



A new *Celastrus* species from the middle Miocene of Yunnan, China and its palaeoclimatic and palaeobiogeographic implications



Xiao-Qing Liang^{a,b}, David K. Ferguson^d, Frédéric M.B. Jacques^a, Tao Su^a, Li Wang^a, Zhe-Kun Zhou^{a,c,*}

^a Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China

^b School of Resource and Environmental Sciences, Yuxi Normal University, Yuxi 653100, China

^c Key Laboratory of Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, CAS, Kunming 650204, China

^d Institute of Palaeontology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

ARTICLE INFO

Article history:

Received 24 September 2014

Received in revised form 7 November 2015

Accepted 11 November 2015

Available online 2 December 2015

Keywords:

Celastrus

Dispersal

Middle Miocene

Palaeobiogeography

Zhenyuan

ABSTRACT

Leaves of a new species of *Celastrus* L. (*Celastrus caducidentatus* Liang XQ et ZK Zhou) are described from the middle Miocene of Zhenyuan, China. They have serrate theoid teeth with clear, deciduous setae and pinnate venation. The species is closely related to *Celastrus paniculatus* ssp. *paniculatus* and probably belongs to subgenus *Celastrus* series *Paniculati*. According to the nearest living relative approach, its presence suggests that Zhenyuan had a warmer and more humid climate in the middle Miocene and that ancestors of *C. paniculatus* probably occurred in East Asia. The distribution history of the genus shows that the North Atlantic corridor and/or Bering continental bridge played an important role in the migration between North America, Europe and Asia. The affinity between *C. caducidentatus* and *Celastrus pringlei* Rose, which is only distributed in Mexico, suggests that a transpacific dispersal existed between East Asia and Central America.

© 2015 Published by Elsevier B.V.

1. Introduction

Celastrus L. is a deciduous or evergreen woody vine. The genus is characterized by a hardy stem with orbicular to ovate lenticels, alternate simple leaves with serrate or subentire margin (Hou, 1955; Zhang and Funston, 2008).

Its classification troubled botanists for its plants have a wide range of morphological diversity, e.g. leaf morphological characters. Leaves are elliptic to oblong, or broadly ovate to orbicular. Except for a dense pubescence on both leaf surfaces in *Celastrus hirsutus* Comber, leaves are usually glabrous or just pubescent on the veins below. Consequently, the genus was once subdivided into more than 500 species, with about half of them distributed in Africa. These do not belong to the genus *Celastrus* but to *Maytenus* Molina (Loesener, 1942). The latter is closely related to the former, but they are distinct from one another based on habits, lenticels, and reproductive organs (Hou, 1955). *Celastrus* itself was also divided into 18 species (Bentham and Hooker, 1862), or nearly 50 species (Loesener, 1942). In 1955, the genus was revised into two subgenera with two series, namely subgenus *Celastrus* with series *Paniculati* (seven species) and series *Axillares* (17 species)

and subgenus *Racemocelastrus* (seven species) based on reproductive organs and distribution (Hou, 1955). Although two nuclear (ETS, ITS) and three plastid (*psbA-trnH*, *rpl16* and *trnL-F*) sequences do not support the classification (Mu et al., 2012b), it is accepted by many botanists (e.g., Zhang and Funston, 2008). These species are restricted to warm temperate and tropical parts of the world (Hou, 1955) (Fig. 1). Twenty-five species are distributed in China, 16 of which are endemic (Zhang and Funston, 2008).

Although the present centre of distribution of *Celastrus* lies in Southeast Asia, its Cenozoic ancestors may have been cosmopolitan (Berry, 1916). Many fossils referred to the genus have been found in the Cretaceous of North America and the Cenozoic of North America, Europe, Asia and Australia (Ettingshausen, 1886; Knowlton, 1902, 1919; Berry, 1939; MacGinitie, 1941; Wolfe, 1960; WGCP, 1978; Mai, 1995; Bozukov, 2000). In China, leaf fossils were collected from the Miocene of Shandong and Taiwang (WGCP, 1978; Huang, 2011). Many Cretaceous and Paleogene *Celastrus*-like leaf fossils were once assigned to two extinct genera, namely *Celastrinites* Saporta (Saporta, 1865) and *Celastraphyllum* Göppert with an entire margin (Göppert, 1853). Many Cretaceous and Paleogene species of these two genera possibly belong to different families or genera. For instance, *Celastraphyllum mimosops* Ettingshausen, an entire-margined, eucamptodromous leaf from the Eocene of the Czech Republic has been transferred to *Dicotylophyllum* Saporta (Kvaček and Teodoridis, 2011). Those fossil leaves with theoid teeth having deciduous setae, typical characters of Celastraceae (Hickey and Wolfe, 1975), are less common.

* Correspondence author at: Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China. Tel./fax: +86 87165219932.

E-mail address: zhouzk@xtbg.ac.cn (Z.-K. Zhou).

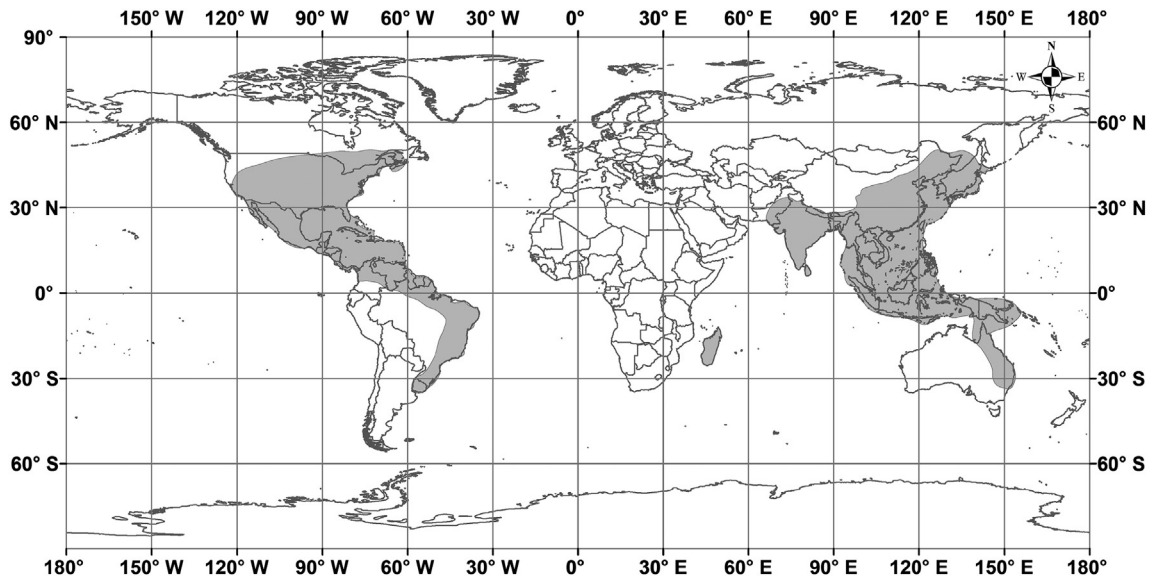


Fig. 1. Distribution of *Celastrus* (grey) at present.

Here, we describe a new species (*Celastrus caducidentatus*) from the middle Miocene of Zhenyuan, Yunnan, China, describe its morphological features, and review its relationship to extant species in order to discuss its palaeobiogeographic and palaeoclimatic implications. And it is shown that plant migration occurred between eastern Asia and North America via transpacific dispersal in the geological past.

2. Material and methods

Compressed and impressed fossil leaves are found in Sanzhangtian (24°06' N, 101°13' E) (Fig. 2), Zhenyuan, Yunnan, China, which is close to Ailao Mountain and has a subtropical climate. The locality also

yielded the lamina and culms of bamboos (Wang et al., 2013) and fern leaves (Jacques et al., 2013). The section belongs to the Dajie Formation dated to the middle Miocene based on stratigraphic studies, and consists of lacustrine and fluvial deposits with conglomerate, sandstone, siltstone, coal, and mudstones (Ge and Li, 1999). Materials were observed and photographed with a Nikon D700 camera and a stereo microscope (S8APO Leica).

