also present in the Huadian palynoflora (Chen 2002).

cf. **Juglandaceae**

Pl. 3, figs 2, 3

Specimens. PEPB 053974, 053969, 054068.

Lamina ovate, est. 5.3–11.0 cm long, 2.6–5.0 cm wide, slightly asymmetrical, base cuneate, apex attenuate. Venation pinnate, craspedodromous, 8 to 10 pairs of secondaries that are curved, sometimes branching; intersecondary veins common, tertiaries percurrent. Margin crenate, teeth acute to right angled.

The leaflets of this species differ from *Carya ezoensis* by more frequent intersecondary veins, and less pronounced asymmetry.

MALVACEAE s.l.

Craigia sp.

Pl. 4, figs 5–7

Specimens. PEPB 054005, 054010, 054016, 054026, 054104, 054020, 054024, 054103, 054031, 054088.

Isolated elliptical capsule valves of *Craigia*, ranging from 11 to 22 mm in length, are common in the Huadian assemblage, They match those of the modern species and of other fossil occurrences in every detail of morphology and venation. Often, the valves are folded along the medial line, such that one half of the valve lies in a different plane from the other. The fusiform outline of the locule is visible along the midsection of the valve.

Craigia, which is native to southwestern China, southeastern Tibet, and Vietnam today, was widespread in the northern hemisphere, ranging from Eocene to Oligocene in western North America and from Oligocene to Pliocene in Europe (Bůžek et al. 1989, as *Pteleaecarpum*; Kvaček et al. 1991, 2002). It is also known from Fushun, Yubari, and other Eocene localities of eastern Asia (Bůžek et al. 1989), the Oligocene Sahne flora of Jilin (Guo & Zhang 2002) and extends to the Miocene of Sikhote-Alin (as *Abronia pliocenica* in Akhmetiev 1973). Traditionally, *Craigia* has been placed either in the Sterculiaceae or Tiliaceae, but these families are non-monophyletic and are now treated as Malvaceae sensu lato (Judd & Manchester 1997).

Plafkeria basiobliqua
(Oishi & Huzioka) Tanai

Pl. 5, figs 1, 2

Specimens. PEPB 053984, 053987, 053993.

These entire-margined leaves are ovate and asymmetrical, and measure 4.5–5.3 cm long by 3.0 cm wide. Venation actinodromous, four to six prominent veins radiating from the base of the lamina, including the primary vein and prominent laterals; tertiaries are percurrent.

These leaves match those known from the Eocene of Hokkaido, Japan (Tanai 1989) and the Oligocene Sahne flora of Jilin (Guo & Zhang 2002). At many localities in western North America and Asia, *Plafkeria* leaves co-occur with *Craigia* fruits. Although they differ from leaves of extant *Craigia* in being entire-margined and have more prominently actinodromous venation, the characters of *Plafkeria* are consistent with the malvalean family to which *Craigia* belongs. It is possible that this leaf type was borne by an extinct species of *Craigia*.

LEGUMINOSAE

Some laminae in the Huadian assemblage resemble those of the Leguminosae, but lack sufficient details to assign more precisely. Leguminous fruits were not found at Huadian but three kinds of legume pods are present in the collections from Fushun (WGCPC 1978).

Legume leaflet type 1

Pl. 5, figs 9, 10, Pl. 6, fig. 6

Specimens. PEPB 054105, PEPB s.n.

Lamina elliptical to ovate, asymmetrical, 2.0–3.5 cm long by 1.0–1.2 cm wide, base rounded to cuneate, apex acute. Margin entire, venation pinnate, with secondary veins barely visible. Petiolule 2–3 mm long, with transverse striations.

The transversely striate, short petiolules indicate that they were probably pulvini. The presence of pulvini, and the shape and venation of the laminae are consistent with assignment to Leguminosae, although the more precise affinities within the family cannot be determined without accompanying fruits or flowers.

Legume leaflet type 2

Pl. 5, fig. 8, Pl. 7, fig. 2

Specimens. PEPB 054072, 054076.

Lamina ovate, symmetrical, 5.4–5.5 cm long and 2.1–3.2 cm wide, base rounded, apex acute. Margin entire, secondaries pinnate, camptodromous.

These leaflets differ from those of type 1 by their symmetrical, and larger laminae. The petiolules were not preserved on these specimens, but the general form of the laminae is consistent with that of many genera in the Leguminosae.

ANACARDIACEAE

Rhus sp.

Pl. 5, fig. 13

Specimen. PEPB 054012.

Endocarp broadly elliptical, 5.5 mm wide, 3.1 mm high, with prominent meridional ribs.

The morphology of extant and fossil *Rhus* endocarps was reviewed by Manchester (1994) along with the record of well preserved fruits from the Middle Eocene of Oregon. The specimen from Huadian shows only the external form of the endocarp, so that the internal anatomy cannot be confirmed, but in the features preserved the specimen is consistent with *Rhus*.

cf. ***Rhus*** sp.

Pl. 2, fig. 1

Specimen. PEPB 053977.

A narrow elliptic leaf, 6.8 cm long, 2.3 cm wide, with rounded base and attenuate apex, prominent teeth (except at base and apex), and about 13 pairs of craspedodromous secondary veins which sometimes extend to the sinus rather than to the apex of the tooth. Intersecondary veins common.

The presence of intersecondary veins, and secondary veins that enter the sinuses rather than the tooth apices, are features consistent with, although not limited to, *Rhus*.

SAPINDACEAE

Koelreuteria sp.

Pl. 4, figs 8–10

Specimen. PEPB 054018.

Elliptical fruit valve, 25 mm long and 16 mm wide, with a midvein and transverse reticulate venation. A longitudinal fracture along the midline of the specimen (Pl. 4, fig. 10) reveals that the median longitudinal septum extended only halfway from the base to the apex of the valve.

This well preserved fruit valve from the Huadian flora provides the earliest unequivocal record of this genus in China, although another specimen was recently reported from the Eocene of Primorye, Far Eastern Russia (Ablaev 2000). The septum to which seeds attached extends only halfway along the locule – a feature diagnostic of the genus (see also Manchester 1999, fig. IIA). Fruits previously identified as *Koelreuteria* from the Eocene of northeastern China and Japan turned out to be incorrectly determined, and were actually fruits of the malvaceous genus *Craigia* (Kvaček et al. 1991). Isolated fruit valves of *Craigia,* which are common in the Huadian assemblage, are distinguished from those of *Koelreuteria* by the fusiform locule area and serial seed attachment of the former, as well as minor differences of venation and smaller size.

cf. ***Acer*** sp.

Pl. 6, figs 1, 3

Specimens. PEPB 054121, 053989.

Trilobed lamina 7.5 cm length, with obtuse base, acute lobes, rounded lobal sinuses, actinodromous venation, with 35 degrees between adjacent primary veins and craspedodromous secondary veins. From base of lamina with 3 primary veins (one in each lobe) radiating, but also two additional strong outer secondaries arising from the same point. Five pairs of curved secondaries arising from midvein. Although the margin is mostly entire in appearance, there are small teeth at the secondary vein endings.

These trilobed leaves differ from *Liquidambar* by more widely spaced, small, nonglandular teeth, and from *Platanus* by teeth and sinuses that are less pronounced. The leaves are similar in general respects to *Acer.* Fruits of *Acer* have not be found at Huadian, although they are present at the Fushun (WGCPC 1978) and Yilan (He & Tao 1997) localities.

RUTALES

Chaneya tenuis (Lesquereux) Wang & Manchester

Pl. 8, figs 4, 5

Specimen. PEPB 054129.

Calyx 2.6 cm in diameter, with four sepals radiating from a common point in a symmetrical pattern suggesting that a fifth sepal was originally present, prior to fragmentation of the specimen. One of the sepals is complete, ovate in shape with a rounded apex, and the two on either side of it are missing their apices but show their lateral margins. Although the forth is still more fragmentary, they all show parallel primary veins that extend longitudinally and which are interconnected by cross veins.

