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Eucommia (Eucommiaceae), a potential biothermometer for the reconstruction of paleoenvironments[1]

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The living trees of *Eucommia ulmoides*, an endemic species in China, grow from 200 to 1700 m above sea level, within the geographic range from 102° E to 118° E and from 25° N to 35° N. Spring temperatures in these regions vary from 12.3°C to 20.1°C. A physiological study (using germination tests) of *E. ulmoides* has been undertaken to test the role of spring temperature as a factor controlling the distribution of *Eucommia*. Results show that the spring temperature is a limiting factor for *Eucommia* seed germination and hence for the distribution pattern of the genus. The suitable range of temperature for seed germination, established experimentally, is from 13°C to 22°C, with an optimum of 18°C. Specimens of fossil *Eucommia* cf. *ulmoides*, preserved as a branch segment and leaves, showing the distinctive latex, were found in Middle Miocene sediments of Shanwang Formation, Shandong Province, East China. If the climatic tolerances documented here for *E. ulmoides* are extrapolated to Shanwang, they are in fact consistent with other predictions of the paleoclimate at this site, indicative of the potential value of *Eucommia* as a biothermometer. These Miocene fossils, and one previously described Eocene fruit specimen, prove the former existence of *Eucommia* in China in addition to North America and Europe. This confirms that the genus is not a recent arrival in China and extends our understanding of the past biogeography of the genus.

Key words: biogeography; China; East Asia; *Eucommia*; Eucommiaceae; Miocene; paleoenvironments.

In order to understand global climate change today, we need to understand the pattern and process of climate change in the past. The evolution of plants was strongly influenced by, and therefore reflects, environmental changes in the geological past. Plants have to tolerate the full climate range in their habitat and are rightly regarded as good biothermometers for the environment. Studies of fossil plants, and their closest relatives involving their systematic status, biogeography, ecology, and physiology may provide a valuable key to reconstruct past terrestrial environments.

Eucommia ulmoides Oliv. is the single extant species of the genus *Eucommia* (Eucommiaceae) (Cronquist, 1981). The living trees of *E. ulmoides* occur only in the hilly area of South China (Fig. 1; Ying, Zhang, and Boufford, 1993). The unicellular latex ducts and the structure of the samaras are unique features of *Eucommia* (Tippo, 1940; Tian and Hu, 1983) and have been used, as a distinctive combination of features, in tracing the history of *Eucommia* in the Northern Hemisphere (Call and Dilcher, 1997).

The earliest macrofossils that can unequivocally be placed in genus *Eucommia* are fruits found in Eocene sediments of Hokkaido, Japan (Huzioka, 1961); Fushun, Northeast China (Geng, Manchester, and Lu, 1999); and the western and southeastern United States (Call and Dilcher, 1997; Manchester, 1999). *Eucommia* macrofossils also occur in western European floras from Oligocene to Upper Pliocene (Mai, 1995; Zhilin, 1989), in North America from Eocene to Oligocene (Call and Dilcher, 1997), and extending into the Miocene of southern Mexico (Magallon-Puebla and Cevallos-Ferriz, 1994). Fossil fruits of *Eucommiodes orientalis* Tao and Zhang (1992) reported from the early Cretaceous of Jilin Province and *Eucommia brevirostria* Guo (1979) found from the early Eocene of Guangdong Province have been rejected due to their lacking key features of the *Eucommia* samara, especially the reticulate pattern of veins and latex filaments over the seed and the medial vascular strand separating the fertile and vestigial infertile carpels (Call and Dilcher, 1997). Mesozoic pollen of *Eucommiidites* Erdtman were considered at one time as early representatives of *Eucommia* but have been more recently proved to be clearly gymnospermous and have been assigned to the new order Erdtmanithecales (Friis and Pederson, 1996).

Our aim in this paper is to explore the potential role of *Eucommia* as a biothermometer in paleoenvironmental reconstruction. The concept of the nearest living relative (NLR) based on recognition of modern genus or even species (Collinson, 1986; Mosbrugger, 1999) and the climate analysis of endemic species (Li, Wang, and Sun, 2001) are adopted and applied in this paper by using the assumption that the fossil species and its NLR species have similar ecological requirements.