Specimens representing 23 extant species and one subspecies, from Herbaria of Xishuangbanna Tropical Botanical Garden, of Kunming Institute of Botany, CAS, and CVH (Chinese Virtual Herbarium, www.cvh.org.cn), were studied. Extant morphological synapomorphies of five leaves from each species were investigated based on the characters

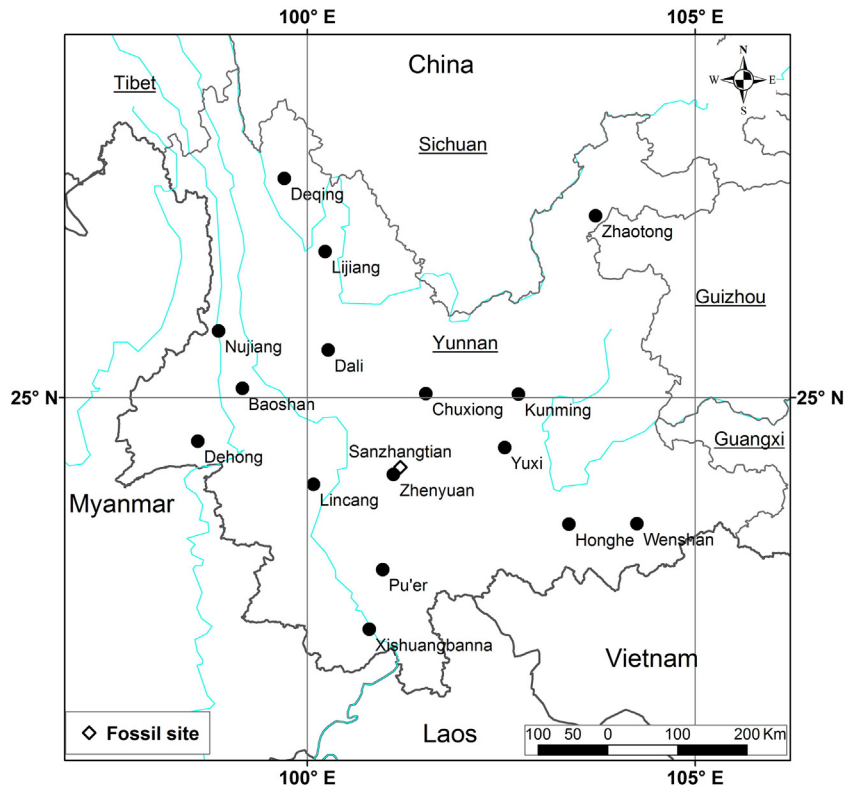


Fig. 2. Locality of fossils in Zhenyuan, Yunnan, China (triangle).

Table 1
Leaf morphological characters of extant and fossil species of *Celastrus*. *C. paniculatus*1 includes *C. paniculatus* ssp. *serratus* (Blanco) Ding Hou with ovate leaves and *C. paniculatus* ssp. *multiflorus* (Roxburgh) Ding Hou with elliptic leaves, and *C. paniculatus*2 is *C. paniculatus* spp. *paniculatus* with obovate leaves. –, st, ss show “no data”, “short and thick”, and “sessile or short”, respectively.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	Reference
<i>C. monospermus</i> Roxburgh	1/2/3	2	5	12.3 ± 2.8	6.2 ± 0.6	2.0	11.0 ± 2.0	1	4.0 ± 0.0	7.5 ± 0.0	45.0 ± 0.0	3	1	
<i>C. orbiculatus</i> Thunberg	1/4	2	1/5	8.6 ± 1.3	6.0 ± 1.2	1.4	16.6 ± 2.2	1	2.4 ± 0.5	5.8 ± 0.4	41.0 ± 2.0	3	1	
<i>C. paniculatus</i> 1	1/2/5/6	2	1/5	8.4 ± 1.3	5.5 ± 1.3	1.5	13.8 ± 2.8	1	3.2 ± 0.8	7.0 ± 0.9	46.0 ± 2.0	3	1/2	
<i>C. paniculatus</i> 2	2	2	1	8.7 ± 1.8	6.7 ± 0.3	1.3	14.1 ± 3.3	1	3.4 ± 0.8	6.4 ± 0.5	43.4 ± 3.5	3	2	
<i>C. stylosus</i> Wallich	1/5	2	5	6.6 ± 0.4	3.8 ± 0.2	1.7	11.4 ± 0.5	1	3.4 ± 0.5	6.0 ± 0.0	46.8 ± 1.8	3	1	
<i>C. virens</i> (Wang et Tang) C.Y. Cheng	1/3	2	5	10.4 ± 1.9	3.7 ± 0.7	2.8	9.8 ± 2.0	1	2.4 ± 0.5	6.8 ± 0.4	60.0 ± 0.0	3	2	
<i>C. hindsii</i> Benthams	1/2	3	5	8.5 ± 0.4	3.7 ± 0.6	2.3	7.6 ± 1.2	1	3.8 ± 0.4	6.6 ± 0.5	60.0 ± 0.0	3	2	
<i>C. gemmatus</i> Loesener	1/6	2	1	11.3 ± 1.2	5.1 ± 1.6	2.2	12.7 ± 3.3	1	2.7 ± 1.0	8.0 ± 1.1	48.3 ± 6.0	3	1	
<i>C. angulatus</i> Maximowicz	1/4	3	1	9.9 ± 1.8	6.4 ± 1.8	1.5	14.4 ± 7.8	1	3.2 ± 0.4	7.6 ± 1.0	50.0 ± 5.5	3	2	
<i>C. aculeatus</i> Merrill	1/5	2	1	8.8 ± 2.4	4.9 ± 1.0	1.8	12.0 ± 4.5	1	2.3 ± 0.8	6.0 ± 0.9	55.5 ± 3.9	3	1	
<i>C. flagellaris</i> Ruprecht	1	2	5	5.0 ± 2.5	3.2 ± 1.0	1.6	8.0 ± 1.2	1	3.5 ± 1.1	5.5 ± 0.5	49.4 ± 7.0	3	2	
<i>C. glaucophyllus</i> Rehder et E.H. Wilson	1	2/3	5	9.9 ± 1.2	5.1 ± 0.5	1.9	12.3 ± 3.2	1	2.4 ± 0.5	5.0 ± 0.0	49.0 ± 3.7	3	1	
<i>C. hirsutus</i> Comber	1/2	3	1	11.6 ± 2.7	7.0 ± 1.2	1.7	20.8 ± 2.9	1	2.6 ± 0.5	8.0 ± 0.6	53.6 ± 4.8	3	1	
<i>C. hookeri</i> Prain	1	3	1	10.6 ± 2.0	6.9 ± 1.5	1.5	11.1 ± 0.5	1	2.6 ± 0.5	5.8 ± 0.4	51.0 ± 5.3	3	1	
<i>C. hypoleucus</i> P.L. Chiu	1/5	3	1/5	13.7 ± 6.2	7.2 ± 0.9	1.9	17.0 ± 4.0	1	4.0 ± 0.0	9.0 ± 3.0	49.5 ± 7.5	3	1	
<i>C. kusanoi</i> Hayata	1	2	1	8.1 ± 1.3	3.9 ± 0.7	2.1	11.2 ± 0.0	1	2.4 ± 0.5	5.0 ± 0.6	48.8 ± 6.7	3	1	
<i>C. pringlei</i> Rose	1	2	1	7.6 ± 0.6	2.7 ± 0.2	2.8	5.3 ± 0.9	1	3.3 ± 0.5	8.0 ± 0.0	41.0 ± 3.7	3	2	
<i>C. punctatus</i> Thunbergh	1	2	1	6.5 ± 0.4	2.9 ± 0.2	2.2	6.8 ± 1.9	1	2.8 ± 0.4	5.0 ± 0.0	48.4 ± 3.3	3	2	
<i>C. rosthornianus</i> Loesener	1	2	1	7.9 ± 3.1	3.7 ± 1.1	2.2	9.6 ± 3.7	1	3.0 ± 0.0	5.4 ± 1.0	50.8 ± 6.6	3	1	
<i>C. rugosus</i> Rehder et E.H. Wilson	1	2/3	4/5	10.3 ± 4.4	6.8 ± 3.2	1.5	11.4 ± 5.5	1	2.4 ± 0.5	5.6 ± 0.5	48.0 ± 4.2	3	1	
<i>C. vaniotii</i> (H. Léveillé) Rehder	1/5	3	1	9.4 ± 1.2	5.8 ± 1.2	1.6	11.8 ± 1.9	1	3.2 ± 0.4	6.2 ± 0.4	54.4 ± 3.9	3	1	
<i>C. oblanceifolius</i> F.T. Wang et P. C. Tsoong	1/2	2	1	10.2 ± 0.6	3.3 ± 0.3	3.0	8.6 ± 1.0	1	3.0 ± 0.0	7.0 ± 0.0	47.4 ± 2.2	3	1	
<i>C. subspicatus</i> Hooker	1	2	1	8.6	3.0	2.7	6.0	1	1.0	8.0	56.0	3	1	
<i>C. caducidentatus</i> Liang XQ et ZK Zhou sp. nov.	2	2	–	5.5 ± 0.1	5.2 ± 0.05	1.06	4.0?	1	5	8	45.0	3	1	this study
<i>C. comparabilis</i> Hollick	5	–	–	9	6.5	–	–	2	–	–	–	2	2	Hollick, 1936; Wolfe, 1977
<i>C. confluens</i> Knowlton	1	2	3	8–9	4–5	–	–	6	–	12	45	2	–	Knowlton, 1902
<i>C. dignatus</i> Knowlton	1/2	4	6	4	3–3.5	–	st	5	–	10	–	2	–	Knowlton, 1902
<i>C. haddeni</i> Knowlton	2	2	4	4	2	–	–	3	–	–	<90	1	–	Lee and Knowlton, 1917
<i>C. lacoiei</i> Knowlton	2/3	2	3/4	3.5	1.3	–	st	4	–	–	<90	1	–	Knowlton, 1916
<i>C. minutus</i> Friedrich	1	2	–	10	0.8	–	–	1	–	11–12	20–30	1	–	Bozukov, 2000
<i>C. serratus</i> Knowlton	5/6	1	1	9–18	5–12	–	11	2	–	10	45	2	–	Lee and Knowlton, 1917
<i>Celastrus</i> sp.	6	2	4	3	1.5	–	–	–	–	5	<90	–	–	Fernández-Marrón and Hably, 2005
<i>C. hesperius</i> Knowlton	1/5	2	3	4.5	3	–	–	4	–	5	–	–	–	Lee and Knowlton, 1917
<i>C. simplex</i> Berry	4	3	4	0.8–1.2	0.8–1.1	–	ss	3	–	–	–	–	–	Berry, 1939
<i>C. pseudo-ilex</i> Ettingshausen	7	–	4	–	–	–	–	–	–	–	–	–	–	Heer, 1862
<i>C. mioangulata</i> Hu et Chaney	5	3	2	8–9	5.4–6.6	–	35.0	1/3	–	5–7	75	2	2	WGCP, 1978

