

# Evolution, palaeobiogeography and palaeoecology of Eucommiaceae

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(Received 26 July 1999; revised version accepted 12 January 2000)

## ABSTRACT

Guo Shuang-xing 2000. Evolution, palaeobiogeography and palaeoecology of Eucommiaceae. Palaeobotanist 49(1) : 65-83.

A comprehensive treatise incorporating morphology, ecology, stratigraphy and systematics of *Eucommia* belonging to family Eucommiaceae, based on extant and extinct records, is presented. Fifteen species of megafossil leaves and fruits of *Eucommia* and about one hundred localities from the northern hemisphere are known. Pollen of *Eucommiidites troedssonii* Erdtman was widely distributed in the Mesozoic sediments of Europe. Authentic pollen records of *Eucommia*, *Eucommiaceapollenites eucommides* Sun and *E. minor* Sun are known from China. They first appeared in East China in the Paleocene.

The validity of *Eucommia* leaves known from the Paleocene of the western United States is doubtful. Other records include *Eucommia brevirostria* from south China, *Eucommia kobayashi* from northern Japan, *Eucommia* sp. from Alaska, United States, *E. browni*, *E. montana* from the Oligocene of United States, *E. sibirica* from the Miocene and Oligocene of Siberia.

During the Miocene *Eucommia* species had widest distribution - *E. japonica* from Japan, *E. caucasica* from Caucasus, *E. kryshstofovichii* from Moldova and Poland, *E. palaeoulmoides* from Caucasus, Ukraine, the Netherlands, Kazakhstan and western Russia and *Eucommia* sp. from Mexico are known.

*Eucommia europaea* is known from the Mio-Pliocene of Siberia, Germany, Poland, France, Italy, the Netherlands and Hungary. Some fossil specimens assigned to the living *E. ulmoides* were found from the Miocene and Pliocene of Germany, Poland and Romania. Several indeterminable species of *Eucommia* were recorded from the Neogene of Poland, Germany, France and Italy. One species of *Eucommia* was found in the Pleistocene of Italy. An evaluation of these records, their geographical distribution, endemism and environmental impact have been discussed.

**Key-words**— Eucommiaceae, Evolution, Palaeobiogeography, Palaeoecology.

## यूकोमिएसी के विकास, पुराजैवभौगोलिकी एवं पुरापारिस्थितिकी का विश्लेषण

गुओ शुआंग जिंग

सारांश

प्रस्तुत शोध पत्र में यूकोमिएसी कुल से सम्बन्धित यूकोमिया के संरचना विज्ञान, पारिस्थितिकी विज्ञान, स्तरिकी एवं वर्गीकृत स्थिति का सम्पूर्ण विवेचन किया गया है, जो इसके विद्यमान एवं विलुप्त अभिलेखों पर आधारित है. यूकोमिया की गुरुपादपाशम पत्तियों एवं फलों की 15 प्रजातियां तथा उत्तरी गोलार्द्ध की लगभग 100 संस्थितियां ज्ञात की गयी हैं. यूकोमाइडाइटीज़ ट्रोएडसोनाइ अर्टमैन के परागकण यूरोप में मीसोजोइक अवसादों में भारी मात्रा में वितरित थे. यूकोमिया,

यूकोमिएसिओयपोलेनाइटीज़ यूकोमिडीज़ सुन एवं ई. माइनर सुन के अभिप्रमाणित परागकण अभिलेख चीन से प्राप्त हुए हैं। ये सर्वप्रथम पेलियोसीन युग में पूर्वी चीन में अवतरित हुए।

पश्चिमी संयुक्त राज्य अमरीका से प्राप्त पेलियोसीन युगीन यूकोमिया पत्तियों का अभिनिर्धारण सन्देहास्पद है। अन्य प्राप्त अभिलेखों में यूकोमिया ब्रीविरोस्ट्रिया दक्षिणी चीन से, यूकोमिया कोबायाशी उत्तरी जापान से, यूकोमिया प्रजाति अलास्का, संयुक्त राज्य अमरीका से, ई. ब्राउनी एवं ई. मॉन्टेना नामक दो ओलिगोसीन युगीन प्रजातियाँ संयुक्त राज्य अमरीका से तथा ई. साइबेरिका प्रजाति मायोसीन एवं ओलिगोसीन युगीन साइबेरिया से प्राप्त हुई हैं।

मायोसीन युग के दौरान यूकोमिया प्रजातियों का प्रचुर वितरण था। इनमें ई. जापोनिका जापान से, ई. काकेशिका काकेशस से, ई. क्रिस्टोफोविचाइ मॉल्डेविया एवं पोलैण्ड से, ई. पेलियोअल्मॉइडीज़ काकेशस, यूक्रेन, नीदरलैण्ड्स, कज़ाकिस्तान एवं पश्चिमी रूस से तथा यूकोमिया प्रजाति मेक्सिको से ज्ञात की गई हैं।

यूकोमिया यूरोपिया प्रजाति मायो-प्लायोसीन युगीन साइबेरिया, जर्मनी, पोलैण्ड, फ़्रांस, इटली, नीदरलैण्ड्स एवं हंगरी से ज्ञात हुई हैं। सर्जीव ई. अल्मॉयडीज़ से सम्बद्ध कुछ पादपाशम प्रादर्श जर्मनी, पोलैण्ड, फ़्रांस एवं इटली में निओजीन युग से खोजे गये हैं। यूकोमिया की एक प्रजाति इटली में प्लीस्टोसीन युग से प्राप्त हुई है। इन अभिलेखों के मूल्यांकन, उनके भौगोलिक वितरण, स्थानिकता एवं पर्यावरणीय प्रभावों की चर्चा करना प्रस्तुत शोध पत्र का प्रमुख उद्देश्य है।

संकेत शब्द—यूकोमिएसी, विकास, पुराजैवभौगोलिकी, पुरापाारिस्थितिकी।

## INTRODUCTION

IT is a comprehensive research of *Eucommia* fossils through geological time. The study is mainly based on the megafossil records of *Eucommia*. The aim of the study is to get a complete knowledge of *Eucommia* and look for its evolutionary relations and its palaeobiogeographic distribution and palaeoclimate.

The living Eucommiaceae is a single genus and species, *Eucommia ulmoides* Oliver growing within China. Its general morphology, systematics, anatomy, pollen, chemical elements, growth, development and habitat are studied in detail by Hutchinson (1931, 1967), Metcalfe and Chalk (1957, 1983), Cronquist (1981), Li Dong *et al.* (1986), Zhang Yu-long *et al.* (1988), Xu Jun-wen *et al.* (1989), Zhang Zhi-yu *et al.* (1990), Zhang Kang-jan (1990) and Cheng Jun-qing *et al.* (1992).

It is often difficult to correctly identify fossil angiosperms, their systematic position because of their morphology and structures are always preserved variously. One cannot easily recognize and judge whether these separate and individual organs preserved belong to the same species, unless those independent organs represent a distinctive characteristics. *Eucommia* fruit is of typically distinctive characteristic organ. *Eucommia samara* an elliptical winged seed with two persistent stigmas at the top of the samara. The seed is in the centre of an elliptic wing fruit. Based on its samara and two persistent stigmas *Eucommia* fruit is very easy to identify. This study is based on the typical representative characteristic of the fossil *Eucommia samara* with elliptic wing with two persistent stigmas at the top. Therefore the fossil species of *Eucommia* should be reliable and are not confused with other fossil species.

## CHARACTERISTICS, HABITAT AND DISTRIBUTION OF LIVING *EUCOMMIA*

Different botanists studied the morphology, anatomy and ecology of *Eucommia*.

**Morphology**—Deciduous tree, 20 m tall, 50 cm in diameter, bark grey and brown, rough, bearing *Eucommia* gum, white slender filament, young twigs with yellow-brown hairs, and later changing smooth, old twigs with obvious lenticulae and pith, bud bodies ovate-rounded, bright in surface, red-brown, scale 6-8, fine trichome in margins.

**Stem anatomy**—The most noteworthy anatomical feature of *Eucommia* is the occurrence of laticiferous cells, containing a substance similar to rubber found particularly in phloem and adjacent tissue of the pericycle. They extend into mesophyll of the leaf. The laticiferous tubes are unicellular (inarticulate), and differ in their mode of development from those of *Cannabis* and *Euphorbia* (Metcalfe & Chalk, 1957).

**Young stem anatomy**—Cork originating in the epidermis, primary cortex collenchymatous. Pericycle containing a loose ring of fibres, together with elongated stone cells with siliceous contents and thin-walled, frequently paired parenchymatous cells each containing an areolate siliceous body. Xylem and phloem in the form of continuous cylinders traversed by narrow rays, pith heterogeneous, the walls of the peripheral cells being thicker than those of cells towards the centre. Laticiferous cells occur in the primary cortex, phloem and pith (Metcalfe & Chalk, 1957).

**Phloem anatomy**—Phellogen of bark 8-10 cells thick, tangential walls of cork cells usually thickened, forming lignified cork cells, phellogen consisting of 1 or 2 flat-oblong cells. Phellogen including cortex 10-12 cells thick, tiny starch grains

in cytoplasm. Several layers of cell groups and minor fibres scattering between phelloderm and phloem, forming usually non-continuous belt in transection. Phloem slightly thick, parenchyma of phloem extend into rubber cells and rubber teams in cells, sometimes rubber depositing in chambers of grit cells. Phloem rays 1 to 3 cells wide, across non-continuous grit cell belt radiating out. Articulated laticifers existing in the phloem and cortex, scattered latex-cells presenting in some of the other tissues, sieve tube S type (Zhang Zhi-yu *et al.*, 1990).

*Xylem anatomy*—Vessels vary to extremely small (mean tangential diameter usually about 25–30  $\mu\text{m}$ ) nearly all solitary, but with occasional radial pairs; 250–350 per sq. mm, semi-ring pores, with spiral thickening, 2 to 3 vessels in tangential rows, wall thin 3–5  $\mu\text{m}$ , and 56  $\mu\text{m}$  in largest tangential diameter, vessel elements 440–820  $\mu\text{m}$  in length; spiral thickening. Perforation plate simple, ovate and elliptic, end wall slightly oblique to short caudate, lateral wall with bordered pits and spiral thickenings (except in immediate neighbourhood of the primary xylem); intervascular pitting uncommon owing to the solitariness of the vessels; small, usually opposite, occasionally alternate, members of medium length. scalariform perforation plate only in vessels of primary wood, pits of ray and wood parenchyma cell similar in size and shape to the intervascular pits. Tyloses very rare, mean length 0.36–0.5 mm or invisible. Parenchyma apotracheal, as isolated cells scattered among the fibres and along the boundaries of the rings, strands usually of 4 cells, diffuse-aggregate and terminal, undeveloped or sometimes absent, terminal wall of parenchyma with obvious nodes thickenings, gum and crystals absent. Wood rays almost homocellular or slightly heterocellular, intermediate between Kribs types heterogeneous IIB and homogeneous I, the others up to 3 (4) cells wide. uniseriate rather a few and composed mostly of procumbent cells, about 5 rays per  $\text{mm}^2$ , with an occasional single marginal row of square to slightly upright cells, the procumbent cells small; terminal wall nodes thickening, horizontal wall of its pit apparent and common, pitting of ray and vessel similar to intervascular pitting, sieve-tubes with S-type plastids. Intercellular pitting absent. Fibres thick, with distinctly bordered pits on both radial and tangential walls, the borders slightly smaller than those of the intervascular pits, walls moderate to very thick, a few cells with spiral thickenings present in some specimens, average length 0.67–0.84 mm and 15 to 20  $\mu\text{m}$  in diameter. Laticiferous cells of root present in the pericycle and phloem (Metcalf & Chalk, 1957; Cronquist, 1981; Zhang Zhi-yu *et al.*, 1990).

*Leaf physiognomy*—Leaves simple, alternate, deciduous, serrate, astipulate, blade elliptical, ovate and oblong, 5–18 cm long and 3–8 cm wide, l/w ratio 1.7; base rounded or broad-cuneate; apex acuminate; hairs simple, unicellular. Young leaves dark green with brown cilium, and becoming smooth before long; old leaf rugulose, leaf back smaragdine, covered by loose castaneous hairs, margin simple serrate, teeth unequal in size,

lower edge two to three times longer than upper edge, glandular at the end of teeth, teeth type violoid; petiole 1–2 cm, texture papyraceous. Venation pinnate, brochidodromous, middle vein medium in thickness, straight; secondary veins 6–10 pairs, lower and upper 1–2 pairs of secondary veins a little thinner than middle ones, subopposite at lower part and alternate at the upper, diverging from middle vein at angles of 35°–55°, upcurved and forming loops at margins, loops diverging many branches forming multifarious moniliform loops within margins; tertiary veins sparse, percurrent between secondary veins, unforked or occasionally forked; quaternary veins forming large irregular multilateral reticulations; quaternary veins forming multilateral areolations; veinlets branched once, twice or three times, endings free or sometimes combined with quaternary veins, forming random fine nets. Veinlet tufted in teeth (Zhang Hong-da *et al.*, 1979; Cronquist, 1981).