MATERIALS AND METHODS

Germination experiments—An experiment was conducted to determine seed vigor in *E. ulmoides* as measured by the number of germinating seeds produced under different temperature conditions. Seed vigor is defined as ''that condition of active good health and natural robustness in seeds which, upon planting, permits germination to proceed rapidly and to completion un-

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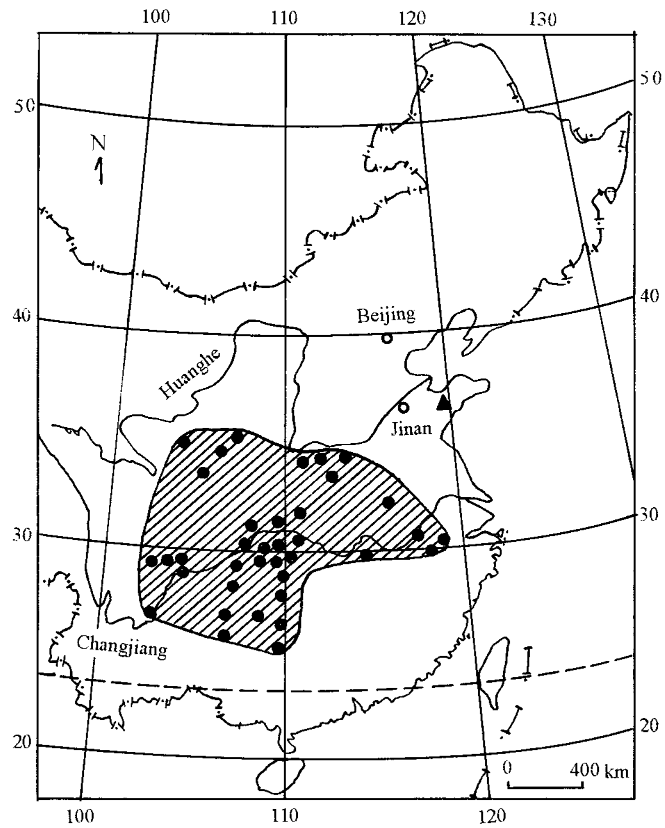


Fig. 1. The fossil locality of *Eucommia* cf. *ulmoides* (triangle) and the distribution of *E. ulmoides* (circles).

der a wide range of environmental conditions'' (Woodstock, 1973, p. 134 and p. 136). The more vigorous the seed is, the bigger the chance of the seedling surviving; the less vigorous it is, the weaker its seedling (Woodstock, 1973; Gu, Xu, and Zheng, 1982; Tao and Zheng, 1991). Seed vigor is affected by factors from both genetic properties and environments. Germination response along a temperature gradient provided a useful measure of seed vigor (Cole, 1972; Woodstock, 1973).

Fresh ripe fruits were collected in autumn from *Eucommia* trees cultivated in Beijing Botanical Garden. Seeds were removed from the fruits in order to avoid imposed dormancy that is otherwise introduced in *Eucommia* by the fruit wall (Lin, Zheng, and Zhang, 1989). Seeds uniform in size and mass, and without mechanical damage, were chosen for the test to ensure that experimental results were not influenced by variations in these factors. The germination experiments were undertaken in the dark. The germination of seeds was established at temperatures of 5°C, 10°C, 13°C, 16°C, 18°C, 20°C, 22°C, and 25°C, respectively, and was controlled by a double direction temperature gradient template. One hundred seeds of each temperature set were divided into four replicates of 25 seeds per dish. Seeds were placed on moist filter paper in petri dishes (9 × 9 cm), which were placed in a seed germinator. A small quantity of distilled water was added regularly to keep the filter paper moist. The number of seeds with radicles was counted every other day for 14 d. After 14 d, the germination percentage, radicle length, and vigor index were recorded. Statistical analysis of all data was conducted using the least significant difference (LSD) test at $P = 0.05$. The vigor index (V) is expressed by the following equation (Tao and Zheng, 1991): $V = S \times G$ representing a synthetic value for seed germination and seedling growth, where S = mean of radicle length, showing seedling growth potential and G (germination index) = $\Sigma G_t/D_t$, indicating the speed for seed germination where G_t = the number of seeds with radicles at day t and D_t (day t) = the number of days since the beginning of the experiment.

Germination percentage, germination index, and vigor index are used here for evaluating seed vigor. Among them, vigor index is the most important value for evaluating seed vigor because it includes both seed germination and seedling growth data.

Source of meteorological data—Spring temperatures, represented by the mean temperature in April from the region where *E. ulmoides* grows today, are cited from a climate database of China (National Meterorological Bureau of China, 1983).

