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Miocene *Ulmus* fossil fruits from Southwest China and their evolutionary and biogeographic implications

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ABSTRACT

The genus *Ulmus* L. (Ulmaceae) has a rich Cenozoic fossil record from the Northern Hemisphere, which provides essential information for evolutionary and biogeographic histories. However, compared to its abundant leaf fossils, fruit fossils of *Ulmus*, which allow accurate identification, are still scarce. In this study, we report two new species of the section *Ulmus*, *Ulmus prelanceaefolia* Q.Y. Zhang et Y.W. Xing sp. nov. and *U. maguanensis* Q.Y. Zhang et Y.W. Xing sp. nov. from the Miocene Huazhige Formation in Wenshan and Maguan basins, southeastern Yunnan, southwestern China. These two species are established based on several well-preserved fossil samaras. *Ulmus prelanceaefolia* represents the only unequivocal record of the ser. *Lanceaefolia* in the world and *U. maguanensis* represents the earliest unequivocal record of the ser. *Nitentes* in East Asia. The evolutionary and biogeographic histories of *Ulmus* are discussed by summarizing and revising the fossil fruit records. We deduce that the narrow-winged fruit may be primitive and the two narrow-winged sections, sect. *Chaetoptelea* and *Trichoptelea* are the early evolved lineages in *Ulmus* and have diversified since the Eocene. The Oligocene was an important epoch for the rapid diversification of broad-winged lineages of *Ulmus*, which was likely due to dispersal advantage in the more open forests originating as the global climate began to cool. We also found frequent exchanges/dispersals and extinction events between or within North America, Asia, and Europe since the Eocene. The North Atlantic and Bering Land Bridges served as important dispersal corridors for *Ulmus* during the Cenozoic.

1. Introduction

Ulmus L. is the most diverse genus in the elm family (Ulmaceae Mirb.), comprising approximately 45 tree or shrub species (Sherman-Broyles et al. 1997; Fu et al. 2003). Most species of *Ulmus* are deciduous and widely distributed or dominant in temperate forests across the Northern Hemisphere with few species extending to the subtropical/tropical regions of Southeast Asia and Central America (Wiegrefe et al. 1994; Sherman-Broyles et al. 1997; Fu et al. 2003). Therefore, revealing the biogeographic history of *Ulmus* is of great interest in respect of floristic evolution in the Northern Hemisphere. *Ulmus* has abundant Cenozoic megafossil records across North America and Eurasia in forms of fruits and leaves (Wolfe 1977; Iljinskaja 1982; Manchester 1989; Xing et al. 2016), which are essential for reconstructing its evolutionary and biogeographic histories. The oldest fossil records of *Ulmus* are represented by fossil leaves dating back to the Paleocene of Asia (Kodrul 1999; Feng et al. 2003), Europe (Kvaček et al. 1994) and North America (Brown 1962). However, as most lineages (sections) of *Ulmus* share similar tooth and venation patterns, leaf fossils provide limited information for understanding evolution within the genus.

According to the latest sectional-level taxonomic system based on molecular and morphological evidence, *Ulmus* may be divided into five sections (Wiegrefe et al. 1994). The circumscription of different sections is mainly based on fruit characters, such as the depth of calyx lobes, perigynous tube shape, the width of fruit wings, and presence or absence of cilia on the samara (Wiegrefe et al. 1994). Therefore, fruit fossils of *Ulmus* could provide vital information for the evolutionary history within the genus. The earliest unequivocal fruit fossils of *Ulmus* associated with leaves which were assigned to the extant section *Chaetoptelea* dated back to the late Early Eocene of western North America (Manchester 1989). Some other fruit fossils were reported across the Northern Hemisphere and unequivocally placed into the sect. *Microptelea* and the sect. *Ulmus* based on fruit morphology (Miki 1937; Straus 1992; Meyer and Manchester 1997). However, compared to abundant leaf fossil records (Oishi and Huzioka 1954; Tanai 1961; Wolfe 1977; Iljinskaja 1982; Burnham 1986), fruit fossils of *Ulmus* are still scarce. Many fruit fossil records are only assigned to generic level without precise determination at the species level. Furthermore, fruit fossil records for several lineages such as the sect. *Blepharocarpa* and

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the ser. *Lanceaefolia* are still lacking, which limits our understanding of evolutionary and biogeographic history within *Ulmus*.

In this study, we report two new fossil species of *Ulmus* based on several broad-winged fruits from the early–middle Miocene of the Wenshan Basin and the early Miocene of the Maguan Basin of Yunnan Province, Southwest China. Our main objectives are to: (1) identify the fossils by comparing with extant and fossil species; (2) review the fruit fossil records of *Ulmus* according to the latest classification system; and (3) discuss the evolutionary and biogeographic histories within *Ulmus* revealed by fruit fossil records.

2. Methods and material

2.1. Fossil localities and age

Three compressed fruit fossil specimens were collected from the Dashidong Village, Wenshan Basin (23° 20′ N; 104° 17′ E, 1271 m a.s.l.) and four fruit fossil specimens from the Maguan Basin (23° 01′ N, 104° 23′ E, 1320 m a.s.l.), Southeast Yunnan Province, Southwest China (Fig. 1).

The Cenozoic sediments in the Wenshan and Maguan basins comprise the Oligocene Yanshan Group, Neogene Huazhige Formation and Quaternary deposits (Zhang 1976; Bureau of Geology and Mineral Resources 1990; Meng et al. 2014; Zhang et al. 2015). The Neogene Huazhige Formation consists of several lithological layers, which lies unconformably on the Oligocene Yanshan Formation and is overlain unconformably by the Quaternary deposits (Zhang 1976; Meng et al. 2014; Zhang et al. 2015).