*Leaf anatomy*—lamina dorsi-ventral, about 750  $\mu\text{m}$  thick, upper and lower epidermises somewhat irregular in shape, a layer of upper epidermal cells compact, cuticle projected, 14  $\mu\text{m}$  thick, lower epidermis consisting of one layer cells, anticlinal walls somewhat wavy, striped under SEM; palisade tissue two layer cells thickness, secondary layer cells shorter, irregular, columnar; spongy tissue 5–6 layer cells thick, intercellular space developed; Stoma confined to the lower epidermis, dense and somewhat protruded, ranunculaceous type, about 49 x 26  $\mu\text{m}$  in size, 5–7 subsidiary cells surround the guard cells, difficult to distinguish from epidermal cells, enclose stoma concentrically. Vascular bundle of middle vein ectophloic and lunar, several layers of parenchymatous cells in the outside enclosed them, rubber cells scattered among them, 2–3 layers of collenchyma cells present under the epidermis of the middle vein. Petiole thick, crescent-shaped, epidermal cells small, crowded, cutin thickened on tangential wall, sclerenchyma 5–6 layers on the lower surface of epidermis, inwards cortex parenchyma inside, cells large, 7 layer-cells thickness; leaf trace single (Metcalf & Chalk, 1957, 1983).

*Flower*—Unisexual, regular, dioecious, borne in bract axil of the same year, racemose arranged on the proximal, bracteate part of a distally leafy shoot, individually solitary and short-pedicellate in the axis of the bracts, but without bracteoles, lack perianth, blossom at or before the time of new leaves; staminate flowers with short pedicel, 3 mm long, basic bracteoid scale obovate, spatulate, 6–8 mm long, apex rounded, margin tricholoma, stamens 5–12, about 1 cm long, filament very short, 1 mm long, anther linear, 9 mm long, tetrasporangiate slender, dithecal, apically prolonged connective, opening by longitudinal slits, pollen-grains binucleated, mature pollen tricolporoidate, with poorly developed pore in each furrow. Pistillate flowers solitary, pedicel 8 mm long, basic bract obovate, ovary flattened, with 2 mm short handle, unilocular, persistent style at apex, stigma bi-cleft and unequal, persistent; ovules 2, only one mature, soland type, ovule

unitegmic with anatropous, nucellus with weakly crassinucellar; perictal cells 2-3 layers, embryo sac polygonum type, endosperm-development cellular (Cronquist, 1981; Heywood, 1979; Hutchinson, 1967).

*Pollen*—Prolate, oblong in equatorial plane, trilobed globe in polar view, polar axis 30.5-54.8  $\mu\text{m}$  in diameter, equatorial axis 27.8-31.3  $\mu\text{m}$  in diameter, tricolporoidate (also tricolpate), pore borders indistinct, pores larger, elliptic, colpus slender, three colpi unequal in length, sometimes two long and one short or in reverse, sometimes one colpus narrows near the equator but expands in the polar region, the two other colpi appearing straight, colpal membrane thin and obscure often, border of pore and colpus slightly thickened along at the lateral of colpus, exine sculpturing being minutely spinecent to verrucate, pollen wall 1.7  $\mu\text{m}$  thick, ectexine homogeneous, a rather thick endexine present and not thickening in the apertural regions. Tectum thin with dense and small granules, columelliform layer consisting of short bacules, foot layer very thick (Zavada & Dilcher, 1986; Zhang Yu-long *et al.*, 1988).

*Fruit*—Samara, flattened, oblong, 2.5-3.5 cm long, 1-1.5 cm wide, base cuneate, bifid at apex, with thin winged, carpodium 2-3 mm long, nutlet in the centre of samara, convex; seed flattened, fusiform, rounded at terminals, 1-1.5 cm in length, 2.5-3.5 mm in width, dicotyledonous embryo embedded in plentiful endosperm. Chromosomes  $2n=34$  (Cronquist, 1981; Heywood, 1979; Zhang Hong-da *et al.*, 1979).

*Chemical components*—Nodes of simple leaf gaps including abundant carbohydrate, e.g., inulin and small amount of tanniferous, medium amount of proanthocyanin, but without ellagic acid and flavone, Calcium carbonate crystals present, some aucubine, articulated laticifers present in phloem and cortex, scattered latex cells present in cells, calcium oxalate crystals invisible. It can be analyzed from the cortex to get the materials using methyl alcohol liquid including n-undetrigintane, (29-ane) n-melissyl alcohol, b-sitosterol, betulin, betulic acid, ursolic acid, vanillic acid, daucosterol, (+)-pinoresinol di-o-b-D-glucopyranoside, liriiodendria and geniposidic acid (Li dong *et al.*, 1986; Xu Jun-wen *et al.*, 1989).

### Habitat

The extant wild *Eucommia* are mainly distributed in the mountains and valleys of Central China. It grows on sunny slopes and in the extending and spacing shrubs. It is a phototropic and heliophytic plant and not unresistant to shade for long duration. The duration and intensity of sunlight deeply affect its growth and development. It grows and develops better in open areas and forest fringes than inner forest lands. It can adapt to various soil conditions, e.g., red, yellow, sandy soils with stones, steep cliffs and precipices with poor soil. However, the optimum soils for growth are the cumulose and fertile soil with good drainage and under the range of 5-7.5 pH value.

They do not favour to grow in over alkaline or exceeding acidic soil. *Eucommia* plants in the wild environment at present favours the mean annual temperature between 11.7° to 17.9°C, mean temperature 0.2° to 5.5° C in cold month and mean temperature 19.9° to 28.9°C in hot month. *Eucommia* plants can not tolerate the minimum temperature less -19.1°C in wild habitation, and less -22.8°C in cultivated conditions, and over 43.6°C of the absolute maximum temperate. They can also not bear temperature of winter because it is not able to satisfy the physiological condition of blossom. The annual precipitation is 478.3 to 1401.5 mm in the *Eucommia* growing areas in South China. The optimum temperature for *Eucommia* growth is 15°C of mean annual temperature and the annual precipitation of 1,000 mm (Zhang Kang-Jan, 1990).

### Distribution

*Eucommia* represent only one native species in China. Its distributional centre of wild plants is now in low mountains and hills of Yangtze River Valley and Central China. It is widely distributed in the south of Qinling mountains of South China and Yellow River Valley of North China, to the north of Nanling Mountains of South China, to west of Yellow Sea and to east of East China Sea and to east of Qinghai-Xizang Plateau and Yunnan-Guizhuo Plateau of Southwest China. Geographically, its distribution is confined in latitude 25°-35° N, across 10° from north to south, and longitude 104°-119° E, across 15° from east to west. The altitude of its growth ranges from 20 m to 2,500 m, and gradually higher and higher from east to west. It is introduced to North America and Europe now (Zhang Hong-da *et al.*, 1979; Zhang Kang-jan, 1990; Cheng Jun-qing *et al.*, 1992).

## FOSSIL RECORDS OF EUCOMMIA

### Pre-Cenozoic *Eucommia*

Before Cenozoic, some pollen grains named *Eucommiidites troedssonii* Erdtman (1948) with a deep colpus and two indistinct shallow colpi was described from the Early Jurassic strata in southern Sweden. Since then some other species of *Eucommiidites* were again found from the Late Triassic to mid-Cretaceous strata (Scheuring, 1970) in the Northern Hemisphere. They appear to be gymnospermous rather than angiospermous. Among them, some *Eucommiidites* pollen grains are probably related to cycads or to *Ephedra* or *Welwithchia* (Hughes, 1961).

Hughes (1961) described some *Eucommiidites* pollen with distal monocolpate and proximal zonosulcate from the Jurassic Bathonian strata in England. Based on materials from the early Cretaceous of eastern North America, Brenner (1967) also recognized another species in its pollen chamber of an ovule with a very long micropyle. Reymanova (1968) also noted the pollen of *Allicospermum retemirum* similar to those of

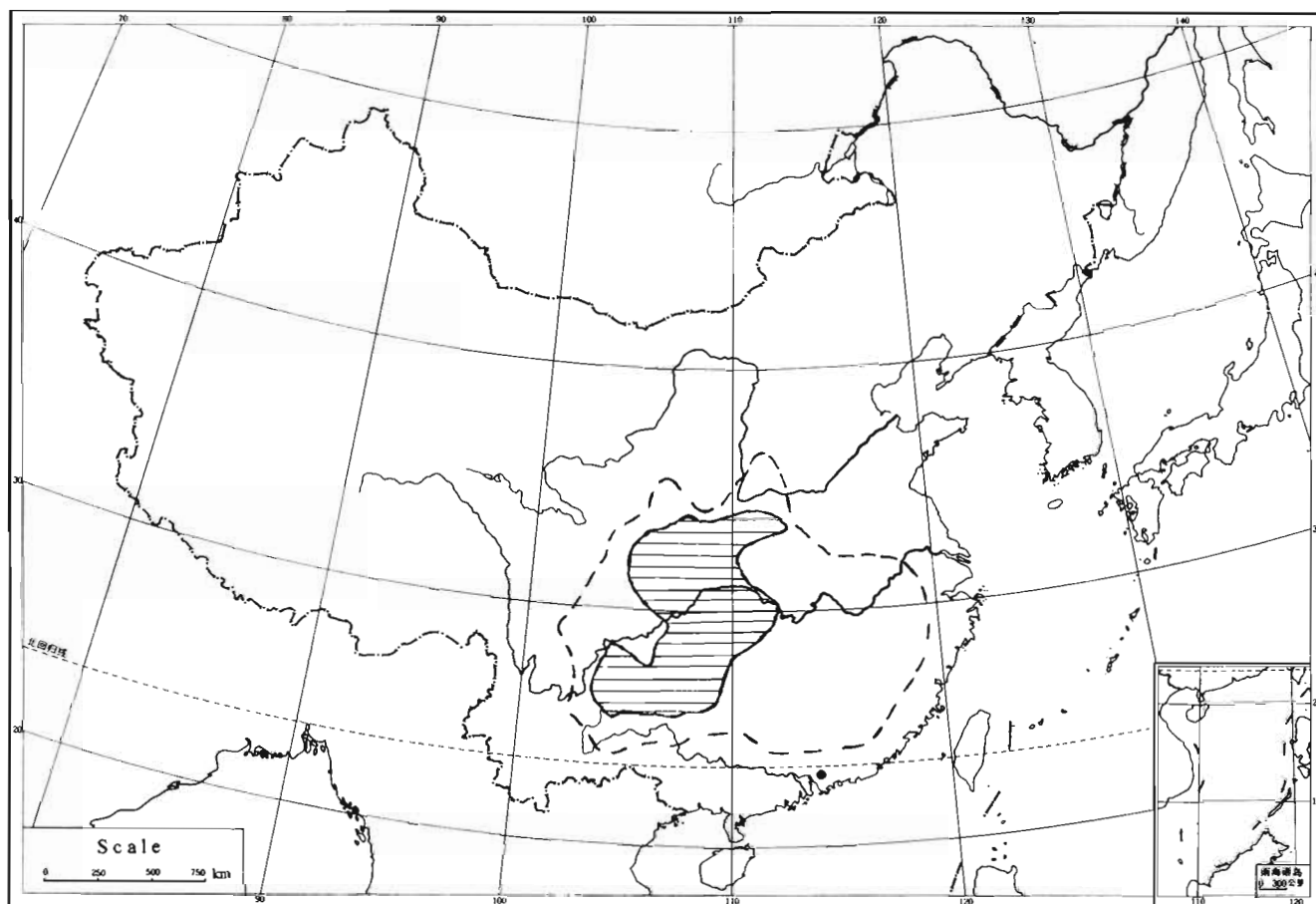


Fig. 1 — The map showing the distributional areas of the living *Eucommia* and the fossil locality in China.

The horizontal lines showing the distributional areas of the wild *Eucommia*.  
The broken lines showing the distributional extent of the cultivated *Eucommia*.  
The black point showing the fossil locality.

*Eucommiidites* from the mid-Jurassic of Poland. These species in their symmetry and orientation are allied to *Classopollis* pollen (Couper, 1958). These characters show that they are related to gymnosperms. Hughes (1976) also considered that although these pollen grains were near to gymnospermous pollen, but are unlike to other gymnospermous pollen. Although *Eucommiidites* consist of the root eucommi- and suffix -idites, it is not probably related to *Eucommia* of angiosperm.

### Paleocene *Eucommias*

In the Paleocene, reliable megafossils of *Eucommia* have not been found yet. Although the leaf fossils of *Eucommia serrata* Brown (1962, p. 72-73) were described from the Lower Fort Union Formation in Montana, Wyoming, South and North Dakota, Coalmont Formation in Colorado, Ferris Formation in Wyoming, Raton Formation in New Mexico and Colorado of Paleocene in the United States; and from the Ravenscrag Formation of Paleocene in Alberta and Saskatchewan of

Canada (Wolfe, 1977, p.70) considered that all of these leaf fossils are doubtfully related to *Eucommia*.