Despite the fragmentary condition of this specimen, it appears to match the shape and venation of the calyx of *Chaneya*, an extinct genus that is well represented in the Yilan (Eocene) and Shanwang (Miocene) floras of China as well as in the Eocene of western North America (Wang & Manchester 2000).

CORNACEAE

Cornus sp.

Pl. 3, fig. 10

Specimen. PEPB 054994.

Lamina elliptical, length incomplete, est. 10.0 cm, width 4.8 cm, base rounded, apex unknown, margin entire; petiole 1.7 cm long and 1 mm thick. Venation eucamptodromous, only some curved secondary veins on the leaf base are visible; tertiary veins percurrent, perpendicular to the midvein, and widely spaced (about 3–5 mm apart).

Cornus is represented by a single specimen, recognizable by strong curved secondary veins, widely spaced percurrent tertiaries that are perpendicular to the midvein, and entire margin.

UNDETERMINED SERRATE LEAVES

The following leaf types remain unidentified, but are summarized because they contribute to the diversity and climate interpretations.

Serrate type 1

Pl. 5, figs 3, 4, 11

Specimens. PEPB 053982, 053990, 053997, 054070, 054071, 054092.

Lamina ovate, slightly asymmetrical, 2.3–8.0, avg. 5.0 cm long, 1.3-5.0 long, avg. 3.0 cm wide, length-width ratio 1.5–1.8. Base rounded, apex acute. Petiole greater than 5 mm long, thin.

Margin serrate, apical side of teeth concave, basal convex. Venation pinnate, craspedodromous, with 7–9 pairs of uniformly curving secondary veins; tertiary veins thin, closely spaced, straight percurrent oriented oblique to the midvein. The secondary veins give off a series of branches to the margin.

This leaf type is relatively common at Huadian. It shows similarities to leaves of Celtidaceae, and Urticaceae, but is distinguished from most extant genera in these families by the small size of the teeth.

Serrate type 2

Pl. 5, fig. 7

Specimen. PEPB 054130.

Lamina ovate, 5.0 cm long and 3.4 cm wide, symmetrical, base obtuse, apex unknown. Venation pinnate, with seven pairs of craspedodromous secondary veins. Margin serrate with blunt teeth distributed one or more per secondary vein.

This is represented by a single specimen, the affinities of which remain undetermined.

Serrate type 3

Pl. 6, figs 2, 4

Specimen. PEPB 054093.

This fragmentary leaf of unknown overall shape was at least 10 cm long, and 9 cm wide with a rounded base and serrate margin. Venation actinodromous, with 5 veins arising from the base of the lamina, secondary veins craspedodromous, one pair of relatively week veins is visible in lower part of lamina. Margin doubly serrate, with secondary teeth on both apical and basal sides of the primary teeth. Sinuses between teeth concave.

The affinities of this leaf fragment with its distinctive doubly serrate, apparently nonglandular teeth, with concave sinuses, remain unknown.

Serrate type 4

Pl. 7, fig. 3

Specimen. PEPB 054037.

Apical half of a leaf ca. 4.5 cm width, venation pinnate, craspedodromous, secondaries widely spaced. Margin crenate, teeth prominent, rounded, not spiny.

Serrate type 5

Pl. 7, fig. 4

Specimen. PEPB 054107.

Lamina palmately lobed, 8 cm long, ca. 9 cm wide. Margin serrate, teeth small. Venation palmate, secondary veins craspedodromous. Petiole 4.0 cm long, 1.1 mm thick.

This leaf is distinctive by its long petiole and palmately lobed outline. The single specimen is folded in such a way as to obscure the original outline of the lamina. The small teeth at the margin are similar to those of the described above *Acer* sp., but that specimen has only three lobes.

Serrate type 6

Pl. 7, fig. 5

Specimen. PEPB s.n.

Lamina narrow obovate, ca. 8.5 cm long, 4.6 cm wide, base cuneate, asymmetrical, venation pinnate, margin serrate in upper half of lamina. Petiole 2.2 cm long, and 1 mm thick.

Because of its asymmetry, this lamina might represent a leaflet. The petiole (or petiolule) is relatively long. There is some similarity to *Fraxinus*, but no fruits of that genus have been recovered.

Serrate type 7

Pl. 8, fig. 1

Specimen. PEPB s.n.

Basal part of leaf est. 6.8 cm long and 2.7 cm wide, with pinnate brochidodromous venation and finely serrate margin.

Serrate type 8

Pl. 8, figs 2, 3

Specimen. PEPB 054117.

Lower part of leaf more than 5.0 cm long and est. 3.0 cm wide, with serrate margin. Venation pinnate, veins entering submedially the acute teeth.

UNDETERMINED ENTIRE-MARGINED LEAVES

The following leaf types remain unidentified, but are included to illustrate the full diversity of the flora as currently known.

Entire-margined type 1

Pl. 5, fig. 5

Specimen. PEPB 054035.

Leaf ovate, 4.8 cm long, 2.3 cm wide, base cuneate, asymmetrical, apex acute, margin entire. Petiole 8 mm long and 0.5 mm thick. Venation pinnate, cuticle thick.

Entire-margined type 2

Pl. 5, fig. 6

Specimen. PEPB 054010c.

Lamina oblong, est. 6.5 cm long, 3.7 cm wide, incomplete at base and apex, entire margined. Venation pinnate, brochidodromous, with thick primary and secondary veins; they arise at angles of 80 degrees from the midvein and arching to the margin. Intersecondary veins common. Tertiary veins percurrent, opposite and alternate. Cuticle thick.

Entire-margined type 3

Pl. 5, fig. 12

Specimen. PEPB 054099

Lamina that appears to be oblong, although only the apical part is preserved, more than 25 mm long and 18 mm wide. Margin entire. Venation pinnate, brochidodromous, midvein straight, secondary veins thin, looping within the margin; intersecondaries common. Intramarginal vein present.

This lamina has excellently preserved details of venation that present a pattern different from the other fossil leaves known from Huadian. Although tentatively treated as a leaf, it could alternatively represent a bract, such as the central lobe of an *Engelhardia* fruiting bract. More complete specimens are needed to determine the affinities of this specimen.

Entire-margined type 4

Pl. 6, figs 7, 8

Specimens: PEPB 054029, 054080.

Leaves very wide ovate, 3.5–3.6 cm long and 3.1–4.0 cm wide, margin entire. Venation pinnate, with 5 pairs of camptodromous secondary veins; lowest pair of secondary veins particularly stout, together with the midvein giving a 3-veined appearance to the lamina.

This lamina type is easily recognized by its shape and the three veins radiating from the base. Although the base of the lamina is visible in these specimens, no petiole was preserved, indicating that the leaf was easily separated at the base of the blade.

Entire-margined type 5

Pl. 6, fig. 5, Pl. 7, fig. 1

Specimens: PEPB 054078, 054082.

Lamina elliptical, est. 4.5–6.5 cm long and 1.8–5.6 cm wide, symmetrical, base cuneate, margin entire. Venation acrodromous, with two strongly ascending secondary veins arising from base of the lamina, such that, with the midvein, there are three main veins in the lower part of the lamina. Apical part of leaf with pinnate secondary veins.

This leaf type is readily recognized by the three main veins arising from base of the lamina. Such leaves may be found in Menispermaceae, Lauraceae, and other families.

DISCUSSION

The Huadian flora is significant in providing the earliest confirmed records of *Koelreuteria*, *Rhus*, and Menispermaceae in the Asian Tertiary, and gives an important glimpse of the flora and vegetation of northeastern China during the Middle Eocene, ca. 45 Ma. The megafossil plants from Huadian that have been identified to living genera mainly represent trees or shrubs. *Ginkgo* and *Metasequoia* grew along with members of the oak, walnut, sumac, sweet gum, and mallow families (*Castanea*, *Quercus*, *Carya*, *Rhus*, *Liquidambar*, and *Craigia*, for example). Woody vines were also present, as indicated by the occurrence of at least two species of Menispermaceae. In addition to the extant genera, some of the species belonged to genera that are now extinct, for example, *Trochodendroides*, *Zyziphoides,* and *Chaneya.*

A large proportion of the species remain unidentified to family and genus level. This is for several reasons. Many of the specimens available so far are only fragmentary, and details of higher order venation are often not well preserved. This means fewer diagnostic characters are available for determination. In addition, we adopted a more strict philosophy for identifying the genera, than was previously employed in Asian and North American Cenozoic leaf studies. We refrained from placing species in a living genus if the only criterion was similarity of shape and major venation, and were concerned about the likelihood that other taxa might look equally similar, given the limited quality of preservation. Only those fossils with especially distinctive architectural patterns were identified.