Table 2
List of morphological characters and states of leaf.

1	Shape	Elliptic, narrow elliptic (1); obovate (2); lanceolate (3); orbicular (4); ovate, broadly ovate (5); oblong (6); linear (7)
2	Base	Cordate (1); cuneate, narrow cuneate (2); round (3); truncate, obtuse (4)
3	Tip	Acuminate, obtusely acuminate (1); cuneate (2); obtuse (3); round (4); straight (5); truncate (6)
4	Length (cm)	Value
5	Width (cm)	Value
6	L/W	Value
7	Petiole (mm)	Value
8	Margin	Serrate (1); dentate, triangular-serrate dentate (2); entire (3); undulate and rounded, undulate teeth (4); coarse tooth (5); large, sharp pointed (6)
9	Teeth/cm	Value
10	Number of 2'vein (pair)	Value
11	Angle of 2'vein to midvein	Value
12	Major 2'vein framework	Camptodromous (1); craspedodromous (2); semicraspedodromous (3)
13	Angle of 3' to midvein	Obtuse (1); perpendicular (2)

that are preserved in the fossil remains. Scoring criteria are presented in Table 2. The cleared leaves of some extant species, taken from the Herbarium of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, were prepared following the methods of Li (1987). Terminology is based on Ellis et al. (2009). One-way ANOVA and cluster analysis (between-groups linkage) were conducted to determine any significant difference between fossil and extant species and to review the relationship of fossil species to extant species by applying SPSS 16.0. The geographic map was made using Arcgis 10.1 software.

3. Systematics

Family: Celastraceae

Genus: *Celastrus* Linnaeus

Species: *C. caducidentatus* Liang X.Q. et Z.K. Zhou, sp. nov.

Holotype: No. SZT-0250 (Plate I, 2)

Paratype: No. SZT-0248 (Plate I, 1)

Type repository: Palaeoecological lab, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS), Yunnan, Mengla, China.

Type locality: Sanzhangtian Village, Zhenyuan County, Yunnan Province, China

Type formation and age: Dajie Formation, middle Miocene

Etymology: the specific epithet, *caducidentatus*, is derived from the theoid tooth with the clear and deciduous seta.

Diagnosis—Fossil leaves obovate and petiolar. Base cuneate. Teeth serrate theoid with a clear, deciduous seta. Venation pinnate. Secondary veins semicraspedodromous with apically elongated arches. Intercostal areas of lower secondary veins narrow and long. Tertiary veins branch. Tertiary marginal veins variable. Quaternary veins reticular.

Description—Leaves are obovate, 5.5 ± 0.1 cm long and 5.2 ± 0.05 cm wide, with cuneate base. Lamina length/width ratio is about 1.05 (Table 1). Petiole is incomplete, 4 mm long. Theoid teeth have clear and deciduous setae (Plate I, 5, 7, 8). A main vein extends into apex of tooth (Plate I, 6–7). Apices turn inwards and look like glands when setae exfoliate (Plate I, 4 and 6). Venation pinnate with eight pairs of semicraspedodromous secondary veins which extend to apex to form a series of arches (Plate I, 1–3). The proximal part of secondary veins is straight. Intercostal areas of basal secondary veins are narrow and long (Plate I, 2 and 3). Principal veins of teeth terminate at apex (Plate I, 6 and 7). Number of teeth per cm is 5 (Plate I, 1–3; Table 1). The tertiary veins branch and are obtuse (Plate I, 2). The marginal tertiary veins are looped (Plate I, 5). The quaternary veins are reticular (Plate I, 9 and 10) and freely ending veinlets branch unequally (Plate I, 10).

Affinity—In the cluster analysis, *C. caducidentatus* is placed in the same clade as *Celastrus paniculatus* ssp. *paniculatus* Willdenow. It shows they have the closest morphological similarity. They are also

close to the Central American species of Series *Axillares*, *Celastrus pringlei* Rose (Fig. 3).

4. Discussion

4.1. Comparison *C. caducidentatus* with extant and fossil species

Fossil leaves from the middle Miocene of Zhenyuan are pinnate and petiolate, and has semicraspedodromous secondary veins with apically elongated arches and theoid teeth with a clear, deciduous seta (Plate I). They probably belong to pinnate Dilleniidae, based on vegetative morphology (Hickey and Wolfe, 1975). Within pinnate Dilleniidae, Ericales, pinnate Malpighiales and Celastrales have leaves with theoid teeth. However, the leaves of Ericales have teeth with an opaque, deciduous cap (Stevens, 2012), while those of pinnate Malpighiales (e.g. Ochnaceae) have brochidodromous secondary veins forming an intramarginal vein by strengthening and straightening of the outer portion of the arc (Hickey and Wolfe, 1975). In Celastrales, leaves of Lepidobotryaceae have an entire margin (Stevens, 2012). Although theoid teeth with deciduous setae also occur in the Aquifoliaceae (Aquifoliales) (Hickey and Wolfe, 1975), their leaves have supervolute (conduplicate) venation (Stevens, 2012). *Celastrus* is distinct from other genera of Celastraceae in characters of veins and margin. *Parnassia* L. and *Lepuropetalon* Elliott have leaves with (sub)palmate venation (Stevens, 2012). *Maytenus* Molina has leaves with festooned semicraspedodromous venation. The leaf margin is entire (e.g., *Acanthothamnus* Brandegee, *Apatophyllum* McGill, *Bhesa* Buchanan-Hamilton ex Arnott, and *Pottingeria* Prain), or glandular-crenate (e.g., *Cassine* L.). Besides, the leaves of *Canotia* Torrey are reduced to scales, while those of *Empleuridium* Sonder et Harvey are sessile (Simmons, 2007). So by a process of elimination, the fossil leaves must belong to the genus *Celastrus*.

C. caducidentatus shares typical morphologic characters with extant species of the genus in leaf venation and teeth. They have pinnate veins, semicraspedodromous secondary veins and serrate theoid teeth having clear, deciduous setae (Plate I, 4–8; Plate II, 3, 4, 6, 8, 15, 17, 18). After the setae drop off, the apices resemble glands (Plate I, 4, 6; Plate II, 3, 4, 8, 15, 17). However, fossil leaves from the middle Miocene of Zhenyuan are significantly different from the extant species of the genus. The ratio of the lamina length/width and number of teeth per cm are about 1 and 5, respectively, while those of the East Asian and Australian species and *C. pringlei* (distributed in Central Mexico) are above 1.2 and 2–4, respectively (Table 1). Leaf morphological characters of the North American species *Celastrus scandens* L. are very similar to those of *Celastrus orbiculatus* Thunberg, so it is distinct from the fossil leaves. Leaves of other extant species distributed in Central and Southern America are elliptic, ovate-elliptic, ovate, oblanceolate-oblong and ovate, and their margins are serrulate or almost entire (Hou, 1955). Leaves of *Celastrus obovatifolius* X.Y. Mu et Z.X. Zhang are obovate, but the proximal part of their secondary veins are curved (Mu et al., 2012a).