Fossil *Eucommia* pollen, *Eucommiaceipollenites eucommides* Sun and *E. minor* Sun were described from some cores of the Paleocene Lingfang Formation in East China (long. 120°-128° E and lat. 25°-32° N). The fossil pollen grains of two species are consistent with those of the living species of *Eucommia* in their morphological characters under light microscope. The fossil plants of these pollen are associated with Myricaceae, Tiliaceae, Oleaceae, Taxodiaceae and a number of other amentiferous plants. These fossil plants were representative of a mixed deciduous and evergreen broad-leaved forest, reflecting a subtropical and humid climate.

### Eocene *Eucommias*

Four megafossil species of *Eucommia* were found from the Eocene strata in Northern Hemisphere. *Eucommia brevirostris* Guo (1979, p. 229) was a complete fruit which

was discovered from the early Eocene Buxin Formation in Sanshui (ca. long. 112°52'E, lat. 23°10'N) of Guangdong, South China. This species could be an earliest one of the Eocene epoch. It inhabited together with *Equisetum* sp., *Lygodium kaulfussii*, *Cinnamomum naitoanum*, *Goepertia ovalifolia*, *Palibinia angustifolia* and *Trapa paulula*. This small flora consists mainly of evergreen trees with microphyllous, coriaceous leaves. The entire and serrate margins were shared by one half each. This flora represented an evergreen broad-leaved forest, reflecting a subarid and southern subtropical climate.

A fruit specimen which was assigned to *Eucommia kobayashi* Huzioka (1961, p. 9-12, pl. 2, figs 5-10) was found from the Eocene Yubari Coal-bearing Formation, at Ishikari Coalfield (ca. long. 124°20' E, lat. 43°15' N) in Yubari city of Hokkaido, Japan. This species was associated with *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Juglans*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Quercus*, *Dryophyllum*, *Ulmus*, *Zelkova*, *Platanus*, *Cercidiphyllum*, *Magnolia*, *Hamamelis*, *Forthergilla*, *Liquidambar*, *Platanus*, *Crataegus*, *Mallotus*, *Rhus*, *Celastrus*, *Acer*, *Paliurus*, *Marlea* and *Fraxinus*. Among the megafossil plants, the hardwoods consist mainly of trees and shrubs with mesophyllous and deciduous leaves. Most leaves of the hardwoods are with serrate margins. Therefore, this fossil flora seems to be a deciduous broad-leaved forest with a few conifers, reflecting a warm temperate or northern subtropical and humid climate.

Recently, Wehr (1995) found an *Eucommia* fruit from the middle Eocene Klondike Mountain Formation at Republic (ca. long. 48°38'N, lat. 118°42'W) in Washington of The United States. This *Eucommia* fossil fruit was associated with conifers: *Pinus*, *Picea* and *Tsuga*; and dicots: *Trochodendroides*, *Cercidiphyllum*, *Nordenskioldia*, *Corylopsis*, *Liquidambar*, *Macginitiea*, *Craigia*, *Tilia*, *Florissantia*, *Zelkova*, *Ulmus*, *Fagopsis*, *Alnus*, *Betula*, *Corylus*, *Pterocarya*, *Juglans*, *Koelreuteria*, *Acer* and others. These fossil plants seem to be a mixed coniferous and broad-leave deciduous forest reflecting a warm temperate or northern sub-tropical and subhumid climate.

Two fossil fruits of *Simarubites eocenicus* (Berry, 1930, p. 94, pl. 44, figs 15, 16) and *Carpolithus banisteroides* (Berry, 1930, p. 134, pl. 33, figs 5, 6) discovered from the Holly Springs Formation of the Wilcox Group in Tennessee (ca. long. 88°34'W, lat. 37°) of United States were transferred to *Eucommia eocenica* Brown (1940, p. 349). Wolfe (1977, p. 70) indicated that these fossil fruits were poorly preserved without typical characteristic of bi-cleft stigmas. Wolfe (1977) regarded that *Eucommia eocenica* (Berry) Brown should not be referred to the genus of *Eucommia*.

Fossil leaves attributed to *Eucommia* sp. (Wolfe, 1977, p. 70, pl. 24, fig. 7), were discovered from the early late Eocene

Middle Ravenian Member of the Kushtaka Formation at Katalla (ca. long. 144° W, lat. 60° 30' N) in Alaska of the United States. It was accompanied by *Lygodium*, *Allantodiopsis*, *Glyptostrobus*, *Carya*, *Engelhardtia*, *Platycarya*, *Pterocarya*, *Dryophyllum*, *Ulmus*, *Tetracentron*, *Calkinsia*, *Cinnamomophyllum*, *Litseaphyllum*, *Liquidambar*, *Leguminosites*, *Allophylus*, *Sapindus*, *Ternstroemites*, *Arctocarpoides*, *Macclintockia*, *Phoenicites* and *Sabalites*. Wolfe believed that these fossil plants were represented by a evergreen broad-leaved forest, which is close to the extant laurel-oak forest in East Asia. This flora from the early Late Eocene Middle Ravenian Formation indicates a northern subtropical climate. Wolfe (1977) indicated that the minimum temperature might be as low as -14°C. The mean annual temperature range was from 13° to 20°C, and the mean temperature of the coldest month varied from 1° to 18°C. The Precipitation was abundant throughout the year.

### Oligocene *Eucommias*

There are three *Eucommia* species known so far, namely *Eucommia browni* Becker, *E. montana* Brown and *E. Sibirica* Dorofeev from the Oligocene sediments. Wolfe and Tanai (1980) while studying the Kenai flora of Alaska, United States, indicated that *E. browni* is actually synonym of *E. montana*. Therefore, the Oligocene eucommias are in fact two species found from three different localities.

*Eucommia browni* Becker (1961, p. 66, pl. 20, figs 1-6) which was assigned Eocene species is actually a synonym of *E. montana* Brown (1940). It was found in the Oligocene Ruby Formation in Ruby River Basin area (ca. long. 112°03'W, lat. 45°26'N) in Southwest Montana, the United States. Besides 82 identifiable species within 61 genera and 37 families have been known. The main genera contain *Equisetum*, *Osmunda*, *Dennstaedtia*, *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Glyptostrobus*, *Metasequoia*, *Chamacyparis*, *Populus*, *Salix*, *Myrica*, *Alnus*, *Betula*, *Carpinus*, *Fagopsis*, *Fagus*, *Quercus*, *Celtis*, *Ulmus*, *Zelkova*, *Morus*, *Cercocarpus*, *Leguminosites*, *Ptelea*, *Ailanthus*, *Cedrela*, *Astronium*, *Cotinus*, *Acer*, *Dipteronia*, *Cardiospermum*, *Dodonaea*, *Koelreuteria*, *Sapindus*, *Paliurus*, *Vitis*, *Cornus*, *Nyssa*, *Fraxinus*, *Holmskioldia*, *Symphoricarpos*, *Typha*, *Potamogeton*, *Cyperacites* and *Smilax*. The Ruby flora indicated a lake and marsh sere, a riparian and main climax association, and a xeric woodland association with a strong and mixture of desert scrub, some areas were ecotones indicative of abrupt topographic changes and accompanied by considerable variations in temperature and humidity. It contains two distinct floral assemblages. The composite flora comprised aquatic, riparian temperate deciduous and coniferous forest xeric-woodland and desert-shrub associations. Both assemblages represent mixed coniferous and broad-leaved deciduous forests, reflecting a subtropical and humid climate.

*Eucommia montana* Brown (1940, p. 349, text-fig. 3) was found from Grant (ca. long. 112°05'W, lat. 45°27'N) of Montana in the United States in Late Oligocene. Later this species was also described by Becker (1969, p. 94-95) from the Beaverhead Basin (ca. long. 112°40'W, lat. 45°20'N) of the uppermost Oligocene to lower-most Miocene in south-west Montana, United States. This species is associated with 160 species of 110 genera. The main genera are *Muccites*, *Equisetum*, *Osmunda*, *Dryopteris*, *Pteris*, *Ginkgo*, *Abies*, *Picea*, *Pinus*, *Pseudolarix*, *Glyptostrobus*, *Sequoia*, *Taxodium*, *Chamaecyparis*, *Juniperus*, *Thuja*, *Populus*, *Salix*, *Myrica*, *Carya*, *Ahus*, *Betula*, *Carpinus*, *Ostrya*, *Castanea*, *Fagopsis*, *Quercus*, *Ulmus*, *Zelkova*, *Nelumbo*, *Nuphar*, *Nymphaeites*, *Cercidiphyllum*, *Berberis*, *Mahonia*, *Cocculus*, *Sassafras*, *Hydrangea*, *Platanus*, *Amelanchier*, *Cercocarpus*, *Crataegus*, *Kerria*, *Potentilla*, *Rosa*, *Vauquelinia*, *Caesalpinites*, *Canavalia*, *Cassia*, *Cladrastis*, *Dalbergia*, *Diphysa*, *Leucaena*, *Mimosites*, *Parkinsonia*, *Pithecolobium*, *Robinia*, *Ptelea*, *Ailanthus*, *Cedrela*, *Astronium*, *Metopium*, *Celastrus*, *Euonymus*, *Acer*, *Dipteronia*, *Athyana*, *Cardiospermum*, *Koelreuteria*, *Sapindus*, *Berchemia*, *Ceanothus*, *Colubrina*,

*Paliurus*, *Reynosia*, *Rhamnites*, *Sterculia*, *Tilia*, *Alangium*, *Cornus*, *Arctostaphylos*, *Vaccinium*, *Diospyros*, *Fraxinus*, *Osmanthus*, *Holmskioldia*, *Paulownia*, *Sambucus*, *Viburnum*, *Viguiera*, *Typha*, *Agrosites*, *Arundo*, *Phragmites*, *Poacites*, *Symplocarpus*, *Smilax* and *Canna*. Becker (1969) regarded that this Oligocene flora consists of various plant communities which range from an aquatic and shore population to the flood plain and humid forest, to mixed coniferous and broad-leaved deciduous forests at higher elevations, to a high-montane, and to a subhumid association of chaparral character. Many fossil plants reflect aspect of the eastern America and Asian deciduous forest, as well as of the coast ranges of Oregon and California. A comparison of the fossil assemblage with analogous modern species suggests that the lake, as a depositional reservoir, stood at about 457-600 m elevation, surrounded by highlands up to 1,800 m. It indicated the minimum temperatures not much below freezing, and a fairly even, annual precipitation between 1,000-1,250 mm.

*Eucommia sibirica* Dorofeev (1963, p. 195, pl. 33, figs 24-26) was found from the Oligocene strata in Rezhenka (ca.

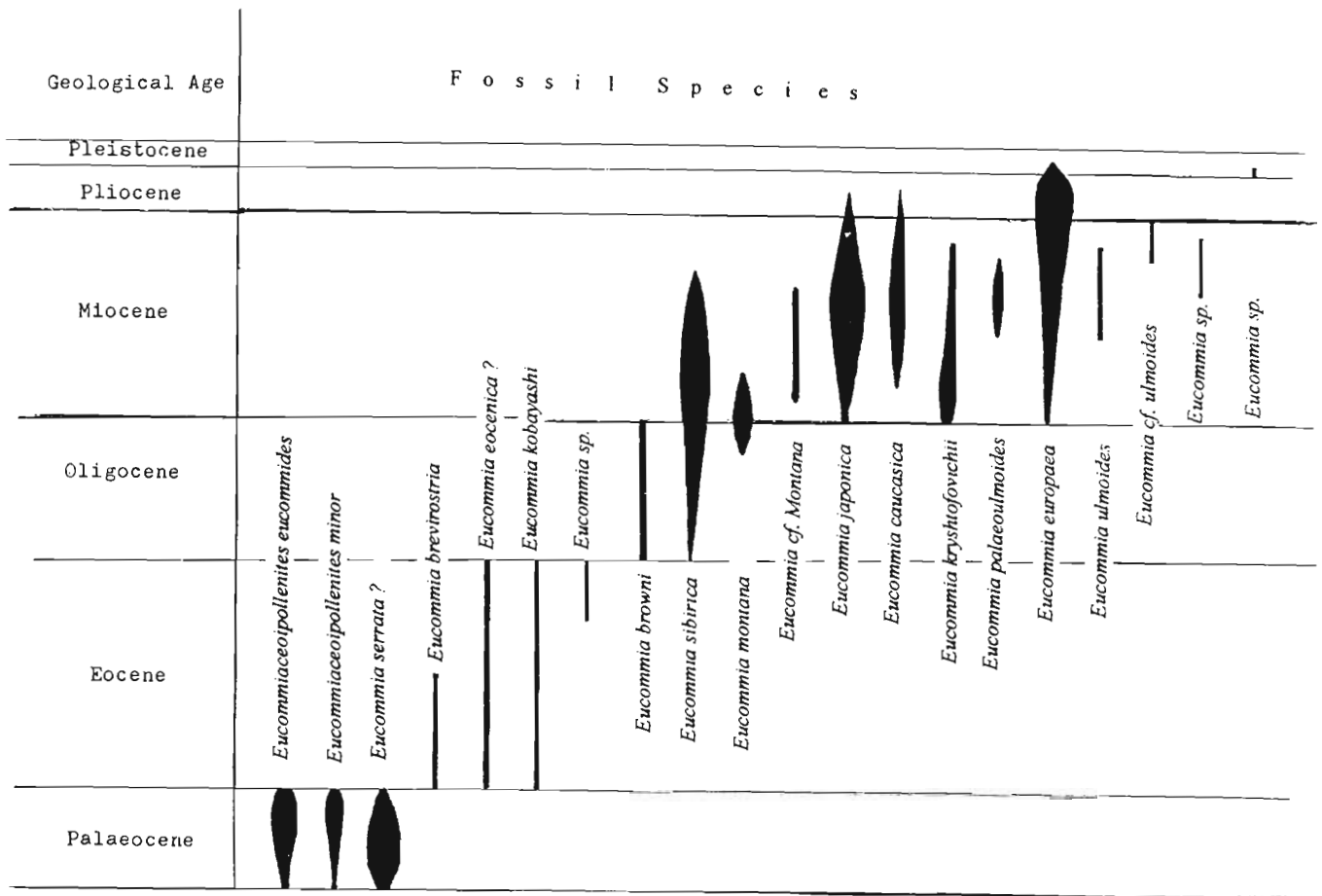


Fig. 2 — The geological ranges of the fossil species of *Eucommia*.