Preliminary investigation also indicates a rich palynoflora from the same sediment as the megafossils (Chen 2002). The pollen assemblage includes unequivocal *Alnus*, as well as *Carya*, Fagaceae and Tilioideae.

COMPARISON WITH OTHER FOSSIL FLORAS

Phytogeographically, the flora contains several taxa that were widespread across the northern hemisphere in the early Tertiary, including *Ginkgo*, *Metasequoia*, *Trochodendroides*, *Zizyphoides*, and *Platimeliphyllum*. These five genera are "holdovers" that are also known from Palaeocene strata in the northern hemisphere. These genera, along with *Fagus* and *Craigia*, are also shared between with the flora of Fushun, Liaoning Province of likely early Eocene age. The seven genera mentioned above, plus *Chaneya* and *Liquidambar*, are also found at the Yilan flora of Heilongjiang Province possibly an indication of shared Middle Eocene age. Compared with the floras of Fushun and Yilan, where there were several species of Pinaceae and Cupressaceae (s.l.), the diversity of gymnosperms at Huadian is lower.

Considering that our current collections have only 120 specimens, the number of species in the Huadian megafossil flora (41) is relatively high, and it may be expected that continued collecting would elevate the diversity. Collecting has not been as intense at the underground mine of Huadian as at the open cast mines of Fushun and Yilan. By comparison, the Fushun flora of similar latitude in Liaoning province, presumed to be early Eocene, has only produced 41 spp. (inventory by Manchester based on examination of the collections of about 1500 specimens at Beijing Institute of Botany). The Middle Eocene Clarno West Branch Creek flora of Oregon, considered similar in age to Huadian, contains about 70 species based on museum collections of about 1500 specimens.

It is instructive to compare the flora of Huadian with Middle Eocene floras elsewhere in the northern hemisphere. In western North America, Middle Eocene floras include the Republic flora of Washington (Wolfe & Wehr 1987, Wehr & Hopkins 1994, Wehr & Manchester 1996) and the West Branch Creek and Nut Beds floras of the Clarno Formation in Oregon (Manchester 1994). In Europe, floras of similar age include Messel (Wilde 1989, Collinson 1988) and Eckfeld (Wilde & Frankenhäuser 1998) of Germany. These floras are compared at the generic level with the taxa present at Huadian (Tab. 1), providing the basis for a simple calculation of percent similarity. The Huadian flora shares 37 % of its 38 genera with the Republic flora of Washington, and 29% with the Clarno West Branch Creek flora of Oregon, USA. The most marked difference is between Huadian and the western European Middle Eocene floras. The percent-

Table 1. Taxonomic comparison of Huadian flora with Middle Eocene floras of North America and Europe

Huadian China	Clarno (Oregon) USA	Republic (Washington) USA	Messel Germany
Ginkgo	X	X	
Metasequoia		X	
Cephalotaxus			X
Diploclisia	X		X
Palaeosinomenium	X		X
Trochodendroides/ *Nyssidium*	X	X	X
Zizyphoides		X	
cf. *Platanus*	X		X
Platimeliphyllum	X	X	
Liquidambar			
cf. *Parrotia*			
Alnus	X	X	
cf. *Quercus*	X		
Castanea			
cf. *Fagus*		X	
Carya		X	X
cf. *Juglandaceae*			
Craigia/*Plafkeria*		X	
Legume leaflet type 1			
Legume leaflet type 2			
Rhus	X	X	
Koelreuteria		X	
cf. *Acer*		X	X
Chaneya tenuis	X	X	
Cornus	X	X	
Serrate types 1–8			
Entire-margined types 1–5			
Total	11	14	6

age of Huadian genera shared with Messel is only about 16 (Tab. 1), and the similarity with Eckfeld is similarly low. The European Middle Eocene floras differ from Huadian in most of the genera represented, and in the general physiognomic aspect. These Middle Eocene European floras possess a higher proportion of broadleaved evergreens (Wilde 1989) than is observed in the Huadian flora.

Wang and Li (1990) noted that the Huadian mammalian fauna shows closer relationship to that of North America than to Europe. The higher proportion of plant and mammal genera shared with western North America than with Europe may be an indication of biotic exchange across Beringia between the eastern Asian and western North American mid-latitudes. The taxa shared between the Middle Eocene of northeastern China and northwestern North America may also reflect similar features of climate; however many of the thermophilic elements known from the Republic and Clarno floras, such as cycads, bananas and diverse Lauraceae, are so far not found from Huadian.

ENVIRONMENTAL INTERPRETATION

Middle Eocene floras of western North America and western Europe include many warm temperate to subtropical genera that are now native to China (Collinson 1988, Mai 1995, Manchester 1994, 1999). The Middle Eocene vegetation of eastern Asia is less well known, partly because of the relatively small number of intensively studied early Tertiary localities and because of uncertainties as to the precise age of the localities. In North America and Europe, the Early to Middle Eocene floras represent the warmest vegetation of the Tertiary. It would be desirable to know if the same situation was true of midlatitude Asian floras.

Wang and Li (1990) identified five genera of mammals from the oil shale at Huadian and inferred that the palaeoenvironment was warm humid forest, based on the habitats of modern mammals related to the Huadian fossils. Based on living relatives, all of the Huadian mammals seem to be forest dwellers – the galcerines usually inhabit only moist areas, while tarsiers tend to live in secondary scrub jungle, usually at low elevations. Because of the oil shale deposition and some preliminary spore-pollen data, they concluded that it was a "forest swamp under warm and moist climate."

Thermophilic elements like palms, bananas, cycads, and aquatic ferns are not in evidence at Huadian. The presence of Menispermaceae at Huadian might be taken as an indication of warm climate, but some extant members of Menispermeae tribe, to which the fossils correspond, are common in temperate deciduous forest. The diversity of vines, although high in the early Eocene of Europe and Middle Eocene of western North America (Manchester 1994), is not certain for Middle Eocene of Asia.

The proportion of dicotyledonous species with entire-margined leaves is about 29% (9/31). If this value is used with the equation of Wolfe (1979; MAT = 1.14 plus 0.306 times percent of entire margined dicot species), the resulting inferred mean annual temperature will be about 10°C. In comparison, other Middle Eocene floras in western North America have warmer inferred MAT of 14 and 17°C (Manchester 2000). The MAT of European floras has not been estimated by the same procedure. However, Wilde (1989) concluded based on physiognomic character of the leaves from Messel, Germany, that the MAT was even higher, likely between 25 and 30°C and the mean temperatures of the coldest month was not under 10°C, with relatively high annual precipitation. These numbers suggest that the floristic differences between these separate Middle Eocene floras may be explained in large part by climate. However, it must be borne in mind that while the North American and European floras indicated in Table 1 are from fissile lacustrine shales, and the oil shales of Huadian also represent lacustrine shales, the Huadian megafossil plants are from nonfissile siltstones that may have been stream-deposited. Some of the differences in leaf margin percentages might thus be due to differences of depositional biases.

We conclude that the floristic similarities between the Middle Eocene Huadian flora and floras of comparable age in western North America reflect the shared component of deciduous taxa that could withstand frost, and the presence of an active dispersal corridor across Beringia. The more marked differences between the floras of Huadian and of Germany may be attributed to a lack of frost in Middle Eocene western European floras, as well as to the presence of a physical barrier, presumably the Turgai seaway, that impeded the direct dispersal of plants between Europe and Asia.