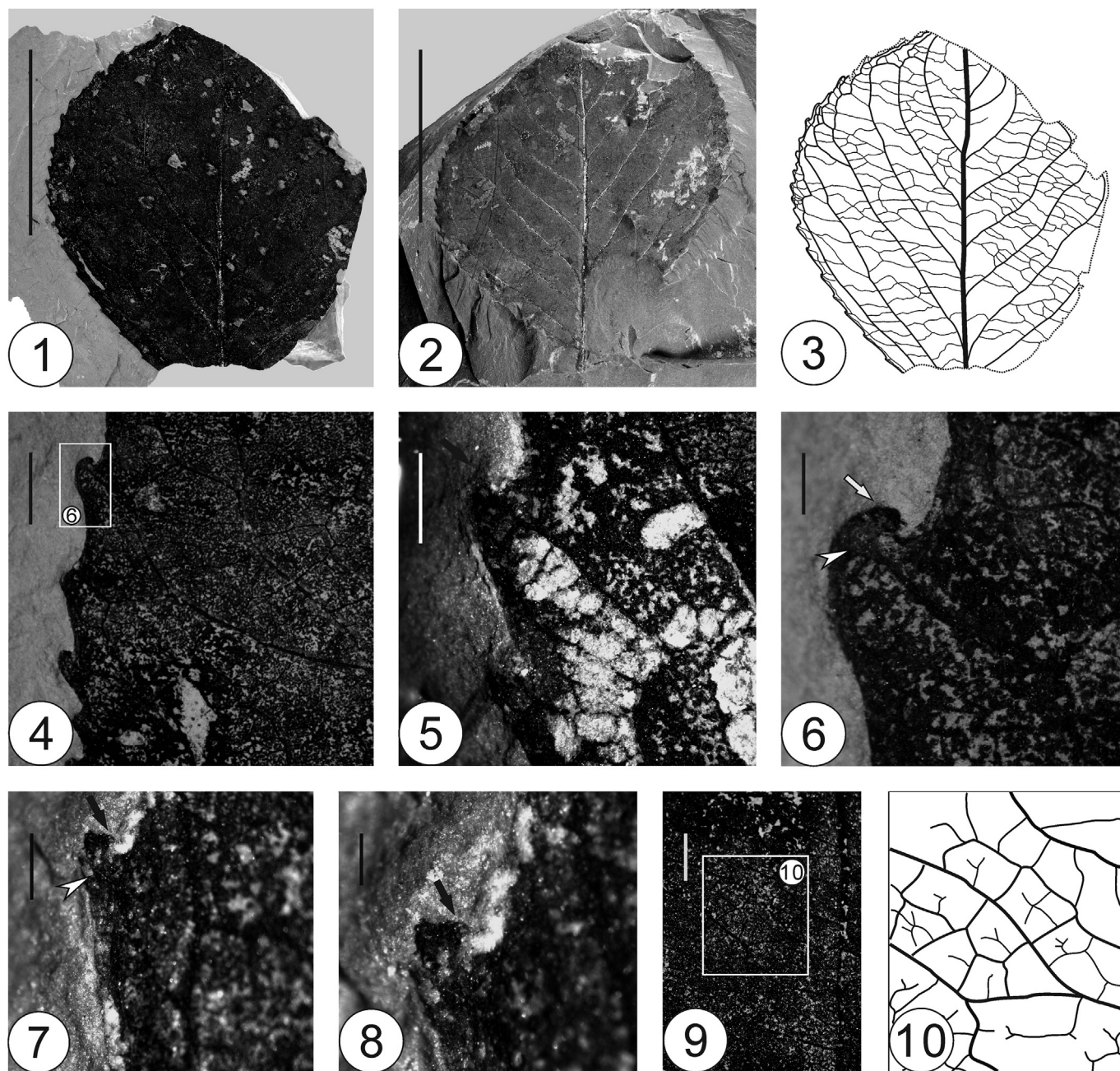


Plate I. Leaves of *Celastrus caducidentatus* from the middle Miocene of Zhenyuan, China. 1 and 2: compressed (paratype) and impressed (holotype) leaf fossil, respectively; 3: illustration of veins of Fig. 1; 4 and 6: deciduous teeth; 5 and 7: theodid tooth with clear, deciduous seta; 8: magnification of Fig. 7; 9: quaternary and freely ending veins; 10: drawing of quaternary and freely ending veins based on Fig. 9. Black and yellow arrows show theodid tooth with clear, deciduous seta and theodid tooth without seta, respectively. White arrow shows principal veins of teeth terminating at apex. Scale bars: 1, 2 = 3 cm; 4 = 2 mm; 5 = 1 mm; 6 = 0.5 mm; 7 = 0.2 mm; 8 = 0.1 mm; 9 = 2 mm.

Leaves of *C. caducidentatus* are easily distinguished from other fossil species by their secondary vein framework, leaf margin and leaf shape. Their leaves possess semicraspedodromous secondary veins with elongated arches and deciduous serrate teeth (Plate 1, 1–7; Table 1). *Celastrus comparabilis* Hollick, *Celastrus confluens* Knowlton, *Celastrus dignatus* Knowlton, and *Celastrus serratus* Knowlton have leaves with craspedodromous secondary veins, and triangular-serrate dentate teeth, large and sharp pointed teeth, coarse teeth and dentate teeth, respectively (Knowlton, 1902, 1919; Hollick, 1936; Wolfe, 1977). Moreover, *C. confluens*, *C. dignatus*, and *C. serratus* have more than ten pairs of secondary veins. The major secondary vein frameworks of *Celastrus haddeni* Knowlton, *Celastrus lacoiei* Lesquereux, and *Celastrus minutus* Friedrich are camptodromous (Knowlton, 1902; Lee and Knowlton, 1917; Bozokov, 2000). The leaf margin of *C. haddeni* is entire, while

that of *C. lacoiei* is undulate and rounded. The number of secondary veins in *C. minutus* is twice that of *C. caducidentatus* (Table 1). Leaves of *C. hesperius* Knowlton and *Celastrus simplex* Berry have undulate-teeth and an entire margin, respectively (Lee and Knowlton, 1917; Berry, 1939). Fossil leaves of *Celastrus* sp. from the Miocene of Spain and *Celastrus pseudo-ilex* Ettingshausen from the Oligocene of England are oblong and linear, respectively (Heer, 1862; Fernández-Marrón and Hably, 2005). *Celastrus mioangulata* Hu et Chaney has ovate or broadly ovate leaves with round base and obtuse apex (WGCP, 1978). Consequently, we assign the leaves from Zhenyuan to a new species.

C. paniculatus Willdenow is divided into three subspecies based on leaf shape: *C. paniculatus* ssp. *paniculatus* (obovate leaves), *C. paniculatus* ssp. *serratus* (Blanco) Ding Hou, (ovate leaves) and *C. paniculatus* ssp.

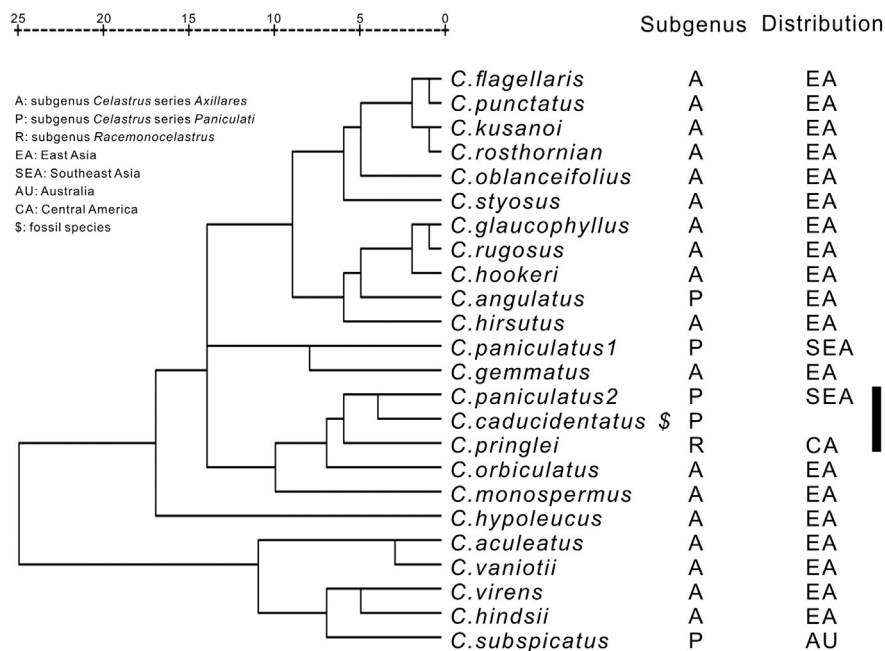


Fig. 3. Nearest living relative of *Celastrus caducidentatus* in leaf morphology shown by cluster analysis (between-groups linkage). Hou's (1955) subgeneric classification of *Celastrus* and distribution are also shown in the tree.

multiflorus (Roxburgh) Ding Hou (elliptic leaves) (Hou, 1955). Transitional forms make it difficult to distinguish them (Zhang and Funston, 2008), but *C. caducidentatus* is similar to *C. paniculatus* ssp. *paniculatus* in leaf shape, leaf margin and secondary veins (Plate I, 1–3, 9, 10; Plate II, 1–5). This close affinity with *C. paniculatus* ssp. *paniculatus* is supported by cluster analysis (Fig. 3). Hence we ascribe the fossil to the subgenus *Celastrus* series *Paniculati*.