long. 84°20'E, lat. 57°20'N) of western Siberia, Russia. And it was also discovered from the Miocene deposits at Esakovka (ca. long. 73°40'E, lat. 55°N) of Omsk province and in Kireevck (ca. long. 85°05'E, lat. 56°30'N) of Tomsk province in western Siberia, Russia. It was widespread in Oligocene in comparison to Miocene. Other fossil plants have not been found associated with this species.

### Miocene *Eucommias*

The most luxuriant and flourishing period of *Eucommia* was in Miocene epoch. The *Eucommia* fossils of Miocene age were most extensive in distribution, nearly covered over the northern part of Eastern Hemisphere and across the Pacific Ocean occupying the western part of North America.

*Eucommia* cf. *montana* Brown (Wolfe & Tanai, 1980, p. 29, pl. 4, fig. 6) was also a member from the middle Miocene Seldovia point flora in Kenai Basin (long. 151°40'W, lat. 58°40'N) of Alaska, United States. Its specimens of fossil fruits are not well preserved. Wolfe and Tanai (1980) considered that these fossil fruits are closely similar to those of living *Eucommia*. And these fossil leaves have ever been found from the Seldovia point flora. Therefore, they regarded that these fossil fruits could be referred to *Eucommia* cf. *montana*. This species was chiefly accompanied by pteridophytes: *Dryopteris* and *Onoclea*; gymnosperms: *Glyptostrobus* and *Metasequoia*; and angiosperms: *Nymphaea*, *Cocculus*, *Cercidiphyllum*, *Liquidambar*, *Platanus*, *Celtis*, *Ulmus*, *Zelkova*, *Fagus*, *Quercus*, *Alnus*, *Betula*, *Carpinus*, *Ostrya*, *Cyclocarya*, *Pterocarya*, *Populus*, *Salix*, *Tilia*, *Hydrangea*, *Crataegus*, *Prunus*, *Sobaria*, *Cladrastis*, *Pueraria*, *Decodon*, *Hemitrapa*, *Acer*, *Nyssa*, *Alangium*, *Kalopanax*, *Fraxinus*, *Lonicera*, *Alisma* and *Potamogeton*. The Seldovia point flora was mainly made up of deciduous trees, shrubs and vines, belonging to a boreal deciduous broad-leaved forest. One third of these fossil plants originated from East Asia, one third from middle latitude of western North America and other one third from high latitude. The temperature regime indicated by the Seldovia point flora was 6°-7°C mean annual temperature. If coniferous forest were not far distant, then a mean annual range of temperature of 26°-27°C was indicated. This in turn indicate that mean annual temperature has declined since the middle Miocene by about 3°-5°C and the present mean range of temperature of the Seldovia point is much higher at present. That is, the present climate at Seldovia is considerably milder than middle Miocene climate. There has been almost no change in winter temperatures, but there has been drastic change in warm month temperatures. The mean temperature of the warmest month has declined by about 7°-8°C. They suggest that it is the strong decline in summer temperatures during the Neogene that was a major factor in the initiation of widespread glaciation during the later Cenozoic (Wolfe & Tanai, 1980).

*Eucommia japonica* Tanai (1961, p. 329) was widely distributed in the Neogene of Japan. It is also known from Ogawa (ca. long. 139°45'E, lat. 42°20'N) and Kanagasawa loc. 2 of Southwest Hokkaido, Japan in the Early Miocene and the Middle Miocene Kudo flora. This species survived along with a fern, *Equisetum*; some gymnosperms: *Keteleeria*, *Picea*, *Pinus*, *Glyptostrobus*, and a lot of angiosperms: *Comptonia*, *Pterocarya*, *Alnus*, *Carpinus*, *Corylus*, *Ostrya*, *Castanea*, *Fagus*, *Quercus*, *Ulmus*, *Zelkova*, *Cercidiphyllum*, *Gleditsia*, *Pueraria*, *Phyllodendron*, *Rhus*, *Tilia*, *Hemitrapa* and *Fraxinus*. These fossil plants are quite close to the temperate deciduous broad-leaved forests, on the mountains of 480 to 560 m in Central Honshu, Japan, and also near to the forests on the northern bank of the middle valley of Yangtze River, Central China. Based on the climatic conditions reflected by the contemporaneous fossil plants in Central China, Tanai and Suzuki (1972) estimated that the palaeoclimate indicated by the Kudo flora was in 10°-12°C in the mean annual temperature and the precipitation was 1,200-1,400 mm. However, it might be still low temperature in winter because of the absence of *Metasequoia* in the Kudo flora.

*Eucommia japonica* was also recorded from the Middle Miocene Yanagida Formation at Takuya in Noroshi (ca. long. 137°E, lat. 42°30' N) of Noto Peninsula in Honshu, Japan (Ishida, 1970). This species was mainly associated with a few ferns: *Onoclea* and *Athyrium* and lots of gymnosperms: *Torreya*, *Keteleeria*, *Picea*, *Pinus*, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Libocedrus*, *Thuja*, and huge angiosperms *Populus*, *Compton*, *Pterocarya*, *Betula*, *Carpinus*, *Ostrya*, *Castanea*, *Castanopsis*, *Fagus*, *Quercus*, *Celtis*, *Ulmus*, *Zelkova*, *Diplodisia*, *Magnolia*, *Michelia*, *Cinnamomum*, *Machilus*, *Liquidambar*, *Parrotia*, *Sycopsis*, *Rosa*, *Albizia*, *Cassia*, *Cladrastis*, *Entada*, *Gleditsia*, *Milletia*, *Mucuna*, *Podogonium*, *Wisteria*, *Ailanthus*, *Buxus*, *Pistacia*, *Rhus*, *Perrottetia*, *Acer*, *Berchimia*, *Paliurus*, *Elaeocarpus*, *Camellia*, *Ternstroemia*, *Cornus*, *Fraxinus*, *Osmanthus*, *Syringa*, *Hemitrapa*, *Livistonia* and *Smilax*. Ishida (1970) regarded that the living equivalents of these fossil plants are mostly found in a wide area of Southeast and Central China, extending eastward to Taiwan province and Southwest Japan. This region is a rainy zone of East Asia. The annual precipitation reflected by the fossil flora is assumed to have been at least 1,600 mm, presumably even as much as 2,000 mm. The mean temperature of coldest and warmest months was estimated to the about 4°-5°C and 26°-27°C and the mean annual temperatures are 14°5'-15°C respectively. Autumn was the rainy season, and even drier month had precipitation of over 100 mm. This fossil flora was a mixed coniferous and deciduous broad-leaved forest, representing a northern subtropical and humid climate.

The fossil fruits of *Eucommia japonica* were found from the Middle Miocene to Early Pliocene Kamigo Formation in



Yamagata (long. 140°35'E, lat. 38°20'N) of northern Honshu, Central Japan as well. Tanai (1961) regarded that fossil specimens of living *Eucommia ulmoides* Oliver discovered by Miki (1941, p. 277) from the Pliocene *Pinus trifolia* bed in Gifu (long. 136°40'E, lat. 35°25'N) of southern Honshu, Central Japan should actually be a synonym of *E. japonica*. This species from the Kamigo Formation was associated with one aquatic fern, *Salvinia* and several gymnosperms: *Pinus*, *Pseudolarix*, *Glyptostrobus*, *Sequoia*, *Metasequoia*, *Cunninghamia* and many angiosperms: *Myrica*, *Carya*, *Pterocarya*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Quercus*, *Celtis*, *Ulmus*, *Zelkova*, *Liquidambar*, *Cinnamomum*, *Rosa*, *Eutada*, *Sophora*, *Robinia*, *Pistacia*, *Rhus*, *Dilodendron*, *Dodonea*, *Sapindus*, *Acer*, *Aralia*, *Tilia*, *Paliurus*, *Stewartia*, *Fraxinus* and *Styrax*. Among the hardwoods, the evergreen elements in number are much less than deciduous ones. The Kamido flora was of a mixed coniferous and deciduous broad-leaved forest, representing a northern subtropical or warm temperate and humid climate.

Some fossil fruits were discovered and assigned as *Eucommia europea* Madler by Dorofeev (1964, p. 582-584, fig. 29) from the late Miocene Sarmatian Formation of Apsheeronsk (long. 39°42'E, lat. 44°28'N) of North Caucasus. After several years, some fossil fruits from the same locality and the same stratum were found again. These fossil fruits were referred as a new species, *E. caucasica* Dorofeev (Dorofeev & Negru, 1970, p. 919, figs 1, 5-8). This species lived together with *Tsuga*, *Abies*, *Cephalotaxus*, *Typha*, *Potamogeton*, *Scirpus*, *Carex*, *Salix*, *Juglans*, *Betula*, *Castanea*, *Alnus*, *Corylus*, *Carpinus*, *Fagus*, *Polygonum*, *Moroidea*, *Corydalis*, *Prunus*, *Crataegus*, *Phyllodendron*, *Acer*, *Meliosma*, *Buxus*, *Daphne*, *Hypericum*, *Eurya*, *Aralia*, *Cornus*, *Ajuga*, *Physalis*, *Solanum*, *Bryonia*, *Fraxinus*, *Styrax*, *Kentranthus*, *Viburnum*, *Santhucus* and others. These fossil plants were mainly composed of montane temperate conifers and deciduous hardwoods. The fossil flora was of a mixed coniferous and deciduous broad-leaved forest, reflecting a warm temperate and humid climate.

*Eucommia kryshstofovichii* Negru (Dorofeev & Negru, 1970, p. 193, figs 1, 9-11) was found from the Early Miocene Sarmatian Formation in Bursuk (long. 29°15'E, lat. 47°40'N) of Moldavia. Later this species was also discovered in great numbers from Northeast Moldavia (long. 28° E, lat. 47°40'N) (Negru, 1972, p. 109, pl. 19, figs 1-7; pl. 20, figs 1-3; text-fig. 8). Negru regarded that some fossil specimens attributed to modern *Eucommia ulmoides* from the contemporaneous age in Gliwice (long. 18°41'E, lat. 52°22'N) of Poland found by Szafer (1951, p. 378, pl. 1, figs 6-13; pl. 2, pl. 4, figs 3-6). They should also be referred as *E. kryshstofovichii*. The fossil specimens of *E. ulmoides* was twice found by Gregor (1979, 1987) from Kishinev (long. 28°50'E, lat. 47°N) of Moldavia. *E. kryshstofovichii* was mainly associated with *Acer*, *Ailanthus*,

*Alangium*, *Ampelopsis*, *Aralia*, *Betula*, *Carpinus*, *Cladium*, *Cleomella*, *Comptonia*, *Cornus*, *Cotinus*, *Decodon*, *Ficus*, *Hypericum*, *Juniperus*, *Morus*, *Myrica*, *Nymphaea*, *Olea*, *Paliurus*, *Physalis*, *Pinus*, *Polycnemum*, *Potamogeton*, *Pyracantha*, *Rubus*, *Ruppia*, *Sambucus*, *Scirpus*, *Sequoia*, *Sparganium*, *Staphylea*, *Swida*, *Taxodium*, *Typha*, *Vitis* and *Zanthoxylon*. The fossil plants comprised mostly deciduous hardwoods, with some softwoods. They were representative of a mixed coniferous and deciduous broad-leaved forests, reflecting a warm temperate and humid climate.