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REFERENCES

ABLAEV A.G. 2000. Paleogene biostratigraphy of the coastal region in south Primorye. Dalnauka, Vladivostok.

ABLAEV A.G., LI CH.-S., TASCHCHI S.M. & WANG Y.-F. 2003. Paleogene of the Hunchun Depression of Pritumanganye (The North-East China). Dalnauka, Vladivostok.

AKHMETIEV M.A. 1973. Sikhote-Alin Miocene flora (River Botchi). Transactions of the Academy of Sciences, USSR, Geological Institute, 247: 1–124.

BEARD K.C. & WANG B. 1991. Phylogenetic and biogeographic significance of the tarsiiform primate *Asiomomys changbaicus* from the Eocene of Jilin Province, Peoples Republic of China. Amer. Jour. Phys. Anthrop., 85: 159–166.

BŮŽEK Č., KVAČEK Z. & MANCHESTER S.R. 1989. Sapindaceous affinities of the *Pteleaecarpum* fruits from the Tertiary of Eurasia and North America. Bot. Gazette, 150: 477–489.

CHANDLER M.E.J. 1961. The Lower Tertiary floras of southern England. 1. Paleocene Floras. London Clay Flora (Supplement). British Museum (Natural History), London.

CHEN J.I. 2002. Middle Eocene palynoflora of Huadian, Jilin Province, Northeastern China. Botany 2002, Botanical Society of America. Program and Abstracts: 54.

COLLINSON M.E. 1988. The special significance of the Middle Eocene fruit and seed flora from Messel, West Germany. Cour. Forsch.-Inst. Senckenberg, 107: 187–197.

CRANE P.R. 1984. A re-evaluation of *Cercidiphyllum*-like plant fossils from the British early Tertiary. Bot. Jour. Linn. Soc., 89: 199–230.

CRANE P.R., MANCHESTER S.R. & DILCHER D.L. 1991. Reproductive and vegetative structure of *Nordenskioldia* (Trochodendraceae), a vessel-less dicotyledon from the Early Tertiary of the Northern hemisphere. Amer. Jour. Bot., 78: 1311–1344.

ENDO S. 1926a. A preliminary report of paleobotanical studies on the Palaeogene plants from the Fushun coal field. Jour. Geol. Geogr., 15 (3): 18. (in Japanese).

ENDO S. 1926b. Plants from the Fushun Coal field. Jour. Geogr. Soc. Tokyo, 38 (453): 627–633.

ENDO S. 1934. The geological age of the Fushun group, south Manchuria. Proceedings of the Imperial Academy, 10 (8): 486–489.

ENDO S. 1942. On the fossil flora from the Shulan Coal-field, Kirin Province and the Fushun Coal-field, Fengtien Province. Bull. Cent. Nat. Mus. Manchoukou 1942(3): 33–47.

GUO SH.-X. & ZHANG G.-F. 2002. Oligocene Sanhe flora in Longjing County of Jilin, Northeast China. Acta Palaeontol. Sinica, 41: 193–210.

HE CH.-X. & TAO J.-R. 1997. A study on the Eocene flora in Yilan County, Heilongjiang. Acta Phytotax. Sinica, 35: 249–256.

HORIUCHI J. 1996. Neogene floras of the Kanto District. Science Report, Institute of Geoscience, University of Tsukuba, sect B., Geological Sciences, 17: 109–206.

JUDD W. & MANCHESTER S.R. 1997. Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological and chemical characters. Brittonia, 49: 384–405.

KODRUL T.M. 1999. Paleogene phytostratigraphy of the south Sakhalin. Transactions of the Geological Institute, Russian Academy of Science, 519: 1–148.

KVAČEK Z., BŮŽEK C. & MANCHESTER S.R. 1991. Fossil fruits of *Pteleaecarpum* Weyland –Tiliaceous not Sapindaceous. Bot. Gazette, 152: 522–523.

KVAČEK Z., MANCHESTER S.R., ZETTER R. & PINGEN M. 2002. Fruits and seeds of *Craigia bronnii* (Malvaceae -Tilioideae) and associated flower buds from the late Miocene Inden Formation, Lower Rhine Basin, Germany. Rev. Palaeobot. Palyn., 119: 311–324.

LIU Y. & FERGUSON D.K. 1996. Catalogue of Cenozoic Megafossil Plants in China. Palaeontographica, B, 238: 141–179.

MAI D.H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena.

MANCHESTER S.R. 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon. Palaeontographica Americana, 58: 1–205.

MANCHESTER S.R. 1999. Biogeographical relationships of North American Tertiary floras. Ann. Miss. Bot. Garden, 86: 472–522.

MANCHESTER S.R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. Oregon Geology, 62: 51–62.

MANCHESTER S.R., CRANE P.R. & DILCHER D.L. 1991. *Nordenskioldia* and *Trochodendron* (Trochodendraceae) from the Miocene of northwestern North America. Bot. Gazette, 152: 357–368.

MANCHESTER S.R. & DILLHOFF R.M. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the

Middle Eocene of Pacific Northwestern North America. Canad. Jour. Bot., 82: 1509–1517.

MASLOVA N.P. 2002. A new plant of the family Platanaceae from the Early Paleogene reconstructed on the basis of leaves and inflorescence. Paleont. Jour., 36: 207–218.

MEYER H.W. & MANCHESTER S.R. 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. Univ. Calif. Publ., Geol. Sci., 141: 1–195.

MINAGAWA, S. 1943. Miscellaneous report (On the age of the oil shale bed developed around Huatien in Jilin Province). Jour. Geol. Soc. Manchoukuo, 4–5: 47–48.

NISHIDA S. 1940. Oil Shale of Kung-tang-tou, Hautien Prefecture, Chi-lin Province (Preliminary Report). Bull. Geol. Inst. Hsing-Ching, 99: 27–31.

QIAN H. 2001. A comparison of generic endemism of vascular plants between east Asia and North America. Intern. Jour. Plant Sci., 162: 191–199.

QIAN H. & RICKLEFS R.E. 1999. A comparison of the taxonomic richness of vascular plants in China and the United States. American Naturalist, 154: 160–181.

STOCKEY R.A., ROTHWELL G.W. & FALDER A. 2001. Diversity among taxodioid conifers: *Metasequoia foxii* sp. nov. from the Paleocene of central Alberta, Canada. Intern. Jour. Plant Sci., 162: 221–234.

TANAI T. 1970. The Oligocene floras from the Kushiro coal field, Hokkaido. Japan. Jour. Faculty Sci., Hokkaido University, ser. 4, 14(4): 383–514.

TANAI T. 1989. The revision of the so-called *"Alangium"* leaves from the Paleogene of Hokkaido, Japan. Bull. Nation. Sci. Mus., ser. C (Geol. Paleont.), 15: 121–149.

TANAI T. 1992. Tertiary vegetational history of East Asia. Bull. Mizun. Foss. Mus., 19: 125–163.

TANAI T. 1995 Fagaceous leaves from the Paleogene of Hokkaido, Japan. Bull. Nation. Sci. Mus. Tokyo, ser. C, 31 (3, 4): 71–101.

TAO J.-R. & XIONG X.-ZH. 1986. The latest Cretaceous flora of Heilongjiang Province and the floristic relationship between East Asia and North America (cont.). Acta Phytotax. Sin., 24: 121–135.

THANIKAIMONI G. 1984. Ménispermaceés: Palynologie et Systématique. Trav. Sect. Sci. Tech., Pondichery, 18: 1–135.

THORNE R.F. 1999. Eastern Asia as a living museum for archaic angiosperms and other seed plants. Taiwania, 44: 413–422.

TRALAU H. 1968. Evolutionary trends in the genus *Ginkgo*. Lethaia, 1:63–101.

WANG B. & LI C. 1990. First Paleogene mammalian fauna from northeast China. Vertebrata PalAsiatica, 28: 165–205.

WANG Y. & MANCHESTER S.R. 2000. *Chaneya*, a new genus of winged fruit from the Tertiary of North America and eastern Asia. Intern. Jour. Plant Sci., 161: 167–178.