4.2. Palaeoclimatic and palaeobiogeographic implications of *C. caducidentatus*

The nearest-living-relative method is a powerful approach to obtain qualitative and quantitative palaeoclimatic (or palaeoenvironmental) information based on the assumption of similarity of a fossil taxon or assemblage to its nearest living relative in morphological characters, although it has some limitations and its accuracy and reliability depend on geological age and identification of taxa and taphonomy (Mosbrugger, 2009). As the nearest living relative of *C. caducidentatus*, *C. paniculatus* ssp. *paniculatus* is mainly distributed in India and Myanmar (Hou, 1955), which has a tropical climate. The presence of the fossil species in Yunnan indicates that Zhenyuan possibly had a warmer and more humid climate in the middle Miocene, and the ancestor of *C. paniculatus* had probably appeared in East Asia in the early Neogene.

Many *Celastrus* leaves have been found (Table 3). *Celastrus* had a very wide distribution in the Cenozoic (Fig. 4). Plants of the genus possibly appeared in the Early Cretaceous of North America (Knowlton, 1919; Wolfe, 1960). They were present in Europe in the Paleocene (Mai, 1995) and in East Asia by the Eocene (Huzioka, 1961). They existed in Australia in the Oligocene (Ettingshausen, 1886), and also dispersed into Cuba in the Miocene (Berry, 1939), even though both

regions were surrounded by oceans. They persisted in Europe until the Pliocene (Kovar-Eder et al., 2006). However, they disappeared at high latitudes, and only remain at 47°N–40°S in America, Asia, Madagascar, and Oceania at present (Hou, 1955) (Fig. 1).

North Atlantic Land Bridge between North America and Europe and Bering Land Bridge between North America and East Asia played an important role in plant change (Tiffney, 1985; Manchester, 1999; Tiffney and Manchester, 2001; Liang et al., 2010) so that *Celastrus* appeared in Europe in the Paleocene and in East Asia in the Eocene (Fig. 4). And, trans-oceanic dispersal is a probable explanation for occurrence in Australia (Ettingshausen, 1886) and the affinity of the Southeast Asian species (*C. caducidentatus*, *C. paniculatus* ssp. *paniculatus*) and the Central American species (*C. pringlei*) (Fig. 3). It is even possible that *Celastrus* migrated between Southeast Asia and Central America via the transpacific route (Fig. 4) based on the morphology of the leaf (Fig. 3) and DNA analysis (Mu et al., 2012b). It gradually evolved different species to adapt to different climate. Consequently, the transpacific dispersal also played an important role in plant dispersal between Eastern Asia and America (Herrera et al., 2011).

Acknowledgements

We thank Prof. Cheng-Sen Li and Prof. Yu-Fei Wang of the Institute of Botany, CAS, Beijing and Prof. Zlatko Kvaček of Charles University, Czech Republic, for their help with the identification. We are also grateful to Anna Monro, Australian National Botanic Gardens, for some photos of *Celastrus subspicatus*. This research was supported by grants from the 973 Programme of MOST of China (2012CB821901), the National Natural Science Foundation of China (NSFC, Nos. U1502231, 41030212, 41272007), and XTBG Postdoctoral Research Funding (PPKP011B13).

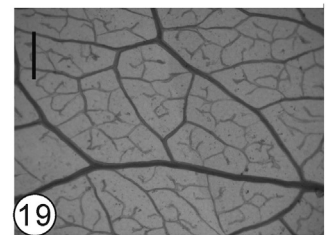
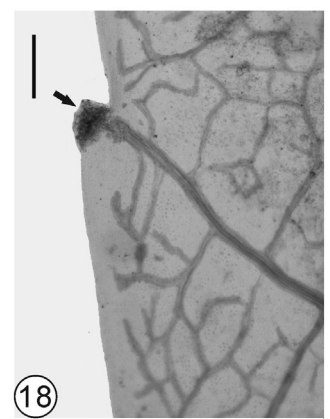
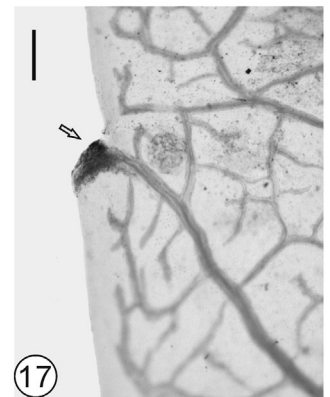
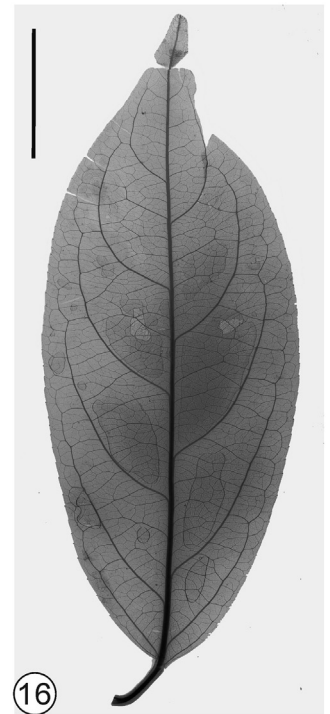
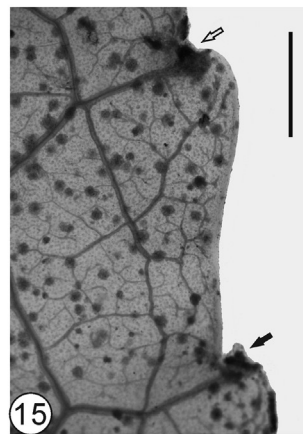
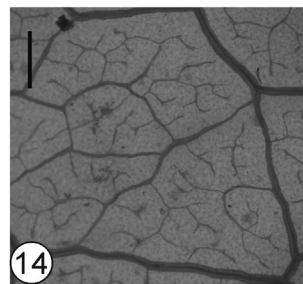
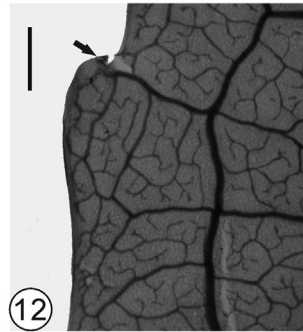
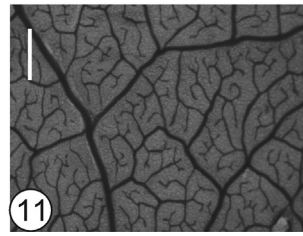
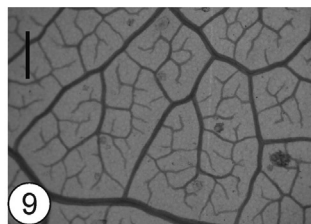
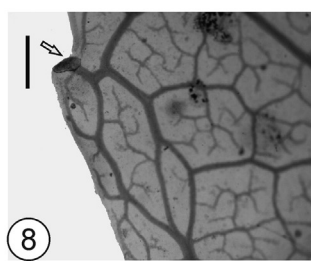
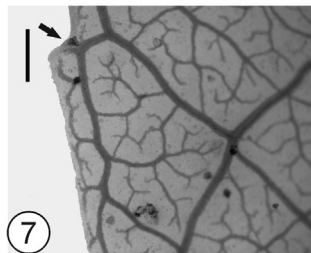
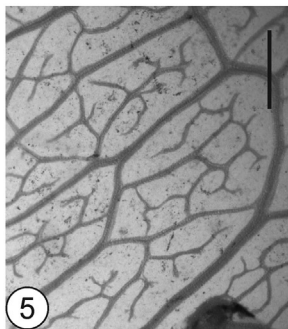
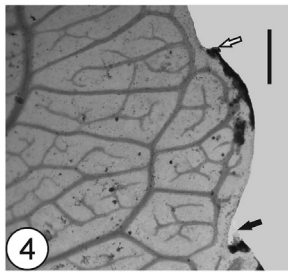
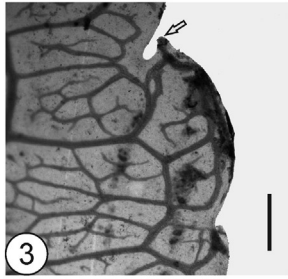
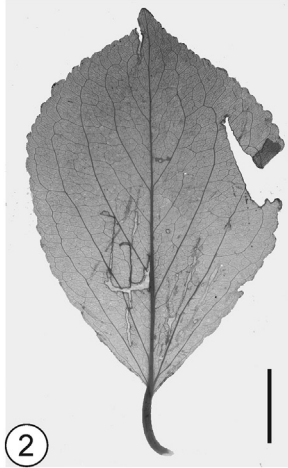


Table 3
Occurrences of *Celastrus* from the Early Cretaceous to Pliocene.