*Eucommia palaeoulmoides* Baikovskaja was extensively distributed in the Miocene strata of Europe, especially of East Europe. Its fossil leaves in morphology are quite close to those of the living *E. ulmoides*. This fossil species was recorded from the Miocene Early Sarmatian age in Ukrainian (long. 35°40'E, lat. 47°15'N) and Moldavia (Kryshstofovich & Baikovskaja, 1965, p.75, pl. 19, fig. 6; Takhtajan, 1974, p. 154, pl. 78, figs 1-6). It was also found from the Aquitanian age of Early Miocene in Krugloe (long. 38°50'E, lat. 47°N) of Kazakhstan (Zhilin, 1989).

Based upon these specimens of fossil fruits from the Lower Sarmatian Formation in Kruka River (long. 30°30'E, lat. 55°N) of West Russia, Kryshstofovich named them under the living species *E. ulmoides* (Kryshstofovich, 1916, p. 1285, text-fig. 1a, figs 1-3). Later, it was transferred to *E. palaeoulmoides*. Its fossil fruits were also found from the Lower Sarmatian Formation in Orehov (long. 35°40'E, lat. 47°15'N) and Naslavcha (long. 28°10'E, lat. 48°15'N) (Yakubovskaja, 1955); and from the Upper Sarmatian Formation in Apsheeronsk (long. 39°42'E, lat. 44°28'N) of Caucasus, and from Kodori (long. 41°10'E, lat. 42°47'N) in Abkhaz of Georgia (Takhtajan, 1974; Kryshstofovich & Baikovskaja, 1966; Kolakovskiy, 1960, 1964). This fossil species was individually recorded from different localities in Pliocene strata in European areas. We have not seen what and how many fossil plants associated with it in the above localities.

Although *Eucommia sibirica* Dorofeev flourished in Oligocene, it was also distributed widely in the Miocene. It was found from Koreevskoe (long. 84°E, lat. 56°30'N) along the Obe River and from Esakovka (74°40'E, 56°20'N) in West Siberia (Dorofeev, 1960, p. 211-213, text-fig. 24; 1963, p. 195-196, pl.33, figs 24-28), from Tegelen (long. 6°09'E, lat. 51°20'N) and Limburg (long. 5°55'E, lat. 51°20'N) (Engelhardt and Kinklin, 1908, s. 257) of the Netherlands, from Mainz (long. 8°07'E, lat. 50°N) (Reid, 1915, p. 139) and Frankfurt a.M. (8°40'E, 50°17'N) (Bass, 1932, p. 139) of Germany. This species lived together with aquatic ferns: *Azolla* and *Salvinia*; gymnosperms: *Glyptostrobus*, *Metasequoia*, *Taxodium*, *Pinus*; and angiosperms: *Typha*, *Sparganium*, *Potamogeton*, *Najas*, *Alisma*, *Cladium*, *Scirpus*, *Carex*, *Epipremum*, *Salix*, *Juglans*, *Pterocarya*, *Carya*, *Betula*, *Alnus*, *Carpinus*, *Corylus*, *Fagus*, *Quercus*, *Morus*, *Broussonetia*.

*Boehmeria*, *Pilea*, *Polygonium*, *Brassenia*, *Eurya*, *Ceratophyllum*, *Ranunculus*, *Magnolia*, *Liriodendron*, *Armeniaca*, *Prunus*, *Cotoneaster*, *Rubus*, *Phyllodendron*, *Ailanthus*, *Phyllanthus*, *Meliosma*, *Vitis*, *Tilia*, *Actinidia*, *Hypericum*, *Viola*, *Decodon*, *Nyssa*, *Trapa*, *Myriophyllum*, *Aralia*, *Cornus*, *Vaccinium*, *Styrax*, *Lycopus*, *Tencrium* and *Weigela*. These fossil plants consisted mainly of deciduous hardwoods. They were represented by a deciduous broad-leaved forest with a few conifers, reflecting a northern subtropical or warm temperate and humid climate.

*Eucommia europaea* Mädlér (1939, s. 103, taf. 8, figs 29-31; taf. 11, figs 9, 10) is the most widely distributed in Europe in Late Tertiary. It was found from Düren (long. 6°30'E, lat. 50°48'N) of western Germany in Late Miocene (Burgh, 1983; Gregor *et al.*, 1989). This species associated with the fossil plants include several gymnosperms: *Glyptostrobus*, *Sequoia*, *Taxodium*, and a great number of angiosperms: *Acer*, *Actinidia*, *Alnus*, *Caldesia*, *Carex*, *Ceratophyllum*, *Cornus*, *Crataegus*, *Decodon*, *Distylium*, *Eurya*, *Fagus*, *Liquidambar*, *Myrica*, *Nyssa*, *Omalanthus*, *Ostrya*, *Paliurus*, *Potamogeton*, *Pterocarya*, *Punica*, *Rubus*, *Sambucus*, *Scirpus*, *Sinomenium*, *Sparganium*, *Styrax*, *Symplocos*, *Urospathites*, *Vaccinium*, *Viola* and *Vitis*. Among them, the deciduous hardwoods were dominated and the evergreen ones were just a few. The fossil plants were represented by a deciduous broad-leaved forest, reflecting a warm temperate and humid climate.

*Eucommia europaea* was also found from the Middle Miocene strata in Schlesien (long. 18°38'E, lat. 50°20'N) of Poland (Kräusel, 1919; Szafer, 1961; Mai, 1964). This species was accompanied by some gymnosperms: *Cephalotaxus*, *Cunninghamia*, *Glyptostrobus*, *Juniperus*, *Pinus*, *Sequoia*, and a great number of angiosperms: *Acanthopanax*, *Acer*, *Actinidia*, *Aesculus*, *Agrimonia*, *Alisma*, *Alnus*, *Ampelopsis*, *Aralia*, *Betula*, *Carex*, *Carpinus*, *Carya*, *Castanopsis*, *Cephalanthus*, *Cladium*, *Clematis*, *Cornus*, *Crataegus*, *Decodon*, *Fagus*, *Fragaria*, *Hartziella*, *Hippuria*, *Hydrocharis*, *Ilex*, *Juglans*, *Leucothoe*, *Linnocarpus*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Meliosma*, *Morus*, *Myrica*, *Nuphar*, *Nymphaea*, *Physalis*, *Polygonum*, *Potamogeton*, *Prunus*, *Pterocarya*, *Quercus*, *Ranunculus*, *Rosa*, *Rubus*, *Ruppia*, *Sambucus*, *Sciadopteris*, *Scirpus*, *Sinomenium*, *Sparganium*, *Symplocos*, *Thalictrum*, *Tilia*, *Typha*, *Viburnum*, *Vitis* and *Zelkova*. The Lauraceae fossils were absent in these fossil plants. These fossil plants indicated a mixed coniferous and deciduous broad-leaved forest with some evergreen hardwoods, reflecting a subtropical and humid climate.

*Eucommia europaea* was found from the Sarmatian Formation of Late Miocene in age as well, in Bujak, Erdobénye, Füzerradvány (long. 20°-22°E, lat. 43°-48°N) of North Hungary and Sály and Balaton (long. 17°40'E, lat. 46°50'N) of West Hungary (Andreánsky, 1959, s. 69; Cziffery, 1955, 1960;

Palfalvy, 1953). This fossil species was associated with several ferns: *Osmunda*, *Pteris*, *Adiantites*, *Onoclea*, *Woodwardites* and *Salvinia*; a lot of gymnosperms: *Ginkgo*, *Taxus*, *Cephalotaxus*, *Abies*, *Pseudotsuga*, *Picea*, *Pinus*, *Glyptostrobus*, *Sequoia*, *Taxodium*, *Cunninghamia*, *Libocedrus*, *Cupressus*; and a great number of angiosperms: *Magnolia*, *Liriodendron*, *Tetracentron*, *Euptelea*, *Cercidiphyllum*, *Laurus*, *Cinnamomum*, *Sassafras*, *Berberis*, *Cocculus*, *Aristolochia*, *Hakea*, *Lomatites*, *Santalum*, *Liquidambar*, *Parrotia*, *Hamamelis*, *Corylopsis*, *Platanus*, *Betula*, *Alnus*, *Carpinus*, *Ostrya*, *Corylus*, *Fagus*, *Castanea*, *Quercus*, *Juglans*, *Carya*, *Pterocarya*, *Engelhardtia*, *Myrica*, *Populus*, *Salix*, *Morus*, *Ficus*, *Ulmus*, *Zelkova*, *Celtis*, *Diospyros*, *Styrax*, *Rapanea*, *Myrica*, *Weinmannia*, *Pittospermum*, *Sporaea*, *Sorbus*, *Crataegus*, *Eriobotrya*, *Rosa*, *Prunus*, *Acacia*, *Cercis*, *Ceratonia*, *Gleditsia*, *Cassia*, *Podogonium*, *Robinia*, *Zichya*, *Desmodium*, *Terminalia*, *Nyssa*, *Daphne*, *Myrtus*, *Tilia*, *Pterospermites*, *Firmiana*, *Zanthoxylon*, *Ptelea*, *Rhus*, *Pistacia*, *Ilex*, *Ailanthus*, *Cedrela*, *Sapindus*, *Acer*, *Rhamnus*, *Zizyphus*, *Vitis*, *Ampelopsis*, *Cissus*, *Euonymus*, *Celastrus*, *Fraxinus*, *Forsythia*, *Ligustrum*, *Hedera*, *Cornus*, *Viburnum*, *Lonicera*, *Catalpa*, *Lyonia*, *Vaccinium*, *Andromeda*, *Clethra*, *Potamogeton*, *Echinodorus*, *Musophyllum*, *Phragmites*, *Arundo*, *Smilax*, *Phoeicites*, *Typha* and *Carex*. Among the fossil hardwoods, the deciduous ones were much more than evergreen ones. Therefore, these fossil plants indicated a mixed coniferous and deciduous and evergreen broad-leaved forest, reflecting a typically subtropical and wet climate.

A few fossil specimens attributed to *Eucommia* cf. *ulmoides* (Givulescu, 1974, p. 153-155, figs 2, 3; 1990, p. 55, pl. 26, fig 8) were reported from the Late Sarmatian Formation of Late Miocene in Chiuzbaia (long. 24°E, lat. 47°30'N) of Romania. The fossils of *E. cf. ulmoides* in Chiuzbaia were associated with a small number of pteridophytes: *Lycopodium*, *Adiantum*, *Osmunda*; a lot of gymnosperms: *Ginkgo*, *Torreya*, *Taxus*, *Amentotaxus*, *Cephalotaxus*, *Glyptostrobus*, *Picea*, *Pinus*, *Sequoia*, *Taiwania*, and a great number of angiosperms: *Liriodendron*, *Magnolia*, *Asimina*, *Persea*, *Sassafras*, *Neolitsea*, *Laurus*, *Daphnogene*, *Epimedium*, *Berberis*, *Mahonia*, *Ceratophyllum*, *Euptelea*, *Cercidiphyllum*, *Liquidambar*, *Parrotia*, *Platanus*, *Alnus*, *Betula*, *Carpinus*, *Ostrya*, *Corylus*, *Fagus*, *Castanea*, *Quercus*, *Ulmus*, *Celtis*, *Myrica*, *Juglans*, *Carya*, *Cyclocarya*, *Spiraea*, *Prunus*, *Sorbus*, *Photinia*, *Malus*, *Itea*, *Cercis*, *Gleditsia*, *Wisteria*, *Zanthoxylum*, *Phellodendron*, *Trapa*, *Pistacea*, *Rhus*, *Koelreuteria*, *Aesculus*, *Acer*, *Celastrus*, *Ilex*, *Paliurus*, *Berchemia*, *Hovenia*, *Ampelopsis*, *Vitis*, *Buxus*, *Loranthus*, *Viscum*, *Cornus*, *Camellia*, *Eurya*, *Populus*, *Tilia*, *Firmiana*, *Daphne*, *Arbutus*, *Clethra*, *Styrax*, *Diospyros*, *Polygonum*, *Lonicera*, *Viburnum*, *Fraxinus*, *Syringa*, *Osmanthus*, *Catalpa*, *Potamogeton*, *Smilax*, *Sasa* and *Glumophyllum*. The evergreen trees and shrubs occupied 20% in species of the total hardwoods. These

fossil plants indicated a mixed coniferous and deciduous and evergreen broad-leaved forest, reflecting a typical subtropical and wet climate.