WEHR W.C. & HOPKINS D.Q. 1994. The Eocene orchards and gardens of Republic, Washington. Washington Geology, 22 (3): 27–34.

WEHR W.C. & MANCHESTER S.R. 1996. Paleobotanical significance of flowers, fruits, and seeds from the Eocene of Republic, Washington. Washington Geology, 24: 25–27.

WGCPC (Writing Group of Cenozoic plants of China). 1978. Cenozoic plants from China, Fossil Plants of China. vol. 3. Science Press, Beijing.

WILDE V. 1989. Untersuchungen zur Systematik der Blattreste aus dem Mitteleozän der Grube Messel bei Darmstadt (Hessen, Bundesrepublik Deutschland). Cour. Forsch.-Inst. Senckenberg, 115: 1–213.

WILDE V. & FRANKENHÄUSER H. 1998. The Middle Eocene plant taphocoenosis from Eckfeld (Eifel). Rev. Palaeobot. Palyn., 101: 7–28.

WOLFE J.A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U. S. Geol. Surv. Profess. Paper, 1106: 1–37.

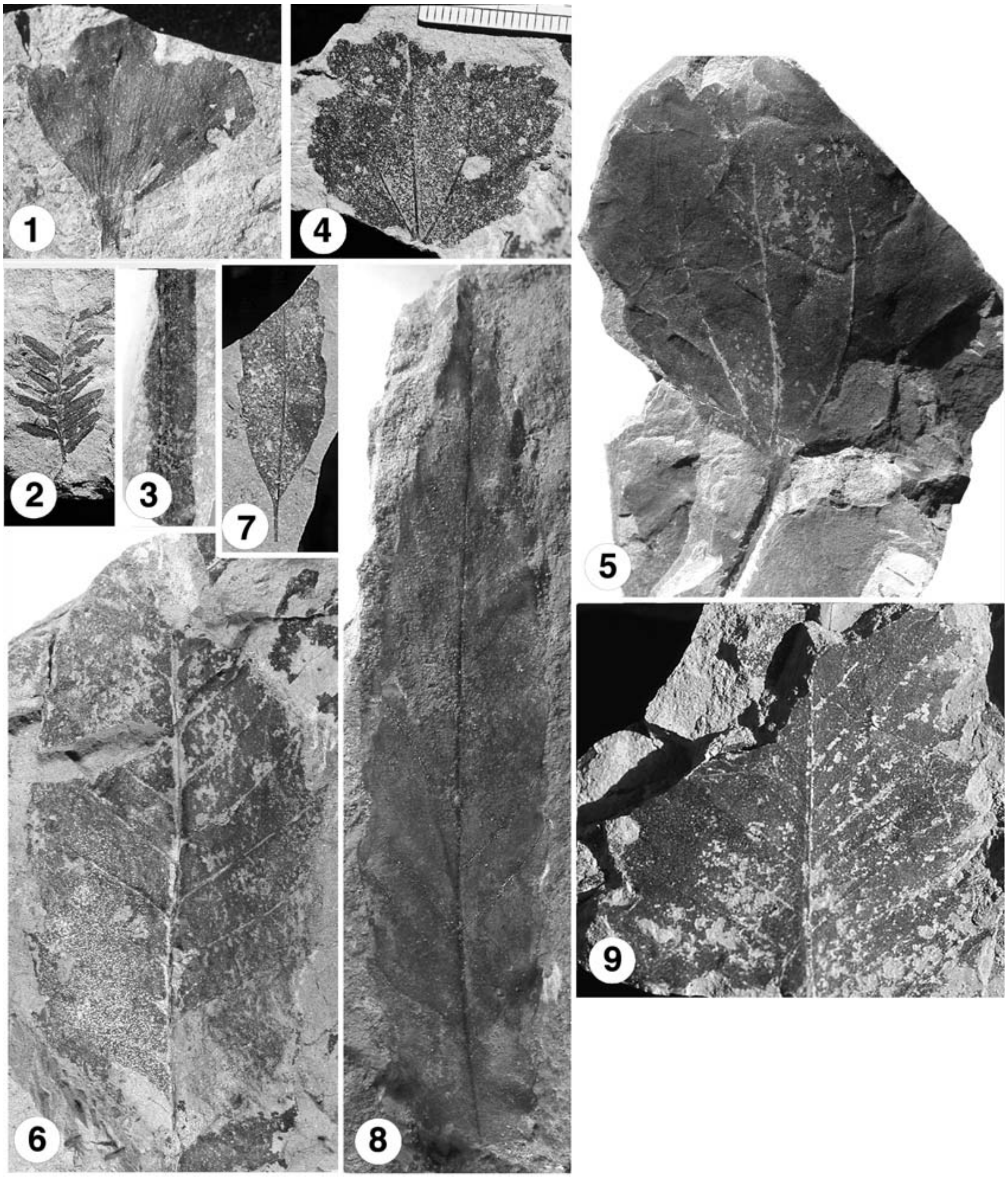
WOLFE J.A. & WEHR W.C. 1987. Middle Eocene dicotyledonous plants from Republic, Northeastern Washington. U.S. Geol. Surv. Bull., 1597: 1–25.

XING Sh. (ed.). 1988. Forest of Jilin Province. Jilin Science and Technology Press and China Forestry Press.

XIONG X.-Zh. 1986. Palaeocene flora from the Wuyun Formation in Jiayin of Heilongjiang. Acta Palaeont. Sinica, 25: 571–576.

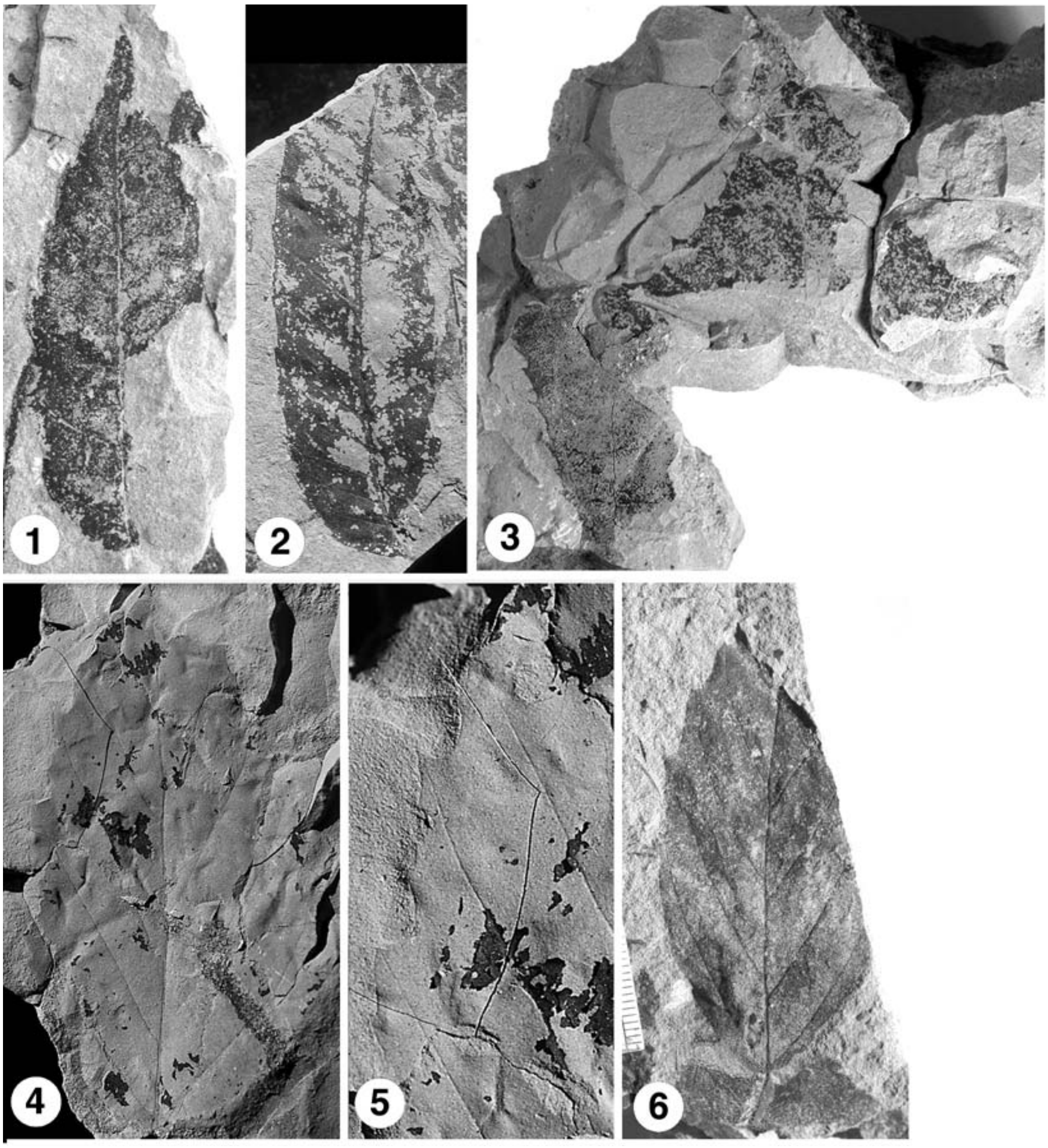
ZHOU J. & SUN J. 1985. A fish fauna is discovered in the late early Eocene of the Huadian Basin, Jilin Province. Vertebrata PalAsiatica, 23: 170.