The fossiliferous deposits of the Wenshan Basin had been previously assigned to the middle and upper part of the Xiaolongtan Formation (synonym of the Huazhige Formation) and estimated to the late Miocene (Su et al. 2013, 2016; Meng et al. 2014, 2015; Zhang et al. 2015; Huang et al., 2016). Recent magnetostratigraphic study suggested that the section of Huazhige Formation in Wenshan is the early–middle Miocene in age (ca. 15.2–16.5 Ma) (Lebreton-Anberrée et al. 2016). The fruit fossils from the Wenshan Basin were preserved in different layers of this section (Fig. 2A). One specimen (KUNPC DMS-0187) was from the yellow fine calcareous mudstone in the upper part of the section, and another two specimens (KUNPC DMS-3709A and its counterpart KUNPC DMS-3709B) were from the grayish yellow siltstone and mudstone in the lower part of the section (Meng et al. 2014; Zhang et al. 2015; Huang et al. 2016, 2017, 2018; Fig. 2A). The outcrop of the Wenshan Basin yields abundant plant fossils. Some species such as *Ailanthus confucii* (Su et al. 2013), *Bauhinia wenshanensis* (Meng et al. 2014), *Palaeocarya hispida* (Meng et al. 2015), *Mahonia mioasiatica* (Huang et al. 2016), *Rosa fortuita* (Su et al. 2016), *Exbucklandia acutifolia* (Huang et al. 2017), *Ficus microtrivia* (Huang et al. 2018) have been previously reported, and indicate a subtropical broadleaved forest vegetation (Huang 2017).

The fossil-bearing layers in the Maguan Basin, characterized by light yellow laminated mudstones, belong to the lower part of the Huazhige Formation according to stratigraphic correlations (Zhang 1976; Bureau of Geology and Mineral Resources 1990; Fig. 2B) and thus has an older age. This was consistent with the finding of the mammal fossil *Gigantamynodon* (Amynodontidae) from the bottom of this section (Qi 1992). *Gigantamynodon* exsisted from the middle Eocene to the early Miocene (Lucas and Emry 1996). The plant fossil-bearing layers were located above the mammal fossil. Many extinct taxa have been identified inculding *Cedrelospermum* and *Divacer* (Jia 2017) which were not found from the Wenshan Section. Therefore, the Maguan plant assemblage should be older than the Wenshan plant assemblage. Recent study of *Cedrelospermum* from different ages suggests that *Cedrelospermum* fossils from the Maguan Basin show more derived morphologies than the fossils from the late Oligocene Lunpola Basin (Jia et al. 2018). Therefore, the fossil-bearing layers in the Maguan Basin are most likely the early Miocene in age (Jia 2017; Jia et al. 2018). Details of the lithological facies represented in the outcrop have been described by Jia (2017). Some other fossils have been previously reported from this outcrop, such as *Cedrelospermum asiaticum* (Jia et al. 2015), *Sequoia maguanensis* (Zhang et al. 2015), and *Pterolobium punctatopsis* (Jia et al. 2017), which indicate a subtropical broadleaved forest vegetation in Maguan flora (Jia 2017).

2.2. Morphological observations

Fossils were photographed using a digital microscope (Zeiss Smart Zoom 5, Germany). Detailed morphology of the fossils was observed under an upright fluorescent microscope (Zeiss Axio Imager A2; equipped with microscope Zeiss AxioCam MRc, Germany). The pictures were generated using the ZEN2012 software (Zeiss, Germany). For comparison, morphological characters of fruit fossils were compiled from published literature, and those of extant species were obtained from

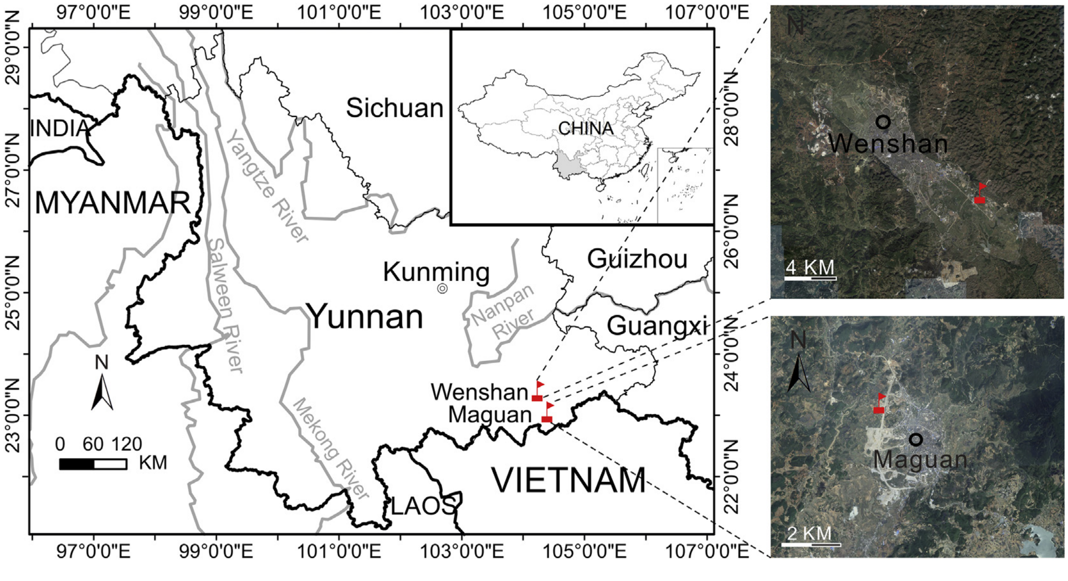

Fig. 1. The fossil localities of the Wenshan and Maguan basins. The two photographs on the right were drawn based on GoogleEarth. The red flags represent the fossil sites.