In the Miocene strata of Europe, some fossil fruits of *Eucommia* which are often badly preserved and it is difficult to identify their species. Hence are referred to *Eucommia* sp. These fossil fruits were found from the late Middle Miocene in Karpaten (long. 20°42'E, lat. 49°38'N) (Lancucka-Srodoniowa, 1979) and Wrocław (17°05'E, 51°05'N) in Schlesien (Kräusel, 1919; Goepfert, 1855; Lancuck-Srodoniowa, *et al.*, 1981) of Poland, and from the Middle Miocene strata in Regensburg (long. 12°10'E, lat. 49°15'N) (Gregor, 1979, 1980, 1982) of Germany. These fossil fruits of *Eucommia* sp. were often associated with a few gymnosperms: *Chamaecyparis* and *Glyptostrobus*, and a lot of angiosperms: *Acer*, *Actinidia*, *Alchenilla*, *Alnus*, *Andromeda*, *Aralia*, *Betula*, *Boehmeria*, *Brasenia*, *Broussonetia*, *Campanula*, *Carex*, *Carpinus*, *Cercidiphyllum*, *Decodon*, *Gratiola*, *Hydrangea*, *Hypericum*, *Ilex*, *Lycopus*, *Magnolia*, *Menyanthes*, *Microdiptera*, *Naja*, *Patrinia*, *Phyllodendron*, *Polygonum*, *Potamogeton*, *Potentilla*, *Ranunculus*, *Rubus*, *Sambucus*, *Schefflera*, *Scirpus*, *Sparganium*, *Stratioites*, *Thalictrum*, *Trapa*, *Urospathites* and *Vaccinium*. They represented a deciduous broad-leaved forest, reflecting a warm temperate and humid climate.

### Pliocene *Eucommias*

*Eucommia europaea* was more luxuriant and flourished in Pliocene than in Miocene in Europe. It was widely discovered from the Pliocene strata such as in Haguenau (long. 7°47'E, lat. 48°49'N), France (Geissert, 1972; Geissert & Gregor, 1981, 1986; Geissert *et al.*, 1989), Karpaten (long. 20°54'E, lat. 50°06'N) Poland and in Valdarno (long. 11°18'E, lat. 45°38'N) and Italy (Azzaroli & Lazzeri, 1979). This species in Pliocene exist together with gymnosperms: *Picea*, *Pinus*, *Tsuga*, *Cephalotaxus*, *Glyptostrobus*, *Taxodium*; and a good number of angiosperms: *Acer*, *Actinidia*, *Aesculus*, *Ajuga*, *Alangium*, *Aldrovanda*, *Alnus*, *Anpelopsis*, *Aralia*, *Brasenia*, *Caldesia*, *Carex*, *Carpinus*, *Carya*, *Ceratophyllum*, *Chenopodium*, *Cornus*, *Corylus*, *Crataegus*, *Cyclocarya*, *Daphniphyllum*, *Dendrobenthamia*, *Dulichium*, *Euphorbia*, *Fagus*, *Fothergilla*, *Halesia*, *Hartziella*, *Ilex*, *Juglans*, *Leitneria*, *Liquidambar*, *Liriodendron*, *Lychnia*, *Lycopus*, *Magnolia*, *Mastixia*, *Meliosma*, *Menispermum*, *Menyanthes*, *Najas*, *Nuphar*, *Nyssa*, *Olea*, *Ostrya*, *Phyllodendron*, *Polugonum*, *Potamogeton*, *Proserpinaca*, *Prunus*, *Pterocarya*, *Pulmonaria*, *Pyracantha*, *Quercus*, *Rubus*, *Sabia*, *Salix*, *Sambucus*, *Sapium*, *Schizandra*, *Schoenoplectus*, *Schindapsites*, *Silene*, *Sclanum*, *Sparganium*, *Staphylea*, *Stellaria*, *Stewartia*, *Stratioites*, *Styrax*, *Swida*, *Syphytum*, *Symplocos*, *Ternstroemia*, *Thalictrum*, *Toddalia* (= *Teclia*), *Trapa*, *Trichosanthes*, *Vicia*, *Viola*, *Viscum*, *Vitis* and *Wikstroemia*. In these fossil plants, a small number of hardwoods were evergreen. The deciduous

hardwoods were dominant. They represented a mixed coniferous and deciduous broad-leaved forest with a small number of evergreen plants, reflecting northern subtropical and humid climate.

In the Late Pliocene, *Eucommia europaea* was found in Tegelen (6°09'E, 51°21'N) in the Netherlands (Reid & Reid, 1915; Mai, 1976), in Frankfurt a.M. (long. 8°40'E, lat. 50°07'N) of Germany (Mädler, 1939). This species in these areas was accompanied by a lot of gymnosperms: *Abies*, *Cephalotaxus*, *Keteleeria*, *Larix*, *Libocedrus*, *Picea*, *Pinus*, *Pseudolarix*, *Sequoia*, *Taxus*, *Taxodium* and *Thuja*; and a great number of angiosperms: *Acanthopanax*, *Acer*, *Aesculus*, *Ajuga*, *Alnus*, *Betula*, *Carpinus*, *Carya*, *Castanea*, *Ceratophyllum*, *Cercidiphyllum*, *Clematis*, *Corylopsis*, *Corylus*, *Dendrobenthamia*, *Dulichium*, *Euryale*, *Fagus*, *Fraxinus*, *Hedera*, *Ilex*, *Juglans*, *Leitneria*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Melissa*, *Nuphar*, *Nyssa*, *Peucedanum*, *Pyrus*, *Polygonum*, *Potamogeton*, *Prunus*, *Pterocarya*, *Quercus*, *Salix*, *Sambucus*, *Scirpus*, *Scleranthus*, *sorbuss*, *Sparganium*, *Staphylea*, *Stewartia*, *Styrax*, *Swida*, *Tilia*, *Trichosanthes*, *Ulmus*, *Viburnum*, *Viola* and *Vitis*. From these fossil plants, we can see that the gymnosperms genera in number in the Late Pliocene are more than in the Early Pliocene. The compositions of angiospermous genera are similar to previous age. These fossil plants represented by a mixed coniferous and deciduous broad-leaved forest, reflecting a warm temperate and humid climate.

Some fossil fruits of *Eucommia ulmoides* (Gregor, 1989) and *Eucommia* sp. (Gregor *et al.*, 1989; Günther & Gregor, 1989) were found from the Late Pliocene age in Frankfurt (long. 8°40'E, lat. 50°07'N) and Aschaffenburg (9°08'E, 49°58'N) of Germany. The two species were accompanied with a few gymnosperms: *Glyptostrobus* and *Pinus*; and a lot of angiosperms: *Acer*, *Aesculus*, *Carex*, *Carpinus*, *Ceratophyllum*, *Decodon*, *Fagus*, *Liquidambar*, *Magnolia*, *Nuphar*, *Nyssa*, *Styrax*, *Tilia*, *Viscum*, and *Vitis*. These fossil plants represented a mixed coniferous and deciduous broad-leaved forest, reflecting a warm temperate and humid climate.

Magallen-puebla and Cevalloz-ferris (1992) reported a Late Cenozoic *Eucommia* fruit from Puebla (98°W, 19°N) of Mexico. This is a far southern fossil record of *Eucommia* in Northern Hemisphere.

### Pleistocene *Eucommias*

*Eucommia europaea* (Bass, 1932) was found from Frankfurt a.M. (8°33'E, 50°03'N) of Germany in Early Pleistocene and some other fossil fruits referred to *Eucommia* sp. (Gregor, 1987) were found from Fidenza (long. 10°03'E, lat. 44°51'N) of Italy in Early Pleistocene. These *Eucommia* fruits were accompanied by some gymnosperms: *Abies*, *Picea*, *Pinus*, *Tsuga*, *Cephalotaxus* and *Juniperus*; and a lot of angiosperms: *Ajuga*, *Alnus*, *Betula*, *Brasenia*, *Carpinus*,

*Carya*, *Ceratophyllum*, *Cenococum*, *Cicuta*, *Cladium*, *Coriaria*, *Cornus*, *Corylus*, *Daphne*, *Dulichium*, *Eriophorus*, *Fagus*, *Hamamelis*, *Hydrocotyle*, *Iris*, *Lycopus*, *Medicago*, *Menyanthes*, *Najas*, *Nuphar*, *Nymphaea*, *Oenanthes*, *Ostrya*, *Paeonia*, *Parrotia*, *Potamogeton*, *Prunus*, *Pterocarya*, *Quercus*, *Rubus*, *Salix*, *Sambucus*, *Solanum*, *Sparganium*, *Tilia*, *Trapa*, *Ulmus* and *Vitis*. These fossil plants represented a mixed coniferous and deciduous broad-leaved forest, reflecting a temperate and humid climate.

## PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY OF *EUCOMMIA*

Fossil records of *Eucommia* through geological ages as reviewed above indicate that *Eucommia* is only restricted in Northern Hemisphere. The *Eucommia* fossil probably earliest appeared in Paleocene epoch in East China (long. 120°-128°E, lat. 25°-32°N) and from then spread into overall Northern Hemisphere. In Eocene, it dispersed probably along East Coast of China to southern reaching Guangdong, South China and northeastward to Hokkaido, Japan. It strode across Bering strait to Alaska, Washington and Tennessee, North America at that time. Its latitudinal distribution was from lat. 23°10'N to lat. 60°30'N spanning across 37°10'N and longitudinal distribution from long. 112°52'E to long. 144°W across 103° in the Eocene. Because the Eocene epoch was the warmest period of Cenozoic era in the earth. Therefore, it was warmer in the high latitude in the Eocene epoch than in other epochs. In the Oligocene, some *Eucommia* species ever grew in Alaska and Montana, the United States and in West Siberia, Russia. In the Early Tertiary, the *Eucommia* was mainly restricted to coasts of the Pacific Ocean.

In the Early Tertiary, China was together connected with Japan as the same continent. The Sea of Japan did not appear yet. *Eucommia* could easily extended into Japan without obstruction. During the Early Tertiary, the Bering strait received mainly continental sedimentation. There is a good evidence that the volcanic rocks and coal-bearing strata were found in Beringia (Parrish, 1987). The Bering area was scarcely marine sedimentation until the beginning of the Miocene. The *Eucommia* migrated from Alaska to Montana and the western part of North America during Early Tertiary.

In the Oligocene, *Eucommia* was only discovered in eastern coast of the ancient Obe Sea, West Siberia. It seems to show that *Eucommia* do not reach Europe in the Palaeogene. Because of the ancient Obe Sea being several thousand km in width and connect the Tethys with Arctic Ocean, it was a major roadblock of *Eucommia* migration from Asia to Europe in the Palaeogene. The Obe Sea began to regress and disappeared by the Oligocene. Since the beginning of Miocene, the *Eucommia* could migrate from Asia to Europe.

During the Miocene, *Eucommia* was the most plentiful in number of species and specimens and the most extensive in space. It grows in Alaska of the United States and the mountains of Puebla of Mexico in the Neogene (probably Miocene) (Magallon-Puebla & Cevallos-Ferriz, 1992) and in Honshu of Japan and Siberia, Asia. It was also widespread in Europe. During the Miocene, *Eucommia* was distributed from long. 5°55'E to long. 98°W across about 256° of longitude and from lat. 19°N to lat. 56°30'N across 37°30' of latitude in Northern Hemisphere. It reached its largest distributive space in geological time. After the Miocene or a little later, the *Eucommia* probably disappeared from the continent of North America. However, it still survived in Asia and Europe since then.

In the Pliocene, *Eucommia* also lived in Japan and Siberia of Asia but it extensively spread in Europe. Its distributional areas were from long. 6°10'E to 136°41'E and lat. 35°30'N to 51°21'N. Its central areas of distribution were in long. 6°-11°30'E and lat. 43°-51°21'N in Europe. It did not survive beyond the Middle Pleistocene in Europe because the cold glacial climate became the stronger and stronger since Pleistocene in northern of the Northern Hemisphere. The *Eucommia* disappeared in Europe in Late Pleistocene at last. Based on the above mentioned, *Eucommia* megafossils have not been found in both sides of the Atlantic Ocean. It seems to imply that *Eucommia* did not stride across the Atlantic Ocean through the Greenland, though it is as a land bridge in connection with Europe and North America in Early Tertiary. There is a possible reason that after the Atlantic Ocean split, it is never closed. *Eucommia* could not span across it but still survives in Central China now.

The above data show that the palaeoclimate indicated by the megafossil plants in association with *Eucommia* showed generally subtropical to warm temperate zones and humid climate in different period of Cenozoic era. This palaeoenvironment is in accordance with the modern climate of the living *Eucommia* habitation in China.

The fossil *Eucommia* species could sometimes live under a southern subtropical and subarid climate, such as in Guangdong of South China in Eocene and in Puebla of Mexico in Neogene. It can also grow under a temperate and humid climate in Italy and Germany in Early Pleistocene. Based on the recent study of living *Eucommia* (Zhang, 1990), it can not grow, develop and reproduce well to south of tropic of cancer in South China and in the too cold climate in North China. Zhang Kang-jan(1990) considered that if the temperature is too hot in summer, *Eucommia* will easily suffer from insect pests and disease, and if over cold in winter it will undergo frigid injury and even death owing to freeze.

Why could *Eucommia* grow in Sanshui (lat. 23°10'N) of Guangdong, South China in Eocene and in Puebla (lat. 19°N) of Mexico in Neogene? If the temperature in Cenozoic era

was consistent and comparable with the modern one, why the *Eucommia* could not grow and develop in Shansui of South China and Puebula of Mexico under the high temperature? How to explain the evidences of the *Eucommia* fossils discovered in the low latitude in the geological time?