PLATES

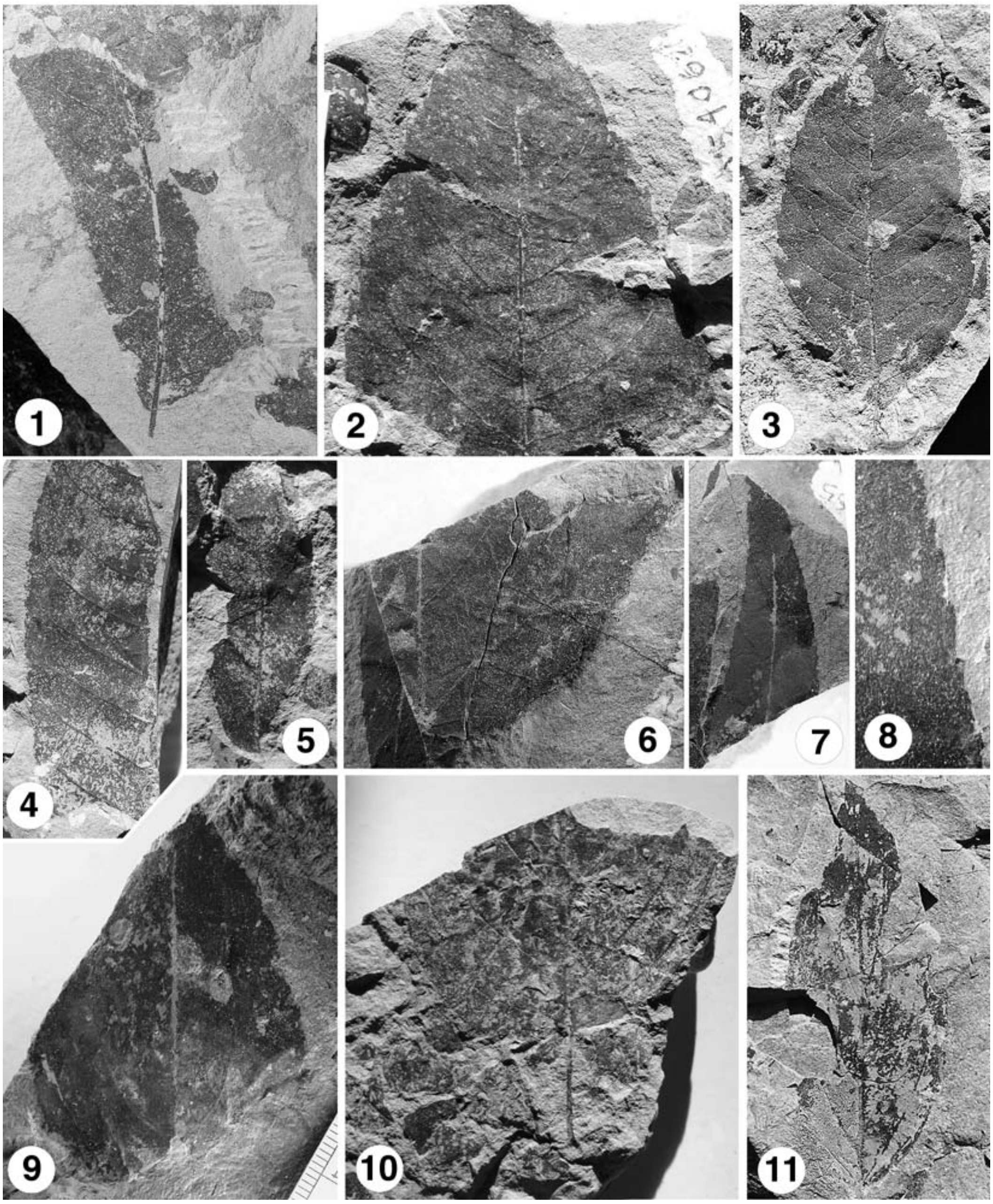


1. *Ginkgo adiantoides* (Unger) Heer, × 2, PEPB 054033
2. *Metasequoia disticha* (Heer) Miki, × 1, PEPB 054040
3. *Cephalotaxus* sp., × 1, PEPB 054084
4. *Trochodendroides arctica* (Heer) Berry, × 1, PEPB 053901
5. *Zizyphoides ezoensis* (Tanai) comb. nov., × 1, PEPB 054061
6. *Castanea fujiyamae* Tanai, × 1, PEPB 054114
7. cf. *Quercus berryi* Trelease., × 1, PEPB 053920
8. cf. *Quercus berryi* Trelease, × 1, PEPB 053852
9. *Castanea fujiyamae* Tanai, × 1, PEPB 054085