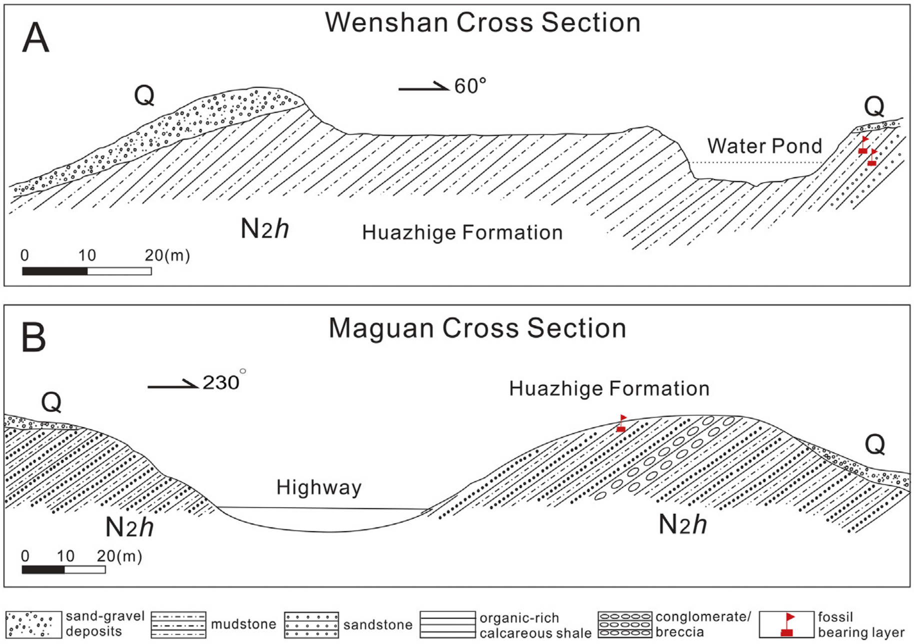

Fig. 2. Cross sections of Wenshan (A) and Maguan (B) basins. Q represents the Quaternary deposits; the arrow represents direction of strata; N2 *h* represents the Neogene Huazhige Formation.

specimens in the herbarium at the Kunming Institute of Botany (KUN, China) as well as from online herbaria, including the Chinese Virtual Herbarium (http://www.cvh.ac.cn/) and JSTOR (https://plants.jstor.org/). Quantitative characters of fossil and extant species, such as fruit size and wing width, were measured using ImageJ 1.50i (Wayne Rasband, National Institutes of Health, USA). Fossil records with uncertain (sub)sectional affinities were then revised based on taxonomy of the (sub)sectional classification of Wiegrefe et al. (1994), and the Flora of China (Fu et al. 2003).

3. Results

3.1. Fruit fossils from the Wenshan Basin

3.1.1. Systematics

Family: Ulmaceae Mirb.

Genus: ***Ulmus* L.**

Section: *Ulmus* Fu.

Series: *Lanceaefolia* Schneider.

Species: *Ulmus prelanceaefolia* Q.Y. Zhang et Y.W. Xing sp. nov.

Holotype: KUNPC DMS-0187 (Plate I, 1).

Paratypes: KUNPC DMS-3709A (Plate I, 4), KUNPC DMS-3709B (Plate I, 5).

Repository: Paleobotanical Collections in the Herbarium, Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Etymology: The specific epithet "*prelanceaefolia*" refers its affinity to the extant *U. lanceaefolia*.

Type locality: Dashidong Village, Wenshan County, Yunnan Province, southwestern China (23° 20′ N; 104° 17′ E, 1271 m a.s.l.).

Stratigraphy: the middle and upper part of the Huazhige Formation (early–middle Miocene).

Diagnosis: Samara elliptical, adjoined by two lateral wings. Fruit wings broad, oblique in shape with two beak-shaped stigmas. A prominent axial vein laterally deflecting in its course from pedicel to stigmatic notch. Surface and margin of samara glabrous. Seed at the center of samara and the apex toward the notch. The seed close to the samara base. Perigynous tube narrow and deep and calyx shallowly lobed. Gynophore visible.

3.1.2. Description

Samaras are elliptical and strongly oblique, 10.8–12.9 mm long and 7.9–8.0 mm wide (Plate I, 1, 4, 5). Two membranous wings are unequal in width with the wider wing ca. 2.6 mm and the narrow wing ca. 1.8 mm (Plate I, 1, 4, 5). Fruit surface and margin are glabrous, and no pubescence is observed on stigmatic surface of notch (Plate I, 1, 4, 5). Two short and beak-shaped stigmas persist on the top of the samara (Plate I, 1, 4, 5). Seed is located at the center of the samara (Plate I, 1, 4, 5). The apex of the seed is toward the stigmatic notch, and the base of the seed is near the base of the samara (Plate I, 1, 4, 5). Seed is 5.9–7.2 mm long and 3.4–3.7 mm wide and is as wide as two wings approximately (Plate I, 1, 4, 5). The distance between seed and samara base is ca. 2.1–2.6 mm (Plate I, 1, 4, 5). The gynophore is clearly visible (Plate I, 1, 3, 4, 5). The pedicel persists a campanulate perianth (Plate I, 1, 3). Perianth is ca. 2.0 mm long and 1.4 mm wide, and perigynous tube is narrow and deep (Plate I, 1, 3). The filaments are flat and extend to corolla tube (Plate I, 1, 3). A prominent axis is laterally deflected in its course from pedicel to stigmatic notch (Plate I, 2). The surface of the seed is covered with reticulate vascular bundles, and the veins within wings are radial to reticular and extend from seed to the samara margin (Plate I, 2). The marginal vein is thick originating from the pedicel and reaching to the stigma (Plate I, 1, 4, 5).

3.1.3. Remarks

The Wenshan fossils are asymmetrically winged fruits, with a vascular bundle originating from the pedicle and running to the stigmatic area along one side of the seed (Plate I, 1, 2, 4, 5). The distinctive characters of the samara indicate the close affinity of our fossils to the genus *Ulmus*. According to the widely accepted classification system of Wiegrefe et al. (1994) and Fu (1980), *Ulmus* may be divided into five sections based on the depth of calyx lobes, the shape of perigynous tube, the width of wings and the presence of hairs on the fruit surface (Table 1). Our fossils represent broad-winged and glabrous samaras, which differ from the sect. *Chaetoptelea* that have narrow wings and densely ciliate wing margins (Plate I, 1, 4, 5; Table 1). Similarly, the sect. *Blepharocarpa* with a densely ciliate margin is distinct from our fossils (Table 1). The Wenshan fossils differ from the sections *Trichoptelea* and *Microptelea* by possessing a shallowly lobed calyx (Plate I, 1, 3;