Fossil material—The twig (Fig. 2) and associated leaves (Fig. 3), one whole leaf and seven other fragments, were all collected from the 22.95 m of diatomaceous shale and mudstone Unit Numbers 6, 7, and 15 as shown in Fig. 2 and Table 1 of Sun et al. (2002) of Shanwang Formation, in Xiejiahe Village (36°54′ N, 118°20′ E), Linqu County, Shandong Province, China. The Shanwang Formation is dated as mid-Miocene, 15 to 17.5 million years ago (mya), based on the data of its fauna and flora as well as of isotope measurements (Li, 1981; Yan, Qiu, and Meng, 1983; Liu and Leopold, 1992; Yang and Yang, 1994; Sun et al., 2002). Specimens studied in this paper are housed at the Department of Paleobotany, Institute of Botany, Chinese Academy of Sciences, Beijing, China. Latex ducts exposed in transverse and longitudinal sections of the branch and leaves were examined under scanning electron microscopy (SEM) in Beijing (Figs. 5–7) and a Hitachi S3000N variable pressure scanning electron microscope (Hitachi, Tokyo, Japan) in low vacuum mode, using back scattered detector with specimens in situ on rock, uncoated, at the University of London, London, UK (Figs. 8–10).

RESULTS

Germination test of Eucommia ulmoides seeds—Preliminary studies have considered aspects of seed physiology of *Eucommia* (Lin and Zheng, 1995; Lin, Zheng, and Zhang, 1989), and we have extended these studies to constrain the temperature controls on seed germination. Our physiologic experiments show that favorite temperatures for the germination of *E. ulmoides* seeds, including optimum and suboptimum temperatures, range from 13°C to 22°C (Table 1, Fig. 11). The optimum temperature is 18°C, as the seeds exhibited the highest vigor index (10.37) and germination rate (98%) at that temperature. The V, G, and S (radicle length) showed no significant differences between 13°C and 16°C or between 20°C and 22°C (Table 1). The lower vigor index (lower than 1% of the highest value) at 10°C indicates much weaker seedlings. Over 25°C, germination ceases (Table 1, Fig. 11; Lin and Zheng, 1995).

Data of spring temperatures cited from meteorological stations—Trees of *E. ulmoides* grow naturally in South China ranging from 200 m to 1700 m above sea level, and from 102° E to 118° E and from 25° N to 35° N (Fig. 1; Ying, Zhang, and Boufford, 1993). The spring temperatures of the distribution region of *E. ulmoides* in nature range from 12.3°C to 21.1°C. They vary from 13.8°C to 20.1°C at altitudes from 206 m to 1527 m at latitudes from 25° N to 27°57′ N, from 15.4°C to 19.3°C at altitudes from 259 m to 972 m at latitudes from 28° N to 30°40′ N, and from 12.3°C to 15°C at altitudes from 396 m to 1131 m at latitudes from 33° N to 35° N (Table 2).

Systematic assignment of fossil material from Shanwang—*Description*—Branch segment, comprising secondary xylem and bark, is 8 cm long, 1.94 cm wide, and 3 mm thick (Fig. 2). Phloem of bark contains abundant unicellular latex ducts arranged in longitudinal strands (Fig. 5; Wang, 1995). Leaves are elliptic, serrate, up to 9.4 cm long and 4.7 cm wide.

Figs. 2–4. **2.** *Eucommia* cf. *ulmoides*. A branch segment. Specimen no. PB-SW-95-0001. Scale bar = 1 cm. **3.** *Eucommia* cf. *ulmoides*. A leaf lamina, showing the leaf architecture with compound teeth (indicated by arrow). Specimen no. PB-SW-98-0015. Scale bar = 1 cm. **4.** *Eucommia ulmoides*. A leaf lamina, for comparison with Fig. 3. Scale bar = 1 cm.

The widest part of the leaf is in the middle of the lamina. Leaf apex is attenuate. Leaf base is acute. Petioles are 1 mm wide and up to 6 mm long. Compound teeth, composed of both main tooth and secondary tooth, are curved apically so that the tooth apex is appressed to the leaf margin (Fig. 3). Leaf venation is camptodromous (Fig. 12), at least six pairs of alternating secondary veins depart from the midrib at an acute angle and arch strongly toward the apex (Fig. 12). The unicellular latex ducts in leaves (Figs. 6 and 8–10) are the same as those in the branch (Fig. 5), at least 0.2 mm long and 4.0 to 5.6 μm in diameter, with inflated ends.