Species	Age	Formation/Locality	Reference
<i>Celastrus herendeensis</i> Hollick	Early Cretaceous	Alaska, USA	(Wolfe, 1960)
<i>Celastrus arctica</i> Heer	Late Cretaceous	Raritan: South Amboy, N. J., USA	(Knowlton, 1902, 1919)
<i>Celastrus arctica</i> Heer	Late Cretaceous	Magothy: Little Neck, Northport Harbor, Long Island, N. Y.; Black Rock Point, Block Island, R. I.; Little Round Bay, Severn River, Md., USA	(Knowlton, 1919)
<i>Celastrus haddeni</i> Knowlton	Late Cretaceous	Vermejo: Coal Creek, Rockvale, Colo., USA	(Lee and Knowlton, 1917; Knowlton, 1919)
<i>Celastrus hesperius</i> Knowlton	Late Cretaceous	Mesaverde: Harper, Wyo., USA	(Knowlton, 1919)
<i>Celastrus</i> sp. Hollick	Late Cretaceous	Raritan: Tottenville, Staten Island, N.Y., USA	(Knowlton, 1919)
<i>Celastrus</i> sp. Knowlton	Late Cretaceous	Vermejo: Vermejo Park, N. Mex., USA	(Knowlton, 1919)
<i>Celastrus lanceolatus</i> Frider	Paleocene	Eisleben, Germany	(Mai, 1995)
<i>Celastrus bruckmannifolia</i> Berry	Lower Eocene	Wilcox (Holly Springs): Holly Springs, Marshall County, Miss., USA	(Knowlton, 1919)
<i>Celastrus minor</i> Berry	Eocene	Kenai: Nenana coal field, Tanana region, Coal Creek, Alaska, USA	(Knowlton, 1919)
<i>Celastrus borealis</i> Heer	Eocene	Fort Union: Elk Creek, Yellowstone National Park, USA	(Knowlton, 1919)
<i>Celastrus culveri</i> Knowlton	Eocene	Fort Union: Burns's ranch, near Glendive, USA	(Knowlton, 1919)
<i>Celastrus curvinervis</i> Ward	Eocene	Bull Mountain field, Mont., USA near Moreau River, S. Dak., USA Lance: West of Miles City, Mont. USA	(Knowlton, 1919)
<i>Celastrus ellipticus</i> Knowlton	Eocene	Fort Union: Elk Creek, Yellowstone National Park, USA	(Knowlton, 1919)
<i>Celastrus eolignitica</i> Berry	Eocene	Wilcox (Holly Springs): Early Grove, Marshall County, Miss. USA Lagrange: Near Grand Junction, Fayette County, Tenn., USA	(Knowlton, 1919)
<i>Celastrus ferrugineus</i> Ward	Eocene	Fort Union: Burns's ranch and Iron Bluff, near Glendive and Bull Mountains, Mont., USA	(Knowlton, 1919)
<i>Celastrus ferrugineus</i> Ward	Eocene	Minturn, 8 miles northeast of Parkman, and Table Mountain, near Black Buttes, Wyo., USA	(Knowlton, 1919)
<i>Celastrus gaudini</i> Lesquereux	Eocene	Denver: Golden, Colo., USA	(Knowlton, 1919)
<i>Celastrus grewiopsis</i> Ward	Eocene	Fort Union: Burns's ranch, Glendive, Mont., USA	(Knowlton, 1919)
<i>Celastrus inaequalis</i> Knowlton	Eocene	Fort Union: Elk Creek, Yellowstone National Park., USA	(Knowlton, 1902, 1919)
<i>Celastrus lindgreni</i> Knowlton	Eocene	Payette: Idaho City, Idaho, USA	(Knowlton, 1919)
<i>Celastrus montanensis</i> Knowlton et Cockerell	Eocene	Fort Union: Burns's ranch, near Glendive and Bull Mountain field, Mont., USA McCord coal bank, Cannonball Kiver, N. Dak., USA Lance: Cannonball River, N. Dak., USA west of Miles City, Mont., USA	(Knowlton, 1919)
<i>Celastrus pterospermoides</i> Ward	Eocene	Fort Union: Burns's ranch and Iron Bluff, near Glendive, Bull Mountains, and 6 miles west of Jordan, Mont., USA near Kirby and Rock Springs area, Wyo., USA Lance: West of Miles City, Mont., USA	(Knowlton, 1919)
<i>Celastrus serratus</i> Knowlton	Eocene	Raton: Primero and Woolton, Colo., USA	(Knowlton, 1919)
<i>Celastrus</i> sp.	Eocene	Yubari, Hokkaido, Japan	(Huzioka, 1961)
<i>Celastrus</i> sp. Knowlton	Eocene	Skykomish, Snohomish County, Wash., USA Raton: Near Yankee, N. Mex., USA	(Knowlton, 1919)
<i>Celastrus taurinensis</i> Ward	Eocene	Fort Union: Bull Mountains and Burns's ranch, near Glendive, Mont., USA Ilo Post Office, Big Horn County, Wyo., USA Wilcox: Coushatta, La., USA Lance: Near Ilo Post Office, Big Horn Basin, Wyo.	(Knowlton, 1919)
<i>Celastrus veatchi</i> Hollick	Eocene	Wilcox: Coushatta, La., USA	(Knowlton, 1919)
	Eocene	Lagrange: Near Trenton, Gibson County, Tenn., USA	
	Eocene	Wilcox: (Holly Springs): Early Grove, Marshall County, Miss., USA	
<i>Celastrus wardii</i> Knowlton et Cockerell	Eocene	Fort Union: Iron Bluff, Glendive, and Miles City, Mont. Lance: Signal Butte, Miles City, Mont., USA	(Knowlton, 1919)
<i>Celastrus winchesteri</i> (Knowlton) MacGinitie	Eocene	Parachute Creek, Colorado, USA Wyoming, USA	(MacGinitie, 1969)
<i>Celastrus comparabilis</i> Hollick	Middle Eocene	Gulf of Alaska, USA	(Wolfe, 1977)
<i>Celastrus confluens</i> Knowlton	Middle Eocene	John Day Basin, Oregon, USA	(Knowlton, 1919)
<i>Celastrus preangulata</i> MacGinitie	Middle Eocene	Nevada County, California, USA	(MacGinitie, 1941)
<i>Celastrus typica</i> (Lesquereux) MacGinitie	Late Eocene	Colorado, USA	(MacGinitie, 1953)
<i>Celastrus minutus</i> Friedrich	Early Oligocene	Sachsen, Germany	(Bozukov, 2000)
<i>Celastrus de stefanii</i> Principi	Oligocene	Sassello, Piedmont Basin, Central Liguria, NW Italy	(Bonci et al., 2011)
<i>Celastrus hippolyti</i> Ettingshausen	Oligocene	Santa Giustina and Sassello, Piedmont Basin, Central Liguria, NW Italy	
<i>Celastrus sordidus</i> Saporta			
<i>Celastrus</i> sp.	Oligocene	near Eugene, Oregon, USA	(Retallack et al., 2004)
<i>Celastrus pseudo-ilex</i> Ettingshausen	Oligocene	Bovey Tracey, England	(Heer, 1862)
<i>Celastrus prae-europaeus</i> Ettingshausen	Oligocene	Vegetable Creek, near Emmaville, N.S.W., Australia	(Ettingshausen, 1886)
<i>Celastrus prae-elaenus</i> Ettingshausen			
<i>Celastrus lefroyi</i> Ettingshausen			
<i>Celastrus spokanensis</i> Berry	Early Miocene	Douglas County, Washington, USA	(Hoffman, 1932)
" <i>Celastrus</i> " <i>oxyphyllus</i> Unger	Early Miocene	Lipovany, Southern Slovakia Znojmo, Moravia, Czech Republic	(Sitar and Kvaček, 1997)
" <i>Celastrus</i> " <i>pyrrhae</i> Ettingshausen	Early Miocene	The main coal seam (Libkovice and Lom Members) in the Most Basin (Czech Republic)	(Teodoridis and Kvaček, 2006)

Table 3 (continued)