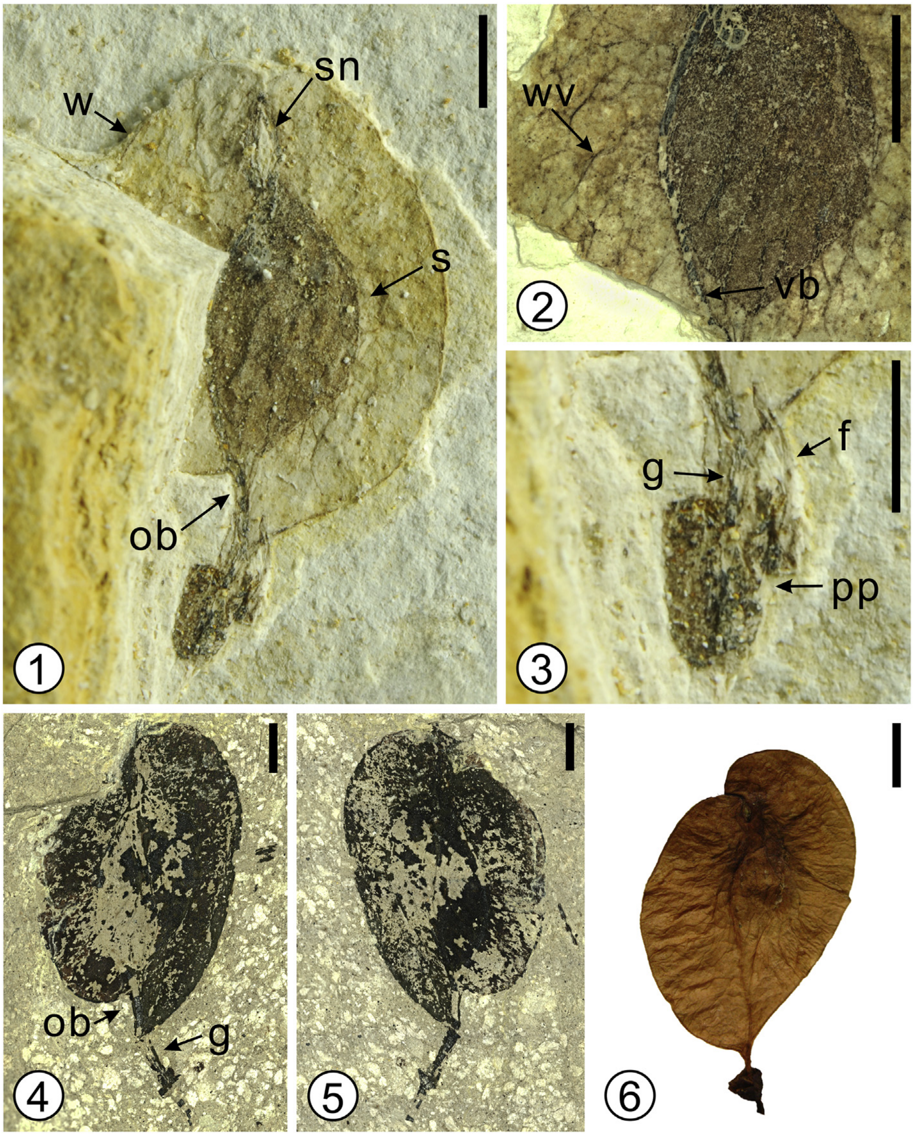

Plate I. Samaras of *Ulmus prelanceaefolia* from the Wenshan Basin and extant *U. lanceaefolia*. **1.** The holotype KUNPC DMS-0187 from a layer of yellow fine calcareous mudstone, scale bar = 2 mm. **2–3.** Amplifications of the holotype, scale bars = 2 mm. **4–5.** The paratypes KUNPC DMS-3709A and its counterpart KUNPC DMS-3709B from a layer of grayish yellow siltstone – mudstone, scale bars = 2 mm. **6.** Samara of extant species *U. lanceaefolia*, scale bar = 5 mm. sn, stigmatic notch; w, wing; s, seed; ob, oblique base; wv, wing veins; vb, vascular bundle; g, gynophore; f, filament; pp., persistent perianth.

Table 1). Moreover, our fossils differ from samaras of the above four sections by having narrow and deep perigynous tubes (Plate I, 1, 3; Table 1). Therefore, our fossils can be confidently assigned to the sect. *Ulmus*. Within the sect. *Ulmus*, four series are recognized according to Fu's (1980) system. The inclusion of ser. *Villosa* in the sect. *Ulmus* might be problematic as the samara of this series possesses densely ciliate margins and stigmas, and narrow or absent wings (Table 1). The seed apex of our fossils is situated toward the notch, which differs from the ser. *Glabrae* where the seed apex is not located toward the notch (Plate I, 1, 2, 4, 5; Table 1). Wings of the Wenshan fossils are strongly oblique and the gynophore is visible between the wings and the perianth, which is distinguished from the ser. *Nitentes* (Plate I, 1, 3, 4, 5; Table 1). The gross morphology of our fossils resembles the monotypic ser. *Lanceaefolia*. However, there are some quantitative differences between the extant species *U. lanceaefolia* and our fossils. For examples, the fruit and seed sizes of our fossils are smaller, and the ratio of seed/samara length of the Wenshan fossils is slightly greater than that of extant species (Plate I, 1, 2, 4, 5, 6); in addition, the distance between seed and samara base of our fossils is shorter than that of *U. lanceaefolia* (Plate I, 1, 2, 4, 5, 6). Moreover, no previous fossils resembling ser. *Lanceaefolia* have been reported. Therefore, we name our fossils as a new species, *U. prelanceaefolia* Q.Y Zhang et Y.W. Xing sp. nov. which refers its affinity to the extant species, *U. lanceaefolia.*

3.2. Fruit fossils from the Maguan Basin

3.2.1. Systematics

Family: Ulmaceae Mirb.
Genus: ***Ulmus* L.**
Section: *Ulmus* Fu.
Series: *Nitentes* Moss.
Species: *Ulmus maguanensis* Q.Y. Zhang et Y.W. Xing sp. nov.
Holotype: KUNPC MG-1086 (Plate II, 1).
Paratypes: KUNPC MG-1409 (Plate II, 2), KUNPC MG-1088 (Plate II, 3), KUNPC MG-0023 (Plate II, 4).

Repository: Paleobotanical Collections in the Herbarium, Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Etymology: The specific epithet refers to the fossil locality, Maguan Basin.

Table 1
Fruit characters used for *Ulmus* sectional/series classification.