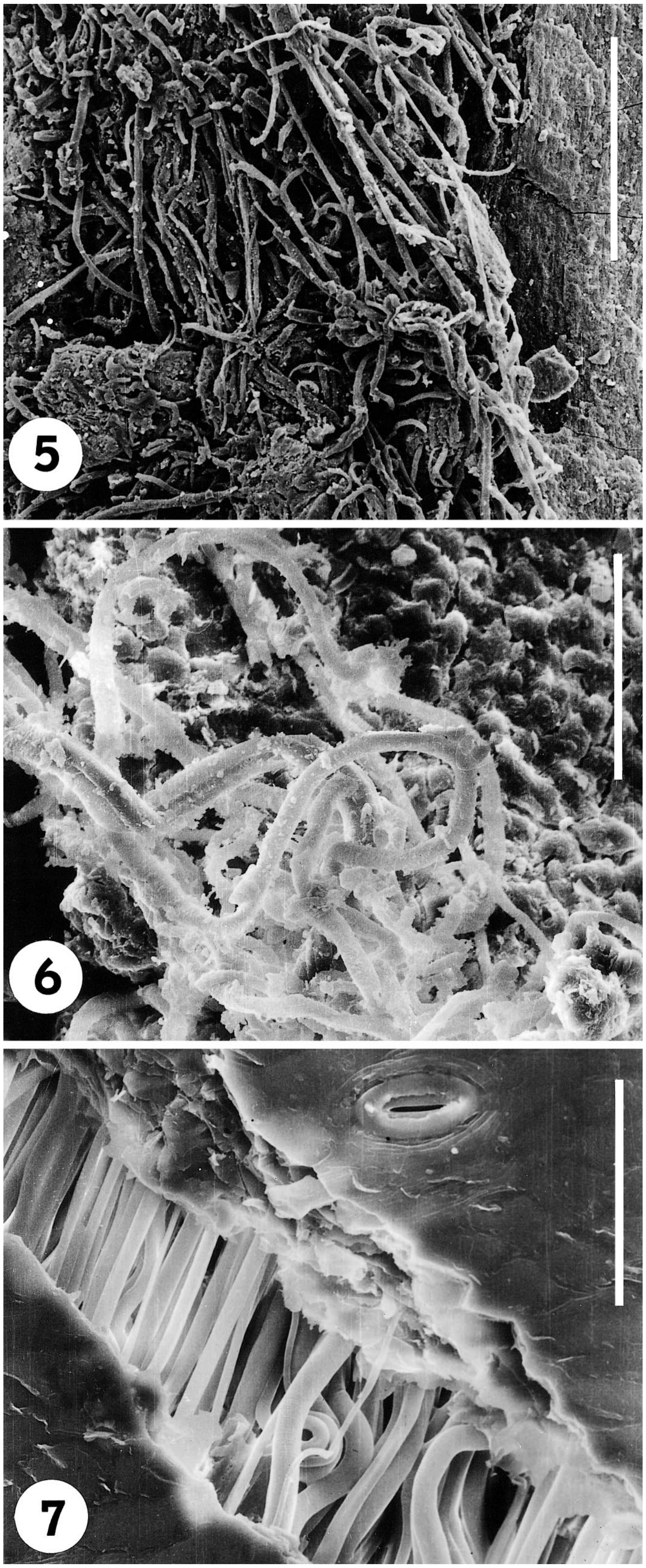
TABLE 1. Temperature effect of seed germination in *Eucommia ulmoides*; within a column the values scored by the same letter are not significantly different (LSD test, $P = 0.05$). The vigor index (V) = $S \times G$, representing a synthetic value for seed germination and seedling growth, where S = mean of radicle length, showing seedling growth potential, and G (germination index) = $\Sigma G_t/D_t$, indicating the speed for seed germination, where G_t = the number of seeds with radicles at day t and D_t (day t) = the number of days since the beginning of the experiment.

Temperature (°C)	Germination (%)	Germination index	Radicle length (cm)	Vigor index
5	0	0	0	0
10	72^{B}	1.66^{C}	0.58^{C}	0.96^{D}
13	70.5^{B}	1.71^{BC}	1.30^{B}	2.22^{C}
16	80^{B}	1.90^{B}	1.69^{B}	3.21^{C}
18	98^{A}	2.81^{A}	3.69^{A}	10.37^{A}
20	74^{B}	2.18^{B}	3.02^{AB}	6.58^{B}
22	76^{B}	2.29^{B}	3.06^{AB}	7.01^{B}
25	5^{C}	0.35^{D}	0.27^{C}	0.09^{D}