Plate 2

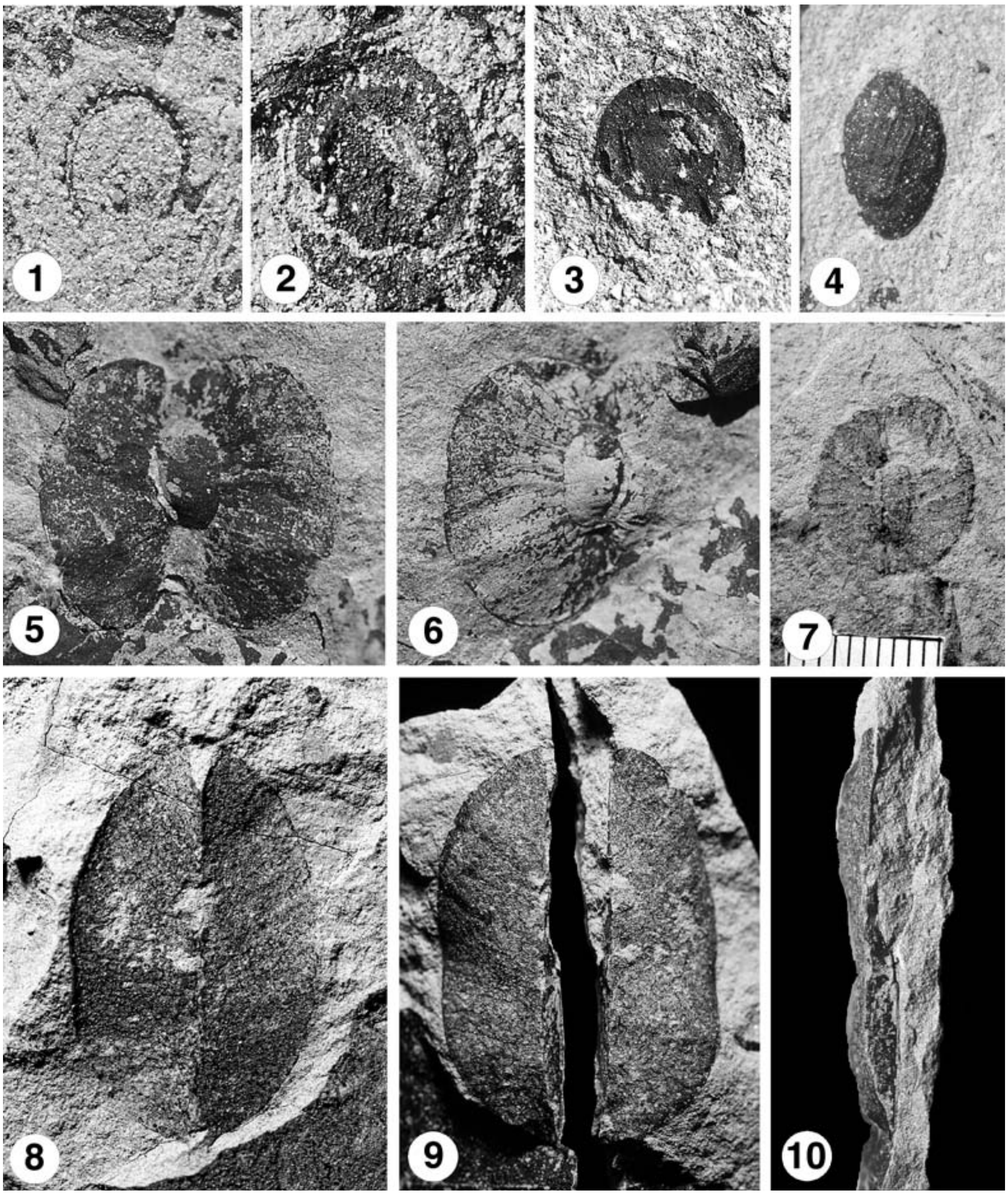


1. cf. *Rhus*, × 1, PEPB 053977
2. cf. *Fagus*, × 1, PEPB 054083
3. cf. *Platanus*, × 1, PEPB 054115
4. *Platimeliphyllum* sp., × 1, PEPB 053987
5. Detail of leaf from 4, × 2
6. cf. *Parrotia* sp., × 1, PEPB s.n.



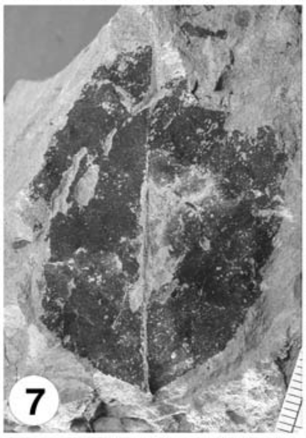
1. *Carya* sp., × 1, PEPB 053976
2. cf. Juglandaceae, × 1, PEPB 054068
3. cf. Juglandaceae, × 1, PEPB 053974
4. *Carya* sp., × 1, PEPB 054060
5. *Carya* sp., × 1, PEPB 054089
6. *Liquidambar* sp., × 1, PEPB 054064
7. *Liquidambar* sp., × 1, PEPB 054065
8. Detail of margin from 7 showing glandular teeth, × 3.5
9. Menispermaceae leaf, × 1, PEPB 054057
10. *Cornus* sp., × 1, PEPB 054994
11. cf. *Parrotia* sp., × 0.6, PEPB 054036

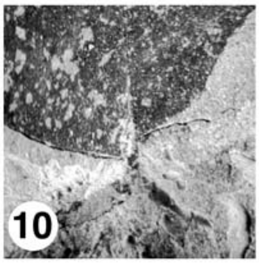
Plate 4

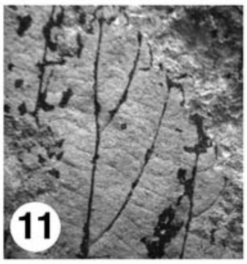


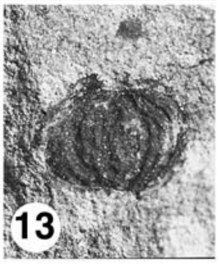
1. *Diploclisia* sp., endocarp, ×6, PEPB 054019a,
2. Counterpart of specimen in 1, ×6, PEPB 054019b
3. *Palaeosinomenium venablesii* Chandler, endocarp, ×6, PEPB 054014
4. *Nyssidium* sp., fruit, ×4.5, PEPB 054022
5. *Craigia* sp., fruit, ×2, PEPB 054010a
6. Counterpart of specimen in 5, ×2, PEPB 05410b
7. *Craigia* sp., fruit, ×2, PEPB s.n.
8. *Koelreuteria* sp., fruit valve, ×2, PEPB 054018
9. Counterpart of the same specimen, broken down the septum
10. Side view of the specimen from 9, showing septum extending only half the length from the base to apex