Section/series	Wing	Fruit surface and margin	Perigynous tube shape	Calyx lobes depth	Seed position	Gynophore	The ratio of fruit stalk/perianth length
Blepharocarpa	Broad, symmetric	Margin densely ciliate	Wide, shallow	Shallow	Toward the notch or not toward the notch	Invisible	2–4
Chaetoptelea	Narrow or broad, symmetric	Margin densely ciliate	Wide, shallow	Shallow	Not toward the notch or whole seed	Invisible	2–6
Trichoptelea	Narrow, symmetric	Surface pubescent, margin densely ciliate	Wide, shallow	Deep	Whole seed	Invisible	~1
Microptelea	Broad, symmetric	Glabrous	Wide, shallow	Deep	Not toward the notch	Visible	≤1
Ulmus/*Villosa*	Narrow, symmetric	Surface pubescent, margin densely ciliate	Wide, shallow	Deep	Whole seed	Invisible	~1
Ulmus/*Glabrae*	Broad, symmetric	Pubescent or glabrous	Narrow, deep	Shallow	Not toward the notch	Invisible	~1
Ulmus/*Lanceaefolia*	Broad, strongly oblique	Glabrous	Narrow, deep	Shallow	Toward the notch	Visible	2–3
Ulmus/*Nitentes*	Broad, symmetric	Pubescent or glabrous	Narrow, deep	Shallow	Toward the notch	Invisible	~1
U. prelanceaefolia	Broad, strongly oblique	Glabrous	Narrow, deep	Shallow	Toward the notch	Visible	?
U. maguanensis	Broad, symmetric	Glabrous	Narrow, deep	Shallow	Toward the notch	Invisible	<1

Characteristics for comparisons are based on Wiegrefe et al. (1994) and Fu (1980) and descripted correspondingly for the *U. prelanceaefolia* and *U. maguanensis*.

Type locality: Maguan Basin, Yunnan Province, southwestern China (23°01′N, 104°23′E; 1320 m a.s.l.).

Stratigraphy: the middle and lower part of the Huazhige Formation (early Miocene).

Diagnosis: Samara asymmetrical with two broad wings, orbicular, broadly elliptic or oblong in shape. Two beak-shaped stigmas at the apex of samara. Samara glabrous except for pubescence on stigmatic notch. A prominent vascular bundle laterally deflecting in its course from pedicel to stigmatic notch. Pedicel short, occasionally persistent perianth and the perigynous tube narrow and deep, filaments flat and extend to corolla tube. Fruit stalk shorter than perianth. Seed at the center of samara and toward the notch, and seed width shorter than or approximately equal to wing width. Gynophore invisible.

3.2.2. Description

Samaras are orbicular, broadly elliptic or oblong in shape, 7.4–11.1 mm long and 6.7–12.2 mm wide (Plate II, 1–4; Table 2). A prominent vascular bundle laterally deflects in its course from pedicel to stigmatic notch (Plate II, 2). Two membranous wings are approximately equal in width with the total width ca. 3.2–7.2 mm (Plate II, 1–4). Fruits are glabrous except for pubescence on stigmatic notch (Plate II, 1–4, 6; Table 2). Two relatively long and beak-shaped stigmas persist on the apex of samara (Plate II, 1, 2, 6). Seed is at the center of the samara and the apex is toward the notch (Plate II, 1–4; Table 1). Seed is 4.8–6.0 mm long and 3.2–5.5 mm wide, and the seed width is shorter than or approximately equal to the wing width (Table 2). The distance between seed base and samara base is ca. 0.8–1.0 mm (Table 2). The gynophore is invisible (Plate II, 1–4; Table 1). The pedicel with ca. 0.6–1.1 mm long is shorter than the persistent campanulate perianth which is ca. 1.7–1.9 mm long (Plate II, 3, 4, 8; Table 1). The perigynous tube is narrow and deep, and the perianth lobes are shallow (Plate II, 3, 4, 7, 8; Table 1). The filaments are flat and extend to corolla tube (Plate II, 3, 7). The marginal vein is thick, the veins within the wings are radial to reticular and extend from the seed to the samara margin (Plate II, 1, 2).

3.2.3. Remarks

The Maguan samaras are broad-winged and glabrous, the perigynous tube is narrow and deep, and the perianth lobes are shallow, suggesting that those features clearly fall within the morphology of sect. *Ulmus* (Plate II, 1–4; Table 1). Its affinity to the ser. *Glabrae* can be eliminated based on the seed position (Table 1). The Maguan fossils differ from the ser. *Lanceaefolia* by having a symmetrical samara, and an invisible gynophore between the samara and perianth (Plate II, 1–4; Table 1). Furthermore, the fruit stalk of ser. *Lanceaefolia* is much longer than that of the Maguan fossils (Table 1). Therefore, the samara characters of the Maguan fossils are consistent with the ser. *Nitentes* (Table 1). Within the ser. *Nitentes*, there are 8–10 extant species (Fu 1980). After detailed comparison, we found that the Maguan fossils cannot be assigned to any extant species (Table 2). The extant species, *U. glaucescens* and *U. castaneifolia* differ from the Maguan fossils by possessing differently shaped samaras and much larger fruits (Table 2). *Ulmus chenmoui* can be distinguished from the Maguan fossils due to its pubescent surface and margin, and a slightly larger samara (Table 2). The Maguan fossils show close similarities in gross morphology to the rest of the Asian species in the ser. *Nitentes*, including *U. davidiana*, *U. prunifolia*, *U. densa*, *U. szechuanica* and *U. microcarpa* (Table 2). However, it is worth noting that the seed lies very close to the bottom of the samara within the Maguan fossils, which differs from these species that have a large space between the seed and samara base (Plate II, 1, 2; Table 2). The seed of the Maguan fossils lies closest to the samara base, while the distance between seed and samara base is usually more than 3 mm in extant species (Table 2). Overall, the Maguan fossils show the closest affinity with *U. microcarpa* from Southeast Tibet, but differs in fruit size (Plate II, 1–4, 5).

Until now, only one fossil species, *U. protojaponica*, was considered to belong to the ser. *Nitentes*, which resembles the extant species *U. davidiana* (Ozaki 1991). However, this fossil samara is poorly preserved, and no further comparisons can be made with the Maguan fossils. According to our re-examination of previously published records (Table 2), fruit fossils from the early Oligocene of Crooked River Basin (Meyer and Manchester 1997) also show affinity with the ser. *Nitentes* due to their seed position. However, they differ from the Maguan fossils by having a different samara shape and a long gynophore (Meyer and Manchester 1997; Table 2). Therefore, we determine the Maguan fossils to be a new species, *U. maguanensis* Q.Y. Zhang et Y.W. Xing sp. nov.