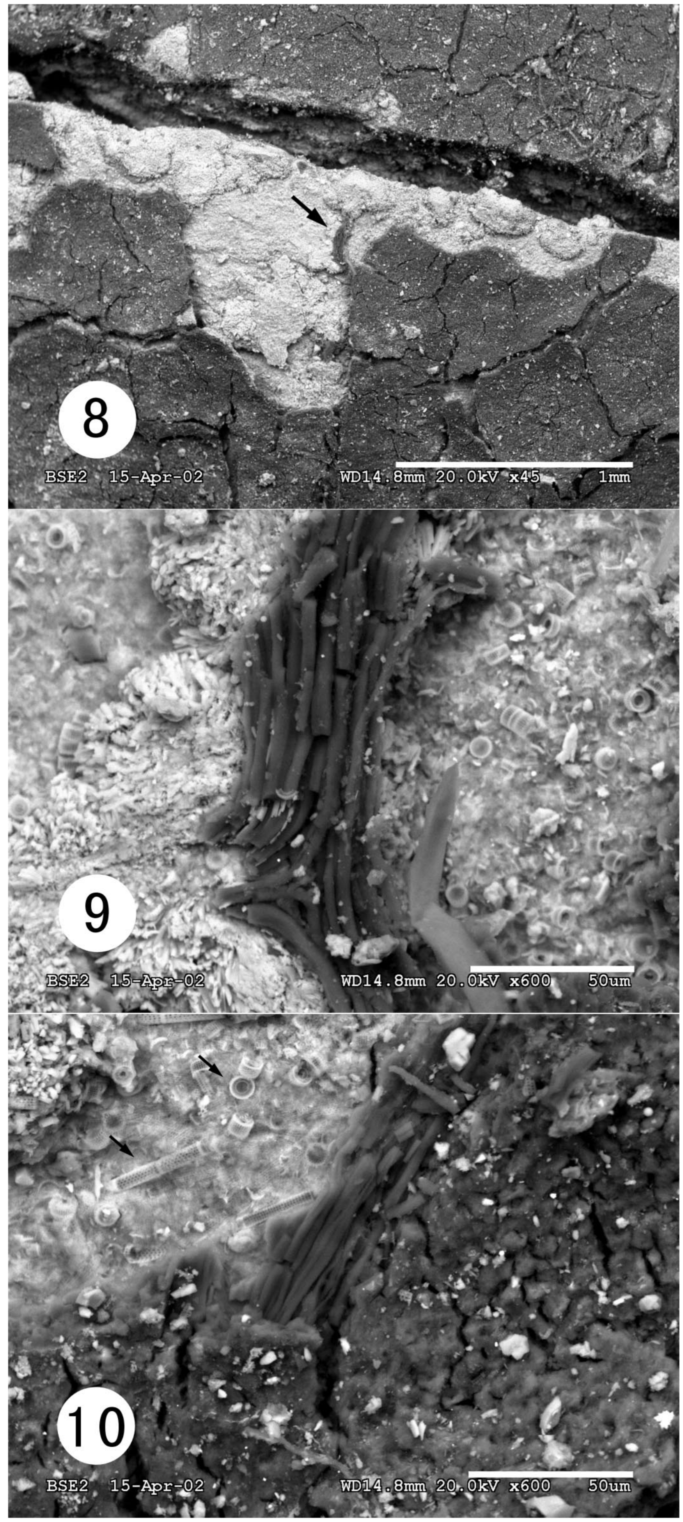
Discussion—Their occurrences in the same rock unit and identity of their latex cells form the basis for regarding both twig and leaves as a single species. The fossil leaves are very similar to those of *E. ulmoides* in terms of leaf venation and compound teeth (Figs. 3 and 4). The latex ducts in phloem of stem, branches, and leaves of *E. ulmoides* range from 0.4 to 3.5 mm long, 3 mm at average, 2.5 to 6 μm in diameter (Tian and Hu, 1983). The unicellular latex ducts of fossil branches (Fig. 5) and leaves (Figs. 6 and 8–10) are very similar to those of *E. ulmoides* (Fig. 7) in dimension and structure. Based on the similarities of fossil specimens to *E. ulmoides*, we assigned these specimens to *E.* cf. *ulmoides*.

DISCUSSION

Habitat of modern Eucommia—Living floras containing *Eucommia* in South China are mostly subtropical; for example, the flora in the Wuling Mountains (108°47′ E–111°33′ E; 27°05′ N–30°09′ N) consists of 164 families of angiosperms, nine families of gymnosperms, and 44 families of pteridophytes (Wang et al., 1995). Trees of *E. ulmoides* in that flora occur together with *Rhus chinensis* Mill, *Liquidambar* mollis



Figs. 5–7. **5.** *Eucommia* cf. *ulmoides*. Latex cells from Fig. 2. Specimen no. PB-SW-95-0001. Scale bar = 250 μm. **6.** *Eucommia* cf. *ulmoides*. Latex cells from specimen no. PB-SW-98-0016. Scale bar = 60 μm. **7.** *Eucommia ulmoides*. Latex cells exposed along a split leaf. Scale bar = 60 μm.