Species	Age	Formation/Locality	Reference
<i>Celastrus aralensis</i> Budantsev	Early Miocene	Altyn-Shokysu-East, Kazakhstan Ashutas, Kazakhstan	(Bruch and Zhilin, 2007)
<i>Celastrus bruckmanni</i> Alex Braun	Miocene	Calvert: Richmond, Va., USA	(Knowlton, 1919)
<i>Celastrus comparabilis</i> Hollick	Miocene	Yakutat Bay, Alaska, USA	(Hollick, 1936)
<i>Celastrus crassifolius</i> Chen H. Wang	Miocene	Dettighofen, Germany	(Scheid, 1929)
<i>Celastrus diana</i> Heer	Miocene	Atanekerdruk, Greenland	(Heer, 1883)
<i>Celastrus dignatus</i> Knowlton	Miocene	Mascall: Van Horn's ranch, John Day Basin, Oreg.	(Knowlton, 1902, 1919)
<i>Celastrus fraxinifolius</i> Lesquereux	Miocene	Florissant, Colo., USA	(Knowlton, 1919; Hollick, 1929)
<i>Celastrus laco</i> Lesquereux	Miocene	Florissant, Colo., USA	(Knowlton, 1916, 1919)
<i>Celastrus minutus</i> Friedrich	Miocene	Satovcha Graben (Western Rhodopes), Bulgaria	(Bozokov, 2000)
<i>Celastrus simplex</i> Berry	Miocene	Matanzas, Cuba	(Berry, 1939)
<i>Celastrus typica</i> (Lesquereux) MacGinitie	Miocene	Beaverhead County, Montana, USA	(Becker, 1969)
<i>Celastrus parvifolius</i> Jennings	Miocene	Missoula, Florissant, Colorado, USA	(Jennings, 1920)
<i>Celastrus decidousseratus</i> sp. nov.	Middle Miocene	Sanzhangtian, Zhengyuan, China	this study
" <i>Celastrus</i> " <i>europaea</i> Unger	Middle Miocene	Parschlug flora, Austria	(Mai, 1995)
<i>Celastrus moravicus</i> Knobloch	Middle Miocene	Znojmo, Moravia, Czech Republic	(Fernández-Marrón and Hably, 2005)
<i>Celastrus mioangulata</i> Hu et Chaney	Middle Miocene	Shangwang, Shangdong, China	(WGPC, 1978)
<i>Celastrus palibinii</i> Kutuzk	Middle/Late Sarmatian	Armavir flora	(Mai, 1995)
<i>Celastrus</i> sp.	Lower Miocene	Magyaregregy, Austria	(Erdei et al., 2007)
<i>Celastrus</i> sp.	Middle Miocene	Erdőbénye	(Mai, 1995)
<i>Celastrus</i> sp.	Middle Miocene	Parla, Madrid basin, Spain	(Fernández-Marrón and Hably, 2005)
<i>Celastrus</i> sp.	Middle Miocene	Taiwan, China	(Huang, 2011)
<i>Celastrus</i> sp.	Middle Miocene	Khanka, Russia	(Pavlyutkin, 2005)
<i>Celastrus</i> sp.	Miocene	Nezhino, Primorye, Russia	(Pavlyutkin, 2009)
<i>Celastrus confluens</i> Knowlton	Late Miocene	Whitebird, Latah, Idaho, USA	(Ashlee, 1932)
<i>Celastrus fernquisti</i> Knowlton	Late Miocene	Spokane Coeur d'Alene, Latah, Idaho, USA	
<i>Celastrus laco</i> Lesquereux	Late Miocene	Spokane Coeur d'Alene and Payette, Latah, Idaho, USA	
<i>Celastrus</i> sp.	Late Miocene	Brandywine, Maryland, USA	(McCartan et al., 1990)
<i>Celastrus</i> sp.	Late Miocene	Chiuzbaia, Maramureş, Romania	(Macovei and Givulescu, 2006)
<i>Celastrus</i> sp.	Late Miocene	Makrilia flora, Crete, Greece	(Mai, 1995)
<i>Celastrus australis</i> Harvey et F. Mueller	Early Pliocene	Papiol, Spain	(Kovar-Eder et al., 2006)
<i>Celastrus gardonensis</i>			
<i>Celastrus poly-morphum</i>			

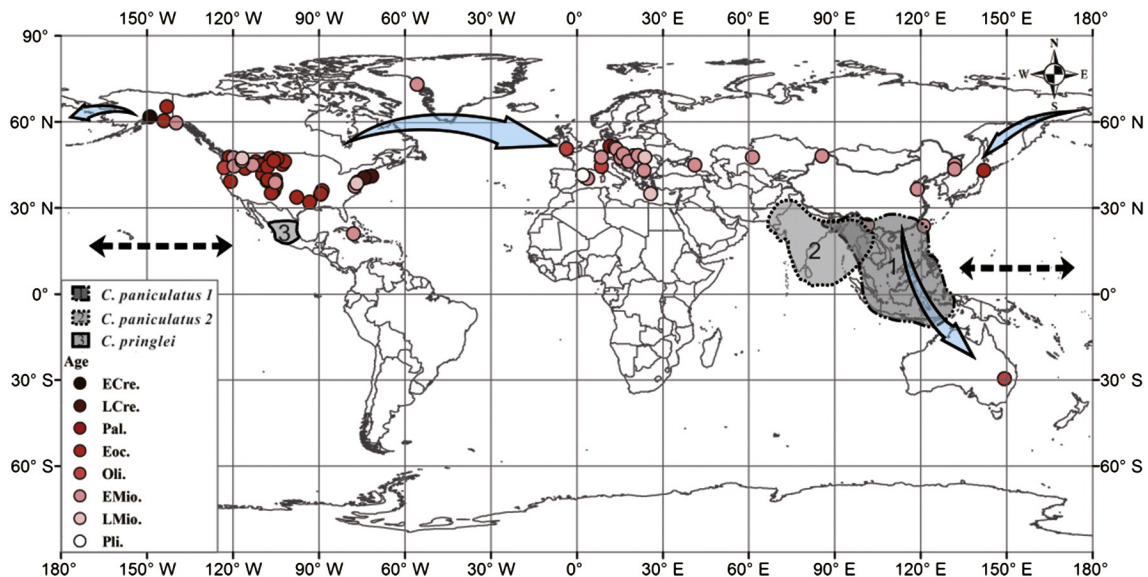


Fig. 4. Map shows migration routes of *Celastrus* from the Paleocene to Miocene. *Celastrus paniculatus*1 includes *C. paniculatus* ssp. *serratus* (Blanco) Ding Hou with ovate leaves and *C. paniculatus* ssp. *multiflorus* (Roxb.) Ding Hou with elliptic leaves, and *Celastrus paniculatus*2 is *C. paniculatus* ssp. *paniculatus* with obovate leaves.