4. Discussion

4.1. The Cenozoic fruit fossil records of Ulmus

Numerous Cenozoic fruit fossils of *Ulmus* have been reported across the Northern Hemisphere (Manchester 1989). We have added recently published fossils and some records not listed in Manchester's (1989) review (Table 3). As the taxonomic affinities of some early records were not designated, we reexamined their morphology based on original pictures and assigned them into sectional/series level according to the classification system of Wiegrefe et al. (1994) and Fu et al. (2003). The fossil *Ulmus* sp. B from Crooked River of North America (Meyer and Manchester 1997) was assigned to the ser. *Nitentes* of the sect. *Ulmus*

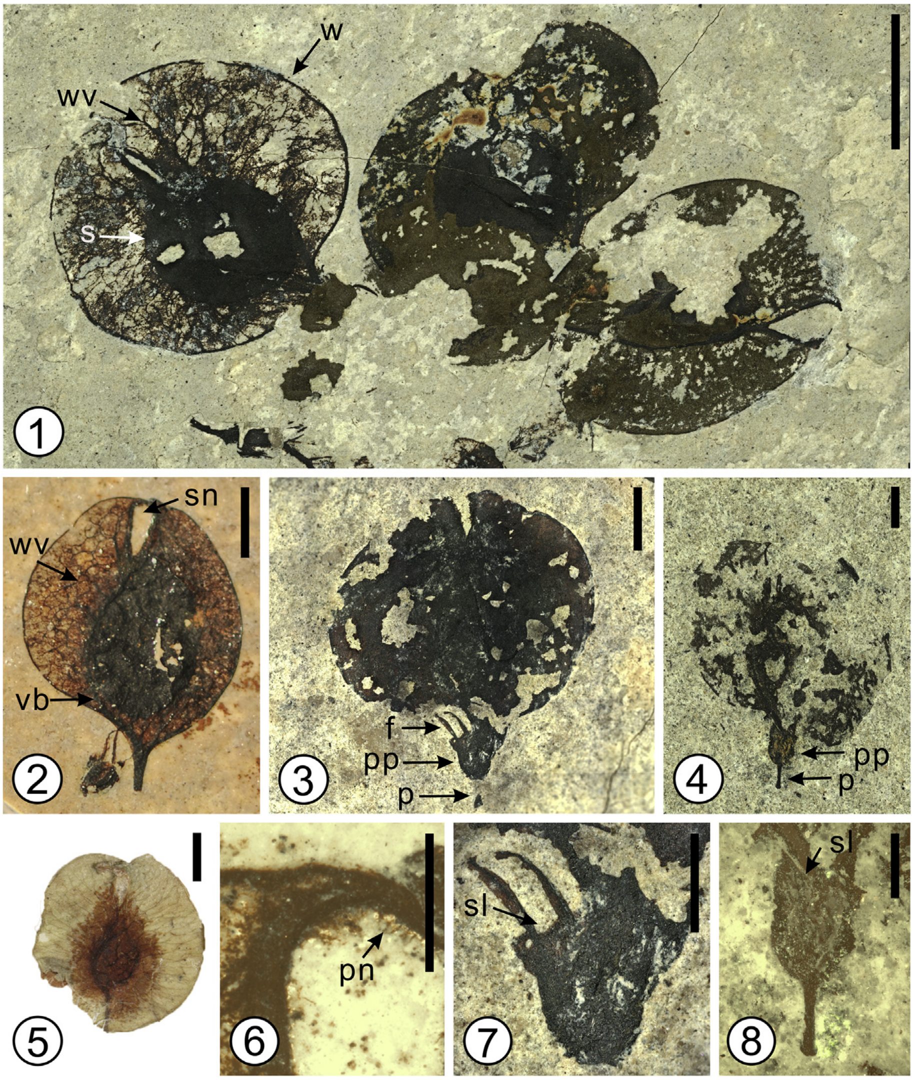

Plate II. Samaras of *Ulmus maguanensis* from the Maguan Basin and extant *U. microcarpa*. **1.** The holotype KUNPC MG-1086, scale bar = 2 mm. **2–4.** The paratypes KUNPC MG-1409, KUNPC MG-1088 and KUNPC MG-0023, scale bars = 2 mm. **5.** Samara of extant *U. microcarpa*, scale bar = 2 mm. **6.** Amplification of the stigmatic notch of KUNPC MG-1409 showing pubescence on notch, scale bar = 1 mm. **7.** Amplification of perianth, scale bar = 1 mm. **8.** Amplification of perianth and pedicle, scale bar = 0.5 mm. w, wing; wv, wing veins; vb, vascular bundle; sn, stigmatic notch; f, filament; pp., persistent perianth; p, pedicle; pn, pubescent on notch; sl, shallow lobed.

due to its broad-winged samara, glabrous surface and margin, shallowly lobed calyx, and seed position that is toward the notch. Fossil samaras from the late Pliocene of Germany (Straus 1992) and *Ulmus drepanodonta* from the late Oligocene of Asia (Iljinskaja 1982) were assigned to the ser. *Glabrae* of sect. *Ulmus* because of their broad wings, glabrous surface and margin, shallowly lobed calyx, and the seed position that is not toward the notch. *Ulmus tenuinervis* from the early Oligocene of North America (MacGinitie 1953) was assigned to the sect. *Microptelea* based on its deeply lobed calyx and visible gynophore. In total, over 20 records with clear sectional affinities were found (Table 3).

North America had the most abundant fossil fruit records from the Paleogene (Table 3). The earliest fossil record was from the early Eocene of Chalk Bluffs flora and McAbee flora of America (MacGinitie 1941; Denk and Dillhoff 2005). Several fruit fossils were also reported in the Oligocene and no records were found in the Neogene (Table 3). In Europe, the earliest fossil was from the late Oligocene of North Bohemia (Bužek 1971) and another two records were from the Neogene (Table 3). The earliest fossil fruit in Asia was from the early Eocene of Northeast China (Wang et al. 2010). From then on, several fruit fossils have been reported from each geological epoch (Fig. 3).