Figs. 8–10. *Eucommia* cf. *ulmoides*. **8.** Surface view of specimen no. PB-SW-98-0017, showing fossil leaf remains attached to diatomite and underlying diatomite. Scale bar = 1 mm. **9.** Enlargement of Fig. 8 (area indicated by arrow), showing fossil latex strands. Specimen no. PB-SW-98-0017. Scale bar = 50 μm. **10.** Enlargement of Fig. 8, showing underlying diatomite (arrows) is visible at top left and a fossil leaf fragment with latex strands exposed in situ between leaf cuticles. Specimen no. PB-SW-98-0017. Scale bar = 50 μm.

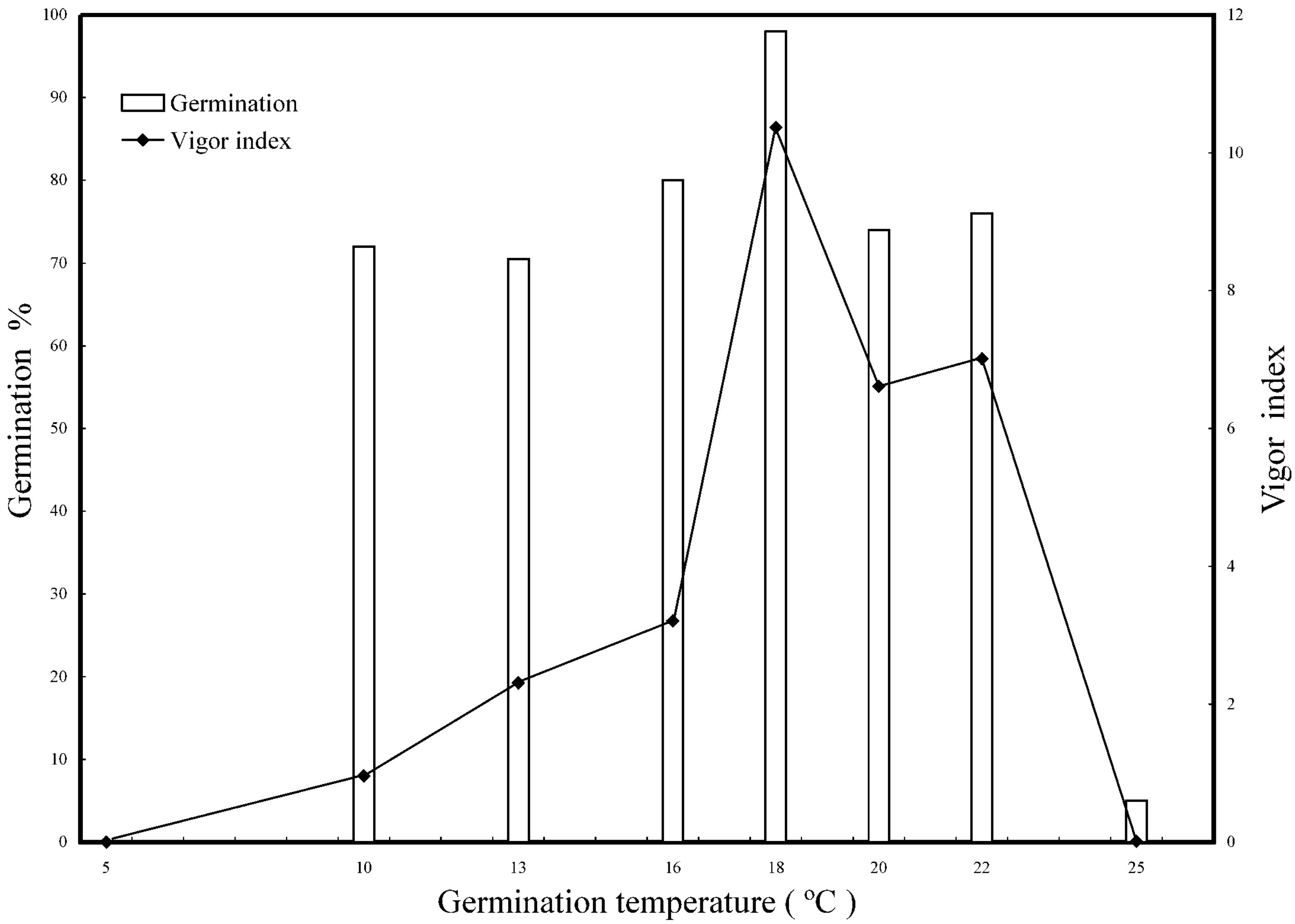


Fig. 11. Temperature effect of seed germination in *Eucommia ulmoides*. Germination percentage, germination index, and vigor index are used here for evaluating seed vigor. Among them, vigor index is the most important value for evaluating seed vigor because it includes both seed germination and seedling growth data.