References

- Ashlee, T.R., 1932. A contribution to the Latah flora of Idaho. *Northwest Sci.* 20, 69–82.
- Becker, H.F., 1969. Fossil plants of the Tertiary beaverhead basins in Southwestern Montana. *Palaentogr. Abt. B* 127, 1–142.
- Bentham, G., Hooker, J.D., 1862. *Genera Plantarum*. Reeve, London.
- Berry, E.W., 1916. The Lower Eocene floras of Southeastern North America. *U.S. Geol. Surv. Prof. Pap.* 91, 1–481.
- Berry, E.W., 1939. A Miocene Flora from the Gorge of the Yumuri River, Matanzas, Cuba. 13. The Johns Hopkins University Studies in Geology, pp. 95–135.
- Bonci, M.C., Vannucci, G., Tacchino, S., Piazza, M., 2011. Oligocene fossil leaves of the Perrando Collection: history, preservation, and paleoclimatic meaning. *Boll. Soc. Paleontol. Ital.* 50, 145–164.
- Bozokov, V., 2000. Miocene macroflora of the Satovcha Graben (Western Rhodopes). *Phytologia Balcanica* 6, 15–30.
- Bruch, A.A., Zhilin, S.G., 2007. Early Miocene climate of Central Eurasia – evidence from Aquitanian floras of Kazakhstan. *Palaeoogeogr. Palaoclimatol. Palaeoecol.* 248, 32–48.
- Ellis, B., Daly, D.C., Hickey, L.J., Johnson, K.R., Mitchell, J.D., Wilf, P., Wing, S.L., 2009. *Manual of Leaf Architecture*. Cornell University Press, New York.
- Erdei, B., Hably, L., Kázmér, M., Utescher, T., Bruch, A.A., 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. *Palaeoogeogr. Palaoclimatol. Palaeoecol.* 253, 115–140.
- Ettingshausen, C.F.v., 1886. Beiträge zur Tertiärflora Australiens. *Denkschr. K. Akad. Wiss. Wien Math-Naturw. Kl.* 53 pp. 81–184.
- Fernández-Marrón, M.T., Hably, L., 2005. A new Miocene plant assemblage from Parla, Madrid basin, Spain. *Rev. Paléobiol., Genève* 24, 647–656.
- Ge, H.R., Li, D.Y., 1999. Cenozoic Coal-Bearing Basins and Coal-Forming Regularity in West Yunnan. *Yunnan Science & Technology Press, Kunming* (in Chinese).
- Göppert, H.R., 1853. Über die Tertiär-Flora Java's, *Neues Jahrb. Mineral. Geol. Paläont.* 433–436 (in German).
- Heer, O., 1862. On the fossil flora of Bovey Tracey. *Philos. Trans. R. Soc. Lond.* 152, 1039–1086.
- Heer, O., 1883. Die fossile Flora Grönlands, *Flora fossilis Grönlandica*. Band II, Zürich (in German).
- Herrera, F., Manchester, S.R., Hoot, S.B., Wefferling, K.M., Carvalho, M.R., Jaramillo, C., 2011. Phytoecogeographic implications of fossil endocarps of menispermaceae from the Paleocene of Colombia. *Am. J. Bot.* 98, 2004–2017.
- Hickey, L.J., Wolfe, J.A., 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Mo. Bot. Gard.* 62, 538–589.
- Hoffman, A.D., 1932. The Douglas Canyon flora of east central Washington. *J. Geol.* 40, 735–738.
- Hollick, A., 1929. New species of fossil plants from the Tertiary shales near De Beque, Colorado. *Bull. Torrey Botanical Club* 56, 93–96.
- Hollick, A., 1936. The Tertiary floras of Alaska. *U.S. Geol. Surv. Prof. Pap.* 182, 1–185.
- Hou, D., 1955. A revision of the genus *Celastrus*. *Ann. Mo. Bot. Gard.* 42, 215–302.
- Huang, S.F., 2011. Historical biogeography of the flora of Taiwan. *J. National Taiwan Museum* 64, 33–63.
- Huzioka, K., 1961. A new Palaeogene species of the genus *Eucommia* from Hokkaido, Japan. *Trans. Proc. Paleontol. Soc. Jpn., New Series* 41, 9–12.
- Jacques, F.M.B., Su, T., Zhou, Z.K., 2013. The first fossil Microsoroid fern (*Palaeosorum ellipticum* gen. et sp. nov.) from the middle Miocene of Yunnan, SW China. *J. Syst. Evol.* 51, 758–764.
- Jennings, O.E., 1920. Fossil plants from the beds of volcanic ash near Missoula, Western, Montana. *Memoirs of the Carnegie Museum* 8, 385–450.
- Knowlton, F.H., 1902. Fossil flora of the John Day Basin, Oregon. *Geol. Surv. Bull.* 204, 7–153.
- Knowlton, F.H., 1916. A review of the fossil plants in the United States National Museum from the Florissant Lake beds at Florissant, Colorado, with descriptions of new species and list of type-specimens. the Proceedings of the United States National Museum. 51, pp. 241–297.
- Knowlton, F.H., 1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *U.S. Geol. Surv. Bull.* 696, 1–815.
- Kovar-Eder, J., Kvaček, Z., Martinetto, E., Roiron, P., 2006. Late Miocene to Early Pliocene vegetation of southern Europe (7–4 Ma) as reflected in the megafossil plant record. *Palaeoogeogr. Palaoclimatol. Palaeoecol.* 238, 321–339.
- Kvaček, Z., Teodoridis, V., 2011. The Late Eocene flora of Kučlín near Bílina in North Bohemia revisited. *Acta Musei Nationalis Pragae, Series B-Historia Naturalis* 67 (3–4), 83–144.
- Lee, W.T., Knowlton, F.H., 1917. Geology and paleontology of the Raton Mesa and other regions in Colorado and New Mexico. *U. S. Geol. Surv. Prof. Pap.* 101, 1–561.
- Li, H.M., 1987. Leaf architecture analysis—a new method for identifying angiospermous fossil leaves. In: Mu, X.N. (Ed.), *New Technologies and Methods in Palaeontology*. Science Press, Beijing, pp. 54–62 (in Chinese).
- Liang, X.Q., Wilde, V., Ferguson, D.K., Kvaček, Z., Ablav, A.G., Wang, Y.F., Li, C.S., 2010. *Comptonia naumannii* (Myricaceae) from the early Miocene of Weichang, China, and the palaeobiogeographical implication of the genus. *Rev. Palaeobot. Palynol.* 163, 52–63.
- Loesener, T., 1942. Celastraceae. In: Engler, A., Harms, H., Mattfeld, J. (Eds.), *Die natürlichen Pflanzenfamilien*. Duncker et Humlot, Berlin, pp. 87–197.
- MacGinitie, H.D., 1941. A Middle Eocene Flora from the Central Sierra Nevada. *Carnegie Inst. Wash. Publ.* 534, 1–178.
- MacGinitie, H.D., 1953. Fossil Plants of the Florissant Beds of Colorado. *Carnegie Inst. of Washington. Contrib. to Paleontology Publ.* 599, 1–198.
- MacGinitie, H.D., 1969. The Eocene Green River Flora of northwestern Colorado and northeastern Utah. *Geol. Sci. Univ. Calif. Publ.* 83, 1–140.
- Macovei, G., Givulescu, R., 2006. The present stage in the knowledge of the fossil flora at Chiuzbaia, Maramureş, Romania. *Carph. J. of Earth and Environ. Sci.* 1, 41–52.
- Mai, D.H., 1995. *Tertiäre Vegetationsgeschichte Europas*. Gustav Fischer Verlag, Jena (in German).
- Manchester, S.R., 1999. Biogeographical relationships of North American Tertiary floras. *Ann. Mo. Bot. Gard.* 86, 472–522.
- McCartan, L., Tiffney, B.H., Wolfe, J.A., Ager, T.A., Wing, S.L., Sirkin, L.A., Ward, L.W., Brooks, J., 1990. Late Tertiary floral assemblage from upland gravel deposits of the southern Maryland Coastal Plain. *Geology* 18, 311–314.
- Mosbrugger, V., 2009. Nearest-living-relative method. In: Gornitz, V. (Ed.), *Encyclopedia of Paleoclimatology and Ancient Environments*. Springer, pp. 607–609.
- Mu, X.Y., Xia, X., Zhao, L., Zhang, Z., 2012a. *Celastrus obovatifolius* sp. nov. (Celastraceae) from China. *Nord. J. Bot.* 30, 53–57.
- Mu, X.Y., Zhao, L.C., Zhang, Z.X., 2012b. Phylogeny of *Celastrus* L. (Celastraceae) inferred from two nuclear and three plastid markers. *J. Plant Res.* 125, 619–630.
- Pavlyutkin, B.I., 2005. The Mid-Miocene Khanka flora of the Primorye. *Dal'nauka, Vladivostok*.
- Pavlyutkin, B.I., 2009. Leaf and fruit remains of *Davidia* (Cornales) from the Nezhino Flora (Miocene of Primorye). *Paleontol. J.* 43, 339–344.
- Retallack, G.J., Orr, W.N., Prothero, D.R., Duncan, R.A., Kester, P.R., Ambers, C.P., 2004. Eocene–Oligocene extinction and paleoclimatic change near Eugene, Oregon. *Bull. Geol. Soc. Am.* 116, 817–839.
- Saporta, G. de, 1865. Etudes sur la végétation du Sud-Est de la France à l'époque tertiaire 5e serie. *Bot. 4 Ann. Sci. Nat.* 5–264 (in French).
- Scheid, W., 1929. Über die Tertiärpflanzen von Baltersweil, Dettighofen und Bühl im Klettgau. *Mitteilungen der badischen geologischen Landesanstalt* 10, 427–543 (in German).
- Simmons, M.P., 2007. Celastraceae. In: Kubitzki, K. (Ed.), *The Families and Genera of Vascular Plants*. Springer-Verlag, Berlin, pp. 29–64.
- Sitar, V., Kvaček, Z., 1997. Additions and revisions to the early Miocene flora of Lipovany (Southern Slovakia). *Geol. Carpath.* 48, 263–280.
- Stevens, P.F., 2012. *Angiosperm Phylogeny Website*. 12th ed. (<http://www.mobot.org/MOBOT/research/APweb/>).
- Teodoridis, V., Kvaček, Z., 2006. Palaeobotanical research of the early Miocene deposits overlying the main coal seam (Libkovice and Lom Members) in the Most Basin (Czech Republic). *Bull. Geosci.* 81, 93–113.
- Tiffney, B.H., 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *J. Arnold Arboretum* 66, 243–273.
- Tiffney, B.H., Manchester, S.R., 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *Int. J. Plant Sci.* 162, s3–s17.
- Wang, L., Jacques, F.M.B., Su, T., Xing, Y.W., Zhang, S., Zhou, Z.K., 2013. The earliest fossil bamboos of China (middle Miocene, Yunnan) and their biogeographical importance. *Rev. Palaeobot. Palynol.* 197, 253–265.
- WGCP, 1978. *Cenozoic Plants of China*. Science Press, Beijing (in Chinese).
- Wolfe, J.A., 1960. Report on Referred Fossils. http://pubs.usgs.gov/ds/760/Downloads/GA/JOHNSON/24V001_PALEO.pdf.
- Wolfe, J.A., 1977. Paleogene floras from the Gulf of Alaska Region. *U.S. Geol. Surv. Prof. Pap.* 997, 1–108.
- Zhang, Z.X., Funston, A.M., 2008. *Celastrus*. In: Wu, C.Y., Raven, P.H. (Eds.), *Flora of China*. Science Press & Missouri Botanical Garden Press, Beijing & St. Louis, pp. 446–474.