4.2. Evolutionary history of *Ulmus* based on fruit fossil records

According to our revision, four out of five sections have fruit fossil records except the sect. *Blepharocarpa* (Table 3; Fig. 3). The earliest fruit fossils are from the early Eocene of North America (MacGinitie 1941) and East Asia (Wang et al. 2010). Additionally, several fossils have been reported from the middle or late Eocene of North America (Table 3; Fig. 3). All these Eocene fruits were narrow-winged and belonged to the sections *Chaetoptelea* and *Trichoptelea*, and no broad-winged fruits have been found in the Eocene (Table 3; Fig. 3). Therefore, we speculate that these two sections might be the early evolved lineages in *Ulmus* and diversified in the Eocene. The narrow-winged fruit may be a primitive character. After the Eocene, no fruit fossils of sect. *Trichoptelea* have been found and only two wingless fruits of sect. *Chaetoptelea* had been reported from the early Oligocene of North America (Meyer and Manchester 1997) and the late Miocene of Europe (Hantke 1954). The scarcity of narrow-winged fruit fossils after the Eocene and their disappearance from Asia might indicate a decrease of richness in the narrow-winged lineages. On one hand, this was likely due to the weak dispersal ability of the narrow-winged fruits by wind. On the other hand, this may simply be due to the preservation bias of the fossil record.

Table 2
Comparison of the Maguan fossils with extant and fossil species of the series *Nitentes* in the section *Ulmus*.

Species	Extant or fossil	Fruit shape	Fruit surface	Fruit size (length × width, mm)	Seed size (length × width, mm)	Seed to samara base (mm)	Seed and wing width comparison
Ulmus glaucescens	Extant	Elliptic, broadly elliptic, or obovate	Glabrous	(20.0–25.0) × (15.0–20.0)	(8.2–11.6) × (5.3–7.7)	4.4–8.0	Seed>wing
U. chenmoui	Extant	Narrowly obovate, oblong – obovate, or broadly obovate	Pubescent	(15.0–25.0) × (10.0–17.0)	(5.2–7.2) × (3.2–4.5)	5.4–7.2	Seed≤wing
U. davidiana	Extant	Obovate	Glabrous or sparsely pubescent	(10.0–19.0) × (7.0–14.0)	(4.2–6.9) × (2.8–3.9)	3.4–5.5	Seed≤wing
U. prunifolia	Extant	Oblong – elliptic to oblong – obovate	Glabrous	(12.0–20.0) × (8.0–13.0)	(5.2–7.9) × (3.2–4.4)	3.7–8.5	Seed≤wing
U. densa	Extant	Oblong, oblong – obovate, obovate, oblong – elliptic	Glabrous	(10.0–16.0) × (8.0–14.0)	(4.9–7.7) × (3.5–5.4)	4.6–8.4	Seed≤wing
U. castaneifolia	Extant	Oblong – obovate, obtriangular – obovate, or obovate	Glabrous	(15.0–33.0) × (10.0–16.0)	(4.1–6.5) × (2.0–2.7)	6.8–10.0	Seed≤wing
U. szechuanica	Extant	Orbicular to obovate – orbicular	Glabrous	(11.0–16.0) × (9.0–13.0)	(3.3–5.9) × (1.9–4.2)	3.3–6.7	Seed≤wing
U. microcarpa	Extant	Orbicular	Glabrous	(7.0–8.0) × (7.0–8.0)	3.0 × 1.9	1.6	Seed≤wing
U. maguanensis	Fossil	Obovate, orbicular, broadly elliptic	Glabrous	(7.4–11.1) × (6.7–12.2)	(4.8–6.0) × (3.2–5.5)	0.8–1.0	Seed≤wing
U. protojaponica[1]	Fossil	Ovate, symmetric	Glabrous	?	?	4.1	Seed<wing
U. protojaponica[2]	Fossil	Elliptical, symmetric	Glabrous	? × (8.8–11.3)	(4.8–6.1) × (2.3–2.6)	3.2	Seed<wing
U. sp. B type1[3]	Fossil	Elliptical, symmetric	Glabrous	9.3 × 6.2	5.6 × 2.9	1.5	Seed≤wing
U. sp. B type4[4]	Fossil	Ovate, symmetric	Glabrous	11.8 × 8.9	3.4 × 3.4	3.5	Seed<wing

1 from Plate 15 of Ozaki (1991); 2 from Fig. 1b and Fig. 2 of Tanai and Suzuki (1965); 3 from Plate 21, Fig. 1 of Meyer and Manchester (1997); 4 from Plate 21, Fig. 4 of Meyer and Manchester (1997).

Compared to the early appearance of narrow-winged fruits, the broad-winged fruits occurred rather late (Fig. 3). The earliest broad-winged fruits were found in the early Oligocene of the Florissant flora of Colorado (MacGinitie 1953), and Crooked River Basin (Meyer and Manchester 1997), which were assigned to the sect. *Microptelea* and the ser. *Nitentes* (sect. *Ulmus*), respectively (Table 3; Fig. 3). Fruit fossils of the sect. *Microptelea* have been reported from the late Oligocene of north Bohemian Basin in Czech (Bužek 1971), and late Oligocene fruits of the ser. *Glabrae* (sect. *Ulmus*) have been found in Amytak, Kazakhstan (Iljinskaja 1982). This indicates that the Oligocene was likely an important period for rapid diversification of broad-winged lineages (Fig. 3). Additionally, this geographic pattern may be due to a dispersal advantage of broad-winged lineages in more open forests, which may have been induced by global cooling during the Oligocene.

Several Neogene broad-winged fruits have been found in the Pliocene of Stegodon Beds, Rubeshibe and Kabutoiwa in Japan (Miki 1937; Tanai and Suzuki 1965; Ozaki 1991) and Wittershausen in Germany (Straus 1992), while no fruit fossils of this age have been reported from North America (Fig. 3). Our fossils from Maguan represented the first record of the ser. *Nitentes* (sect. *Ulmus*) in East Asia (Fig. 3). The Wenshan fossils represent the only unequivocal fossil record of the ser. *Lanceaefolia* (sect. *Ulmus*, Fig. 3) in the world. During the same period, numerous fossils belonging to Ulmaceae were found in the Wenshan and Maguan basins, such as the fossil leaves of *Zelkova* and

Table 3
Fossil fruit records of *Ulmus* during the Cenozoic according to the order of the section/series and age.