Oliv., *Quercus acutissima* Carr., and *Q. variabilis* Bl. (Zhang, Gao, and Chen, 1990). Close fossil relatives of the latter four species were also found in the Shanwang flora (WGCPC, 1978).

Occurrence of fossil Eucommia and related paleoenvironments—The discovery of fossil *Eucommia* in the Tertiary sediments of China (Wang, 1995; Geng, Manchester, and Lu, 1999) proves the former existence of *Eucommia* in China in addition to North America and Europe. This confirms that the genus is not a recent arrival in China and refutes previous suggestions that the genus migrated to China from North America via Europe during the Tertiary (Szafer, 1952).

Wang (1995) briefly reported *Eucommia* cf. *ulmoides* as a new occurrence in the Shanwang Flora. The specimens, a piece of branch and leaves collected from Shanwang Formation of Middle Miocene in Shandong Province, China, are here shown to be much closer to the extant species *E. ulmoides* than to any other fossil *Eucommia* species and are therefore assigned to *Eucommia* cf. *ulmoides*.

The Shanwang flora is Miocene in age and composed largely of angiosperms, including 43 families, 87 genera, and 125 species (Hu and Chaney, 1940; WGCPC, 1978). These families of angiosperms are mainly typical temperate trees, such as those in Betulaceae, Aceraceae, Ulmaceae, Fagaceae, Salicaceae, Tiliaceae, Juglandaceae, Rhamnaceae, and some subtropical evergreen trees, i.e., *Cinnamomum* (Lauraceae), *Magnolia* (Magnoliaceae), *Ficus* (Moraceae), and *Eriobotrya* (Rosaceae) (Hu and Chaney, 1940; WGCPC, 1978). The paleoclimate inferred from this Shanwang flora and its associated fauna is warm temperate to subtropical (Hu and Chaney, 1940; WGCPC, 1978; Yan, Qiu, and Meng, 1983; Zhang, 1986; Liu and Leopold, 1992; Yang and Yang, 1994; Sun et al., 2002).

Estimate of spring temperatures for natural regeneration of Eucommia—Seeds of *E. ulmoides* mature in the autumn and then germinate in the following spring. Therefore, a suitable temperature for seed germination in the spring is an important factor in the life cycle of *E. ulmoides*. The range of spring temperatures in the area or distribution region of this species is consistent with the results of the temperature test for seed germination of *E. ulmoides*, although experimental data yield slightly higher temperatures than meteorological data. The overlapping temperature range (from 13°C to 20°C) between experimental data and meteorological data represents the natural germination conditions of living *Eucommia*. Nat-

TABLE 2. Data from Chinese meteorological stations based on 30-yr averages from 1951 to 1980 for spring temperatures (represented by the mean temperature in April) in the area of the recent distribution of *Eucommia ulmoides*. Data taken from a climate database of China (National Meteorological Bureau of China, 1983).

Station no.	Latitude (°N)	Longitude (°E)	Altitude (m asl)[a]	Spring temperature (°C)
57006	34°35′	105°45′	1131.7	12.3
57036	34°18′	108°56′	396.9	14.1
57127	33°04′	107°02′	508.4	15
56294	30°40′	104°01′	505.9	17
57405	30°30′	105°35′	278.2	18.1
57447	30°17′	109°28′	437.2	16.5
56287	29°59′	103°00′	627.6	17
57504	29°35′	105°03′	352.3	18.7
57516	29°35′	106°28′	259.1	18.8
56386	29°34′	103°45′	424.2	18.2
56376	29°21′	102°41′	795.9	19.3
57537	29°18′	108°10′	310.6	17.8
57602	28°53′	105°26′	334.8	18.9
56492	28°48′	104°36′	340.8	19
57606	28°08′	106°50′	972	15.4
57731	27°57′	108°15′	416.3	17.4
57722	27°46′	107°28′	792.8	15.3
57741	27°43′	109°11′	283.5	16.8
57713	27°42′	106°53′	843.9	15.8
57745	27°27′	109°41′	272.2	16.4
57707	27°18′	105°14′	1510.6	13.8
57766	27°14′	111°28′	248.6	16.6
57816	26°35′	106°43′	1071.2	16.3
57806	26°15′	105°55′	1392.9	15.3
58921	25°58′	117°21′	206	19.6
57922	25°50′	107°33′	972.2	15.7
56793	25°47′	104°37′	1527.1	17.2
57902	25°26′	105°11′	1378.5	17
58927	25°06′	117°01′	341.9	20.1

[a] asl = above sea level.