The Milankovitch's hypothesis and the astrogeology (Wolfe, 1978; Xu *et al.*, 1983) gave a good explanation about the climatic change. It is that the inclination of the earth's rotational axis has always been changing in each geological time. The change of inclination of the earth's rotational axis has influenced climatic fluctuations. From the Paleocene to the middle Eocene, inclination became to decrease gradually

from a value of perhaps 10° to a value of 5°. It results in the difference of radiant flux in winter and summer became less. The temperature difference of higher and lower latitudes and the range of mean annual temperatures also were low. It means that the temperature of lower latitudes in summer is not so hot and the higher latitude in winter not so cold. Thus, *Eucommia* could widely grow and reproduce either in lower latitude or in higher latitude. The *Eucommia* might have lived in the Sanshui in South China which was a little south of the tropic of Cancer. In contrary, the inclination became to increase to the present average value of 23.5° (Wolfe, 1978). It resulted in the elevation of temperature difference of winter and summer. Consequently,

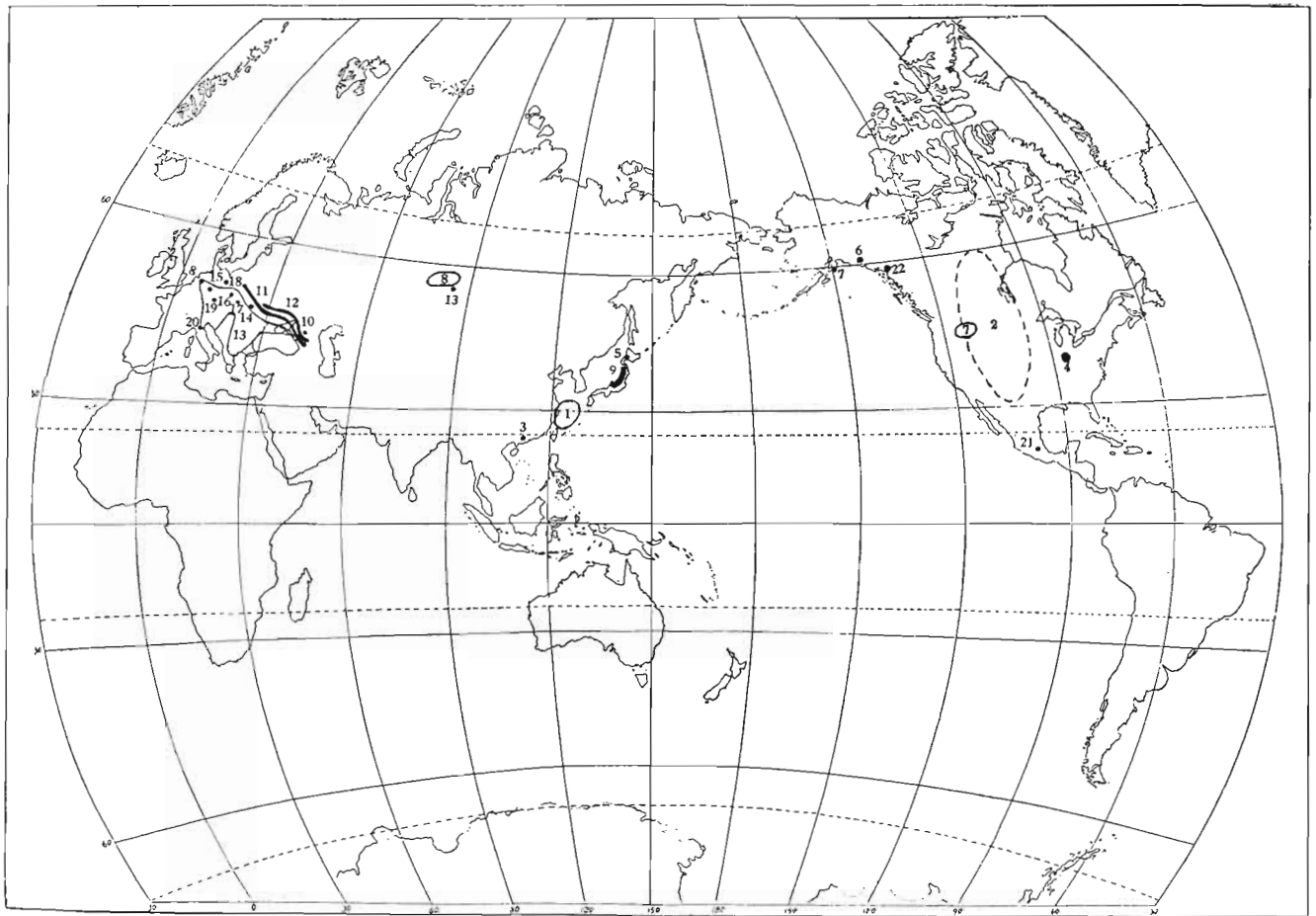


Fig. 3 — The map showing the distribution of the fossil species of *Eucommia* in the world.

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| 1 <i>Eucommiaceipollenites eucommides</i> and <i>E. minor</i> , pollen, Paleocene; | 12. <i>E. palaeoulmoides</i> , fruits, and leaves, Miocene;                |
| 2. <i>Eucommia serrata?</i> leaves, Eocene;  | 13. <i>E. europaea</i> , fruits, Miocene-Pliocene;                         |
| 3. <i>E. brevirostria</i> , fruit, Early Eocene;                                   | 14. <i>E. cf. ulmoides</i> , fruits, Miocene;                              |
| 4. <i>E. eocenica?</i> fruits, Eocene;   | 15. <i>E. ulmoides</i> , fruits, Miocene-Pliocene;                         |
| 5. <i>E. kobayashi</i> , fruits, Eocene;   | 16. <i>Eucommia</i> sp3., fruits, Miocene;                                 |
| 6. <i>Eucommia</i> sp., leaves, Eocene;  | 17. <i>Eucommia</i> sp4., fruits, Pliocene;                                |
| 7. <i>E. montana</i> (= <i>E. browni</i> ), fruits, Oligocene-Miocene;             | 18. <i>Eucommia</i> sp5., fruits, Pliocene;                                |
| 8. <i>E. sibirica</i> , fruits, Oligocene and Miocene;                             | 19. <i>Eucommia</i> sp6., fruits, Pliocene;                                |
| 9. <i>E. japonica</i> , fruits, Miocene-Pliocene;                                  | 20. <i>Eucommia europaea</i> and <i>Eucommia</i> sp., fruits, Pleistocene; |
| 10. <i>E. caucasica</i> , fruits, Miocene-Pliocene;                                | 21. <i>Eucommia</i> sp., fruits, Neogene;                                  |
| 11. <i>E. kryshstofovichii</i> , fruits, Miocene;                                  | 22. <i>Eucommia</i> sp., fruit, Eocene.                                    |

Fig. 4—The geological ages and geographical distributions of fossil *Eucommia*.

Fossil species	Organ	Age	Stratigraphy	Longitude/Latitude	Locality	Reference
<i>Eucommiaceoi</i>	pollen	Paleocene	Lingfang Fm.	120-128°E, 25-32°N	East China	Sun, 1990
<i>-pollites ecommides</i>						
<i>E. minor</i>	pollen	Paleocene	Lingfang Fm.	120-128°E, 25-32°N	East China	Sun, 1990
<i>Eucommia serrata?</i>	leaves	Paleocene	Fort Union Fm.	95-115°W, 31-60°N	North America	Brown, 1962
<i>E. brevirotria</i>	fruit	Eocene	Buxin Fm.	112°52'E, 23°10'N	South China	Guo, 1979
<i>E. eocenica?</i>	fruit	Eocene	Holly Spring Fm.	88°34'W, 37°40'N	Tennessee, USA	Berry, 1930; Brown, 1940
<i>E. kobayashi</i>	fruits	Eocene	Yubari Fm.	141°50'E, 43°15'N	Hokkaido, Japan	Huzioka, 1961
<i>Eucommia</i> sp.	leaves	Eocene	Kushtaka Fm.	144°W, 60°30'N	Alaska, USA	Wolfe, 1977
<i>Eucommia</i> sp.	fruits	Eocene	Klondike Mt. Fm.	118°42'W, 48°38'N	NW, USA	Wehr, 1995
<i>E. brownii</i>	fruits	Oligocene	Ruby R. Fm.	112°03'W, 45°26'N	Montana, USA	Becker, 1961
<i>E. montana</i>	fruits	Oligocene		112°05'W, 45°27'N	Montana, USA	Brown, 1940
<i>E. montana</i>	fruits	Oligocene	Beaverhead Fm.	112°40'W, 45°20'N	Montana, USA	Becker, 1969
<i>E. cf. montana</i>	fruit	Miocene	Seldovia Point Fm.	151°40'W, 58°40'N	Alaska, USA	Wolfe & Tanai, 1980
<i>E. sibirica</i>	fruits	Oligocene		84°20'E, 57°20'N	Western Siberia	Dorofeev, 1960, 1963; Takhtajan, 1974
<i>E. sibirica</i>	fruits	Miocene		74°40'E, 56°20'N	Western Siberia	Dorofeev, 1963; Takhtajan, 1974
<i>E. sibirica</i>	fruits	Miocene		74°10'E, 56°10'N	Western Siberia	Dorofeev, 1963; Takhtajan, 1974
<i>E. sibirica</i>	fruits	Miocene		6° 10'E, 50°10'N	Netherlands	Engelhardt & Kinklin, 1908; Reid, 1907; Reid & Reid 1915
<i>E. sibirica</i>	fruits	Miocene		84°00'E, 56°30'N	Western Siberia	Dorofeev, 1960, 1963
<i>E. sibirica</i>	fruits	Miocene		6°09'E, 51°20'N	Netherlands	Reid, 1907
<i>E. japonica</i>	fruits	Mio-Pliocene	Kamigo Fm.	140°35'E, 38°20'N	Japan	Tanai, 1961
<i>E. japonica</i>	fruits	Pliocene	<i>Pinus trifolia</i> Bed	136°41'E, 35°30'N	Gifu, Japan	Miki, 1941
<i>E. japonica</i>	fruits	Miocene	Kudo Fm.	139°45'E, 42°30'N	Ogawa, Japan	Tanai & Suzuki, 1972
<i>E. japonica</i>	fruits	Miocene	Yanagid Fm.	137°E, 42°30'N	Japan	Ishida, 1970
<i>E. caucasica</i>	fruits	Miocene		39°42'E, 44°28'N	North Caucasus	Dorofeev, 1964; Dorofeev & Negru, 1970
<i>E. caucasica</i>	fruits	Pliocene		41°10'E, 42°47'N	Geogia	Kolakovsk, 1960
<i>E. kryshstofovichii</i>	fruits	Miocene	Sarmatian Fm.	29°15'E, 47°40'N	Moldovia	Dorofeev & Negru, 1970, Negru, 1977
<i>E. kryshstofovichii</i>	fruits	Miocene	Sarmatian Fm.	28°E, 47°42'N	Moldovia	Negru, 1972; Gregor, 1979
<i>E. kryshstofovichii</i>	fruits	Miocene	Sarmatian Fm.	18°41'E, 50°22'N	Poland	Szafer, 1951
<i>E. palaeoulmoides</i>	leaves	Miocene	Aquitanian Fm.	38°50'E, 47°00'N	Kazakhstan	Zhilin, 1989
<i>E. palaeoulmoides</i>	fruits	Miocene	Sarmatian Fm.	38°40'E, 46°40'N	West Russia	Kryshstofovich, 1916
<i>E. palaeoulmoides</i>	fruits	Miocene		35°40'E, 47°15'N	Ukraine	Kryshstofovich, 1916
<i>E. palaeoulmoides</i>	fruits	Miocene	Sarmatian Fm.	28°10'E, 48°15'N	Moldovia	Yakubovskaja, 1955
<i>E. palaeoulmoides</i>	fruits	Miocene	Sarmatian Fm.	39°42'E, 44°28'N	North Caucasus	Kryshstofovich, 1916
<i>E. palaeoulmoides</i>	fruits	Miocene		41°10'E, 42°47'N	Geogia	Kolakovsk, 1960, 1964; Baikovska, 1963
<i>E. europaea</i>	fruits	Miocene		39°42'E, 44°28'N	North Caucasus	Madler, 1939; Dorofeev, 1960, 1963
<i>E. europaea</i>	fruits	Miocene		84°00'E, 56°30'N	Western Siberia	Dorofeev, 1960, 1963
<i>E. europaea</i>	fruits	Miocene		6° 30'E, 50°52'N	Germany	Burgh, 1983; Gregor <i>et al.</i> , 1989
<i>E. europaea</i>	fruits	Miocene		18°38'E, 50°20'N	Poland	Gregor <i>et al.</i> , 1989; Kräusel, 1919; Mai, 1964; Szafer, 1961 Goeppert, 1855
<i>E. europaea</i>	fruits	Miocene		20°36'E, 49°40'N	Poland	Lancucka-Srodoniowa, 1979; Milek, 1959
<i>E. europaea</i>	fruits	Miocene		6°09'E, 51°20'N	Netherlands	Reid, 1907
<i>E. europaea</i>	fruits	Miocene		8°45'E, 51°10'N	Germany	Engelhardt & Kinklin, 1908
<i>E. europaea</i>	fruits	Miocene		6°10'E, 51°20'N	Netherlands	Reid, 1915
<i>E. europaea</i>	fruits	Miocene		8°50'E, 50°02'N	Germany	Bass, 1932
<i>E. europaea</i>	fruits	Miocene	Sarmatian Fm.	20°22'E, 47°48'N	NE Hungary	Andreansky, 1959; Cziffery, 1955, 1960
<i>E. europaea</i>	fruits	Pliocene		17°40'E, 46°50'N	Hungary	Palfalvy, 1953