Plate 5



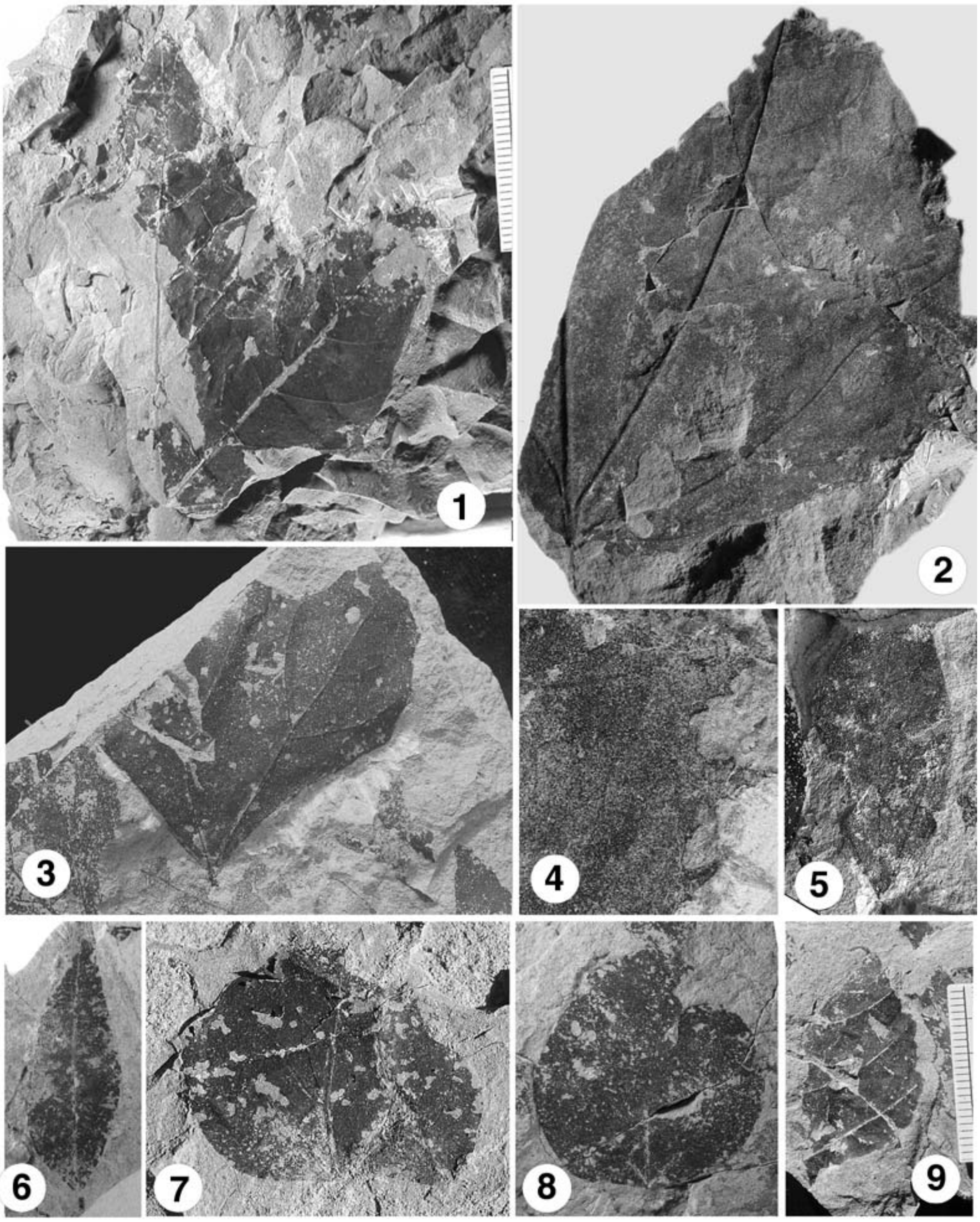






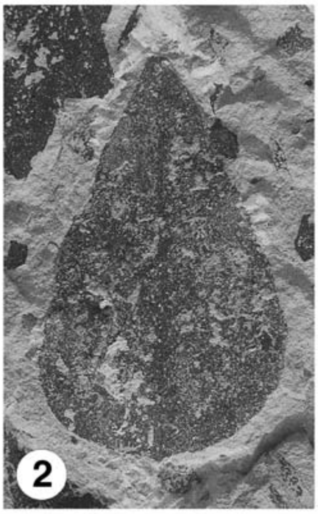
1. *Plafkeria basiobliqua* (Oishi & Huzioka) Tanai, × 1, PEPB 053984
2. *Plafkeria basiobliqua* (Oishi & Huzioka) Tanai, × 1, PEPB 053987
3. Serrate type 1, × 1, PEPB 053982a
4. Serrate type 1, × 2, PEPB 053997
5. Entire-margined type 1, × 1, PEPB 054035
6. Entire-margined type 2, × 1, PEPB 054010c
7. Serrate type 2, × 1, PEPB 054130
8. Legume leaflet type 2, × 1, PEPB 054072
9. Legume leaflet type 1, × 1, PEPB 054105
10. Detail from 9, showing transversely striate pulvinus on petiolule, × 5
11. Detail from 3, marginal teeth of serrate type 1, × 3
12. Entire-margined type 3, × 1.25, PEPB 054099
13. *Rhus* sp., fruit, × 4, PEPB 054012

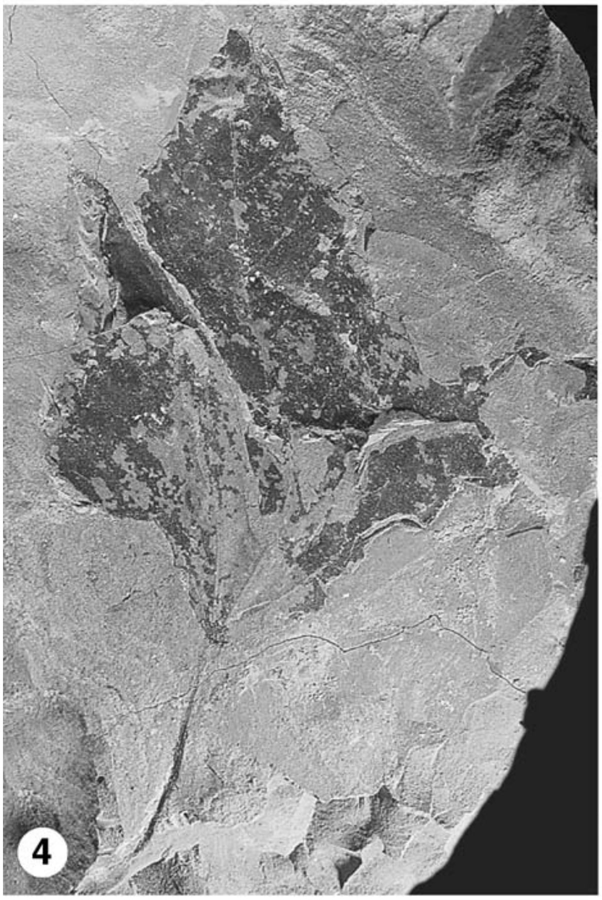
Plate 6



1. cf. *Acer* sp., × 1, PEPB 054121
2. Serrate type 3, × 1, PEPB 054093
3. cf. *Acer* sp., × 1, PEPB 053989
4. Detail of margin from 2, × 2.25
5. Entire-margined type 5, × 1, PEPB 054078
6. Legume leaflet type 1, × 1, PEPB s.n.
7. Entire-margined type 4, × 1, PEPB 054029
8. Entire-margined type 4, × 1, PEPB 054080
9. cf. *Alnus* sp., × 1, PEPB 053980

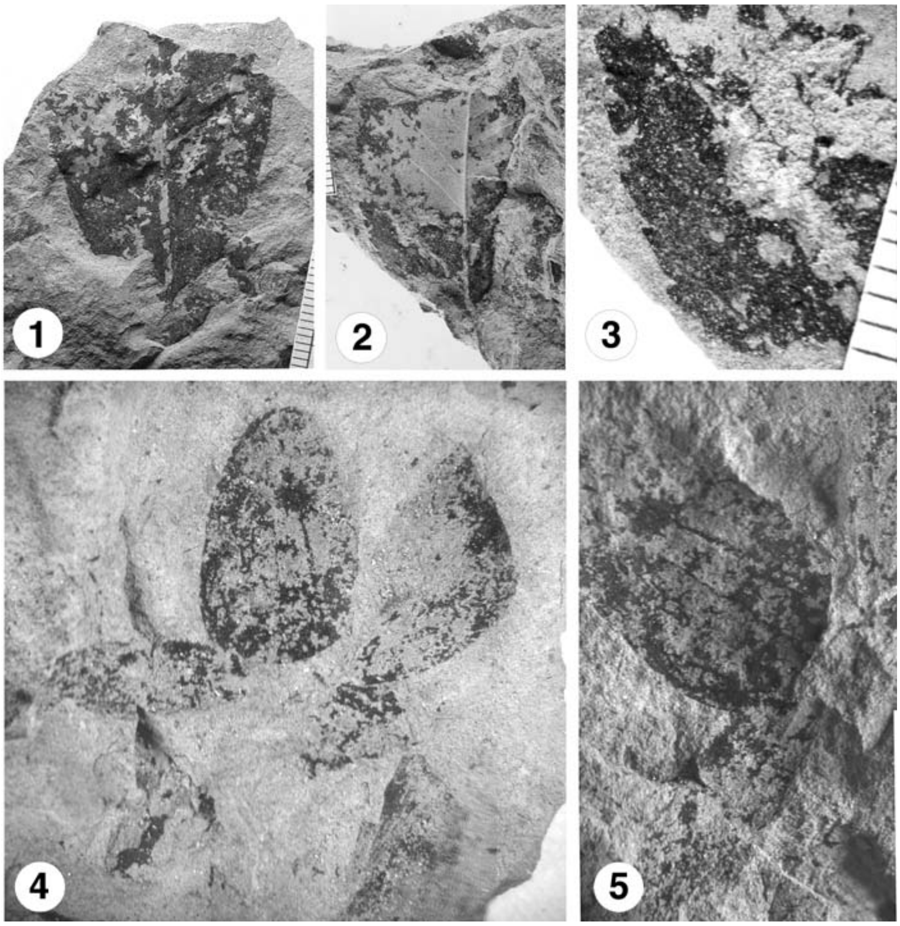
Plate 7





1. Entire-margined type 5, × 1, PEPB 054082
2. Legume leaflet type 2, × 1, PEPB 054076
3. Serrate type 4, × 1, PEPB 054037
4. Serrate type 5, × 1, PEPB 054107
5. Serrate type 6, × 1, PEPB s.n.

Plate 8



1. Serrate type 7, × 1, PEPB s.n.
2. Serrate type 8, × 1, PEPB 054117
3. Detail of 2, × 3.8
4. *Chaneya tenuis* (Lesquereux) Wang & Manchester, calyx, × 2.5, PEPB 054129
5. Same, with oblique lighting oriented to emphasis venation details, × 3