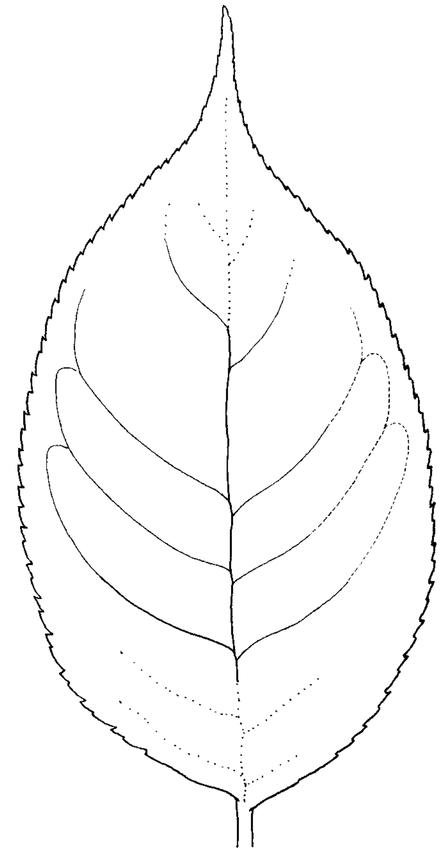


Fig. 12. Partial reconstruction of leaf architecture of *Eucommia* cf. *ulmoides*, showing camptodromous venation, alternating secondary veins, and compound teeth (see Fig. 3; specimen nos. PB-SW-98-0015 and PB-SW-98-0016).

ural regeneration, from germinating seeds, is of fundamental importance for the maintenance of natural plant populations, especially in trees like *Eucommia* where vegetative reproduction is lacking or very limited. Our results, combining evidence from experimental studies of seed vigor and the climatic conditions under which modern *Eucommia* grows today, show that spring temperature is an important factor controlling *Eucommia* distribution. We do not exclude the possibility that other factors may also be relevant but these would require further research.

Considering the concept of NLR (Collinson, 1986; Mosbrugger, 1999) and the climate analysis of endemic species (Li, Wang, and Sun, 2001), the temperature requirement for seed germination of fossil *E.* cf. *ulmoides* is inferred to have been close to that of its nearest living relative species. The spring temperatures of the Shanwang locality in the Middle Miocene are therefore estimated to be from 13°C to 20°C, ranging from 0.1°C to 7°C higher than present 12.9°C in spring, which is cited from Weifang meteorological station [36°45′ N, 119°11′ E] near Shanwang [36°54′ N, 118°20′ E]. This is consistent with other research work depicting the climate of Middle Miocene in Shanwang locality as warm temperate to subtropical (see above). The global warming in the Middle Miocene (Tanai, 1967; Wolfe, 1978; Graham, 1999), together with the paleolatitude of Shanwang being at 27°30′ N (Ye and Yuan, 1980), or between 28.3° N and 32.4° N (Liu and Shi, 1989) as indicated by paleomagnetic data, might be responsible for the higher spring temperature of Shanwang in the Middle Miocene than the present day.

Paleoclimatic and paleobiogeographic significance—Combined evidence from the natural distribution and germination experiments has shown that spring temperatures of 13°C to 20°C are a limiting factor on the distribution of *Eucommia ulmoides* (Eucommiaceae). If this climatic tolerance is extrapolated to the Middle Miocene of Shanwang (with fossil *E.* cf. *ulmoides*) it proves to be consistent with other predictions of palaeoclimate at this site. This new evidence for climatic tolerances of *Eucommia* can in future be incorporated into palaeoclimate analysis of other fossil assemblages containing this genus. The Miocene fossils, and one previously described Eocene fruit specimen, prove the former existence of *Eucommia* in China in addition to North America and Europe. This confirms that the endemic genus *Eucommia* is not a recent arrival in China and focuses attention on the significance of Chinese fossils for understanding the evolution and biogeography of the genus.

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