Fossil species	Organ	Age	Stratigraphy	Longitude/Latitude	Locality	Reference
<i>E. europaea</i>	fruits	Pliocene		11°30'E, 43°33'N	Italy	Azzaroli & Lazzeri, 1979; Gregor 1989,
<i>E. europaea</i>	fruits	Pliocene		8°E, 48°48'N	France	Geissert, 1972; Geissert & Gregor, 1981, 1986; Geissert <i>et al.</i> , 1989
<i>E. europaea</i>	fruits	Pliocene		6°06'E, 51°19'N	Netherlands	Reid, 1907; Reid & Reid 1915;
<i>E. europaea</i>	fruits	Pliocene		8°45'E, 50°06'N	Germany	Engelhardt & Kinklin, 1908; Mädler, 1939
<i>E. europaea</i>	fruits	Pliocene		8°15'E, 51°10'N	Germany	Engelhardt & Kinklin, 1908
<i>E. europaea</i>	fruits	Pliocene		6°10'E, 51°20'N	Netherlands	Reid & Reid 1915; Mai, 1976
<i>E. europaea</i>	fruits	Pliocene		20°54'E, 50°06'N	Poland	Szaffer, 1954
<i>E. europaea</i>	fruits	Pleistocene		8°33'E, 50°03'N	Germany	Bass, 1932; Kovar & Gregor, 1984
<i>E. cf. ulmoides</i>	fruits	Miocene	Sarmatian Fm.	24°00'E, 47°30'N	Romania	Givulescu, 1974, 1990
<i>E. ulmoides</i>	fruits	Pliocene		8°51'E, 50°06'N	Germany	Gregor <i>et al.</i> , 1989
<i>E. ulmoides</i>	fruits	Miocene		18°39'E, 50°21'N	Poland	Kräusel 1919; Szafer 1961, Mai 1964
<i>Eucommia</i> sp.3	fruits	Miocene		20°42'E, 49°39'N	Poland	Kräusel, 1919; Goeppert, 1855
<i>Eucommia</i> sp.	fruits	Miocene		17°42'E, 51°52'N	Poland	Lancucka-Srodonioda <i>et al.</i> , 1981
<i>Eucommia</i> sp.	fruits	Miocene		12°06'E, 49°09'N	Germany	Gregor, 1979, 1980, 1982
<i>Eucommia</i> sp.	fruits	Pliocene		8°57'E, 50°03'N	Germany	Gregor, 1989
<i>Eucommia</i> sp.	fruits	Pliocene		8°03'E, 48°48'N	France	Geissert, 1972; Geissert <i>et al.</i> , 1989
<i>Eucommia</i> sp.	fruits	Neogene		98°00'W, 19°00'N	Mexico	Magallon-Puebla & Cevalloz-Ferriz, 1992
<i>Eucommia</i> sp.	fruits	Pleistocene		11°24'E, 44°52'N	Italy	Gregor, 1987, 1989

the winter became colder and summer became hotter. It was the reason why the *Eucommia* could not grow to south of tropic of Cancer in South China. In Neogene, the global temperature was gentle and warm. The temperature was not so cold and not so hot in the lower latitudes. Thus the *Eucommia* could also adapt to upland or lower mountain in Puebla of Mexico (Xu *et al.*, 1983).

## SYSTEMATIC EVOLUTION OF *EUCOMMIA*

*Eucommia* was established by Oliver (1891) based on the herbaria collected from Hunan province, Central China. He put *Eucommia* into Urticales according to the fruit feature which look like those of Ulmaceae. Engler (1909) put *Eucommia* on an individual family. Hutchinson (1931) referred it to the Hamamelidaceae. Engler and Diels (1936) transferred it to Rosales. Nemejc (1956) elevated it to an order level. Takhtajan (1969, 1980) considered that Eucommiales is in relation to Urticales, both orders probably had a common origin. Thorne (1989) put Eucommiaceae into Hamameliales and indicated that it had no relation to Urticales. Cronquist (1981, 1988) believed that Eucommiales is close to Urticales in morphology. The two orders should belong to Hamamelidae. Echartd (1963) considered that Eucommiales with two ovules is more primitive than Urticales with solitary ovule. However, the presence of unitegm, weak developed and crassinucellate ovule and missing stipules in Eucommiaceae are evidently

advanced characters. He indicted further that Eucommiales is probably between Hamamelidales and Urticales in systematic position. The three meridional furrows of unequal length and with rounded ends represent the germinal apertures of *Eucommia* pollen. These characteristics of *Eucommia* pollen are similar to those of *Cercidiphyllum* and *Euptelea* (Erdtman, 1969).

The evolution and systematic relationship of modern and fossil *Eucommia* is discussed.

1. After research on the wood anatomy of the living *Eucommia*, Zhang Zhiyu *et al.* (1990) supported Keng's viewpoint that spiral thickenings on lateral walls of vessels in *Eucommia* are remnant of a primitive character, which is similar to those of some genera of Hamamelidaceae. However, the lateral walls of vessels in Ulmaceae are lacking spiral thickenings on lateral walls. The simple perforation plates of Eucommiaceae are more specialized than those of Hamamelidaceae.

2. Zhang Zhi-yu *et al.* (1990) noticed that the *Eucommia* contains iridoid compound and having unitegm ovules and cellular endosperm. Dahlgren (1980, 1983) put with uncertainty Eucommiaceae into Corniflorae, Loasiflorae and Lamiiflorae, as a member of evolutionary lineage. This treatment is widely discrepant from those of Takhtajan (1980), Cronquist (1981) and Thorne (1989). Though Eucommiaceae contains iridoid compound, it is different from the super order

of corniflorae in its external morphology, wood anatomy and embryology. The iridoid compound has also been found in *Liquidambar* (Hamamelidaceae) but not in Ulmaceae.

3. The development of microsporangia and megasporangia of Eucommiaceae was studied by Tang (1962) and Eckardt (1963). Zhang Zhi-yu *et al.* (1990) observed firstly the haustoria present both at the micropylar end and at the chalazal end and 4-celled proembryo of the solanad type.

Both families Eucommiaceae and Hamamelidaceae share some embryological characters, e.g., glandular tapetal cells usually being multinuclear, cytokinesis of meiosis of pollen mother cells being simultaneous, microspores developing tetrahedrally; ovules presenting anatropous, crassinucellate; embryo sacs being of the monosporic polygonum type and endosperm being cellular. Embryologically, Eucommiaceae is more specialized than both families of Ulmaceae and Hamamelidaceae. There is a proembryo of the solanad type, coexistence of micropylar haustorium and chalazal haustorium, especially the epidermis and the endothecium being widely separate in Eucommiaceae. These characters are more specialized than both families of Ulmaceae and Hamamelidaceae.

4. Zhang Yu-long *et al.* (1988) and Zhang Zhiyu *et al.* (1990) regarded the tricolporate pollen grains of Eucommiaceae and Hamamelidaceae are obviously different from the pored pollen of Ulmaceae. Based on the characters of anatomy, embryology and pollen morphology, the Eucommiaceae has more close relation to Hamamelidaceae than to Ulmaceae. The *Eucommia* pollen has sometimes been compared to that of *Cercidiphyllum*, although it differs in details (Cronquist, 1981).

5. Zhang Zhiyu *et al.* (1990) postulated that the Ulmaceae and Eucommiaceae diverged from an earlier common ancestor. Cronquist (1981) wrote that Eucommiaceae with two ovule is more primitive than the Urticales with only one, but more advanced than in several other features such as unitegmic, not fully crassinucellate ovules and absence of stipules. It seems likely that the Eucommiaceae originated from the Hamamelidales as an independent order - Eucommiales. He wrote further that because of the combination of both advanced and primitive features, Eucommiaceae could not be regarded as directly transitional taxon between the Hamamelidales and Urticales, though Eucommiaceae supports the idea of an evolutionary link between the two orders.

6. After the research of the foliar architecture of Hamamelidae, Wolfe (1989) pointed out that Eucommiaceae should be put in the subclass of Hamamelidae. However, the foliar physiognomy of Eucommiaceae is not quite similar to that of Hamamelidae, but close to the Violales of Dilleniidae. Wolfe also noticed that the anatomy, venation, teeth type and habit of Eucommiaceae are very close to those of Stachyuraceae of Violales, but not to either Hamamelidaceae

or Ulmaceae. Meanwhile, he pointed out again that the characteristics of foliar physiognomy, xylem and pollen of *Stewartia pautagana* of Theaceae are analogous to Eucommiaceae. Wolfe (1989) believed that *Eucommia* is related to *Stachyurus* of Stachyuraceae in Violales and *Stewartia* of Theaceae in Theales.

7. It is difficult to know the evolutionary relation of fossil fruits of Eucommiaceae. Morphologically, the fossil fruits in earlier ages are a little smaller than those in the present day. Perhaps it might be an evolutionary tendency of Eucommiaceae fruits.

## DISCUSSION AND CONCLUSION

According to the present evidences of *Eucommia* fossils, some reports of pre-Cenozoic remains are unreliable. The earliest records of *Eucommia* fossils are Paleocene pollen grains (Cronquist, 1988) which occurred from East China. The Paleocene pollen remains of *Eucommia* from North America are not universally recognized. So *Eucommia* probably originated from East China. Since Eocene, the fossil fruits and leaves of *Eucommia* are commonly found in Northern Hemisphere.

Latitudinally, the widest distribution of *Eucommia* fossils in space is from lat. 23°10'N to 60°30'N, across 37°20' in the Eocene and longitudinally from long. 6°10'E to 98°10'W, across 255°40' in the Miocene. *Eucommia* mainly occurred in Eastern Hemisphere. It has survived in North America from Eocene to Late Miocene and in Europe from Miocene to Early Pleistocene, and in Asia from Paleocene to present day.

The palaeobiogeographic distributions of *Eucommia* were consistent with paleogeographic evolution of Northern Hemisphere in Cenozoic era. The region of Bering Sea received mainly continental deposits in Early Tertiary. Therefore, *Eucommia* might be interpreted as a transcontinental plant which migrates from East Asia to North America via the Bering area. The Ancient Obe Sea (Turgayan Sea) situated in West Siberia was vast and spacious area, connected from the Tethys to the Arctic Ocean across several kilometers, so the migration of *Eucommia* from Asia to Europe was barred by the ancient Obe Sea in Early Tertiary. The regression of Obe Sea did not occur until the Late Oligocene. The transmission of *Eucommia* between Asia and Europe occurred since Late Oligocene, but transgression and extensive sea in Late Tertiary barred its migration across the Bering area.

The Palaeoclimatic environment reflected by the fossil plants in association with *Eucommia* is generally in accordance with the modern habitation where the wild *Eucommia* is growing now. The climatic environment represents a subtropical to warm temperate and humid conditions. It seems to show that the modern climatic environments of the wild *Eucommia* now are also reflected by the fossil plants in geological time.



From the foregoing account of the endemic family Eucommiaceae of China, we recognize that the "endemic family, genus and species" are limited in time and space. The present endemic taxa not only restricted in a local and narrow area, but did not show the same restriction in the past time. The present endemic taxa might have extensively distributed in other areas in the past geological times. It can be deduced that the present endemic taxa could migrate and disperse to any place in different geological times. The ecological habitation of the present endemic plants might represent their optimum environment in the past. Therefore, the present endemic plants of a local area are not equal to the endemic plants of same local area in the past.

**Acknowledgements**—I am very grateful to Wu Zheng-yi and Tang Yangcheng for their suggestions of this research about the endemic family Eucommiaceae within China and for their encouragement to the author; to Peter Raven, the Director of Missouri Botanical Garden and late Author Cronquist, in New York Botanical Garden, for their many valuable and precious books and papers presented. I would like to thank Steven R. Manchester, in Florida Museum of Natural History, for critically reading the manuscript and for helpful suggestions to K. S. Saraswat of Birbal Sahni Institute of Palaeobotany, Lucknow, India. This study is supported by National Natural Science Foundation of China no. 9390010.

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