Section/Series	Species	Age	Wing type	Occurrence	Reference
Ulmus/*Nitentes*	*Ulmus protojaponica*	Early Pliocene	Broad	Rubeshibe, Japan	Tanai and Suzuki 1965
Ulmus/*Nitentes*	*U. protojaponica*	Late Miocene–early Pliocene	Broad	Kabutoiwa, Japan	Ozaki 1991
Ulmus/*Nitentes*	*U. maguanensis*	Early Miocene	Broad	Maguan Basin, China	This Study
Ulmus/*Nitentes*	*U.* sp. B 1	Early Oligocene	Broad	Crooked River, US	Meyer and Manchester 1997
Ulmus/*Nitentes*	*U.* sp. B 4	Early Oligocene	Broad	Crooked River, US	Meyer and Manchester 1997
Ulmus/*Glabrae*	*U.* sp.	Late Pliocene	Broad	Wittershausen, Germany	Straus 1992
Ulmus/*Glabrae*	*U. drepanododonta*	Late Oligocene	Broad	Amytak, Kazakhstan	Iljinskaja 1982
Ulmus/*Lanceaefolia*	*U. prelanceaefolia*	Early–middle Miocene	Broad	Wenshan Basin, China	This Study
Microptelea	*U. parvifolia*	Late Pliocene	Broad	Stegodon Beds, Japan	Miki 1937
Microptelea	*U. pyramidalis*	Late Oligocene	Broad	north Bohemian Basin, Czech	Bužek 1971
Microptelea	*U. tenuinervis*	Early Oligocene	Broad	Florissant flora, US	MacGinitie 1953; Manchester 1989
Trichoptelea	*U.* sp.	Early–middle Eocene	Narrow	Driftwood Creek/Smithers, Quilchena, British Columbia, Canada; Republic flora, US	Denk and Dillhoff 2005
Chaetoptelea	Section *Chaetoptelea*	Late Miocene	Wingless	Schrotzburg, Switzerland	Hantke 1954
Chaetoptelea	*U.* sp. A	Early Oligocene	Narrow	Crooked River Basin, Oregon, US	Meyer and Manchester 1997
Chaetoptelea	Sect. *Chaetoptelea*	Middle Eocene	Wingless	Republic flora, US	Burnham 1986
Chaetoptelea	*U.* sp.	Middle Eocene	Wingless	West Branch Creek, Oregon, US	Manchester 1989
Chaetoptelea	*U.* sp.	Middle Eocene	Wingless	Horsefly, Black Creek Rd., British Columbia, Canada	Willson and Lindoa, 1978
Chaetoptelea	*U.* sp.	Middle Eocene	Wingless	One Mile Creek,Princeton, British Columbia, Canada	Manchester 1989
Chaetoptelea	*U. pseudo-fulva*	Late early Eocene	Narrow	Chalk Bluffs, US	MacGinitie 1941; Manchester 1989
Chaetoptelea	*U. okanaganensis*	Late Early Eocene	Wingless	McAbee flora, US	Denk and Dillhoff 2005
Chaetoptelea	*U. fushunensis*	Early Eocene	Wingless	Fushun, China	Wang et al. 2010

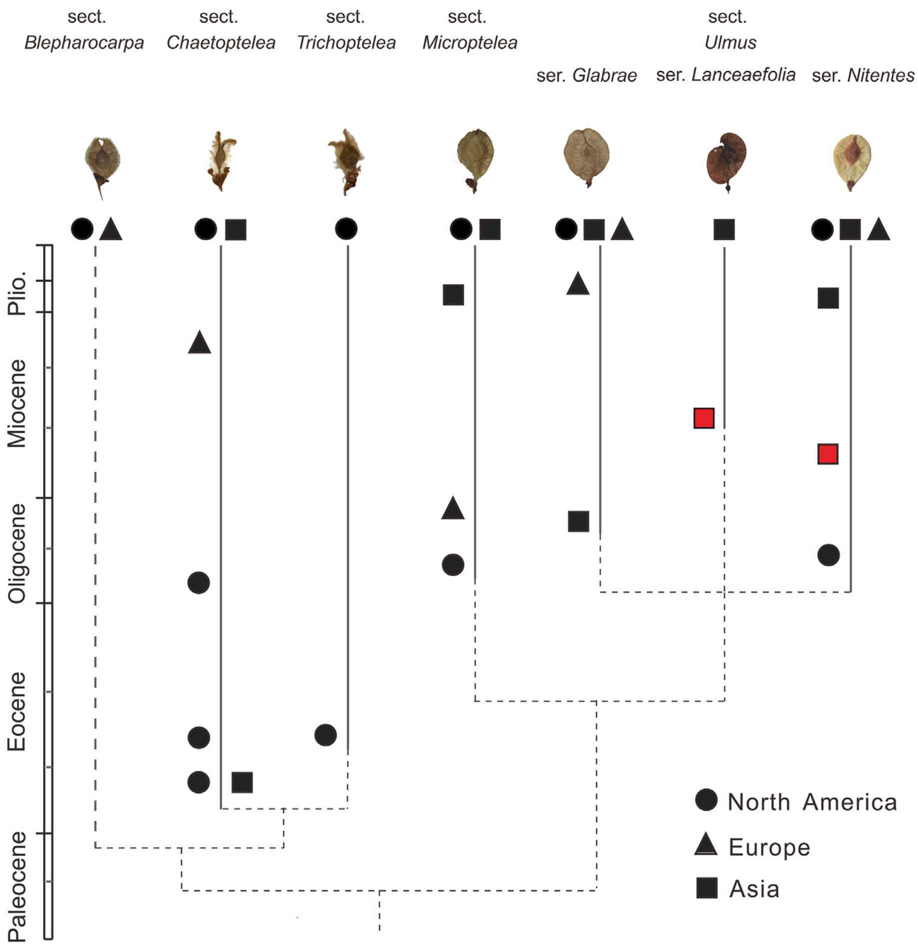

Fig. 3. The Cenozoic fossil fruits of *Ulmus* and the evolution and biogeography of each section or series. The black color represents the fossil fruits from published literature. The red color represents the fossil fruits from the Wenshan and Maguan basins. The phylogenetic relationships are based on Wiegrefe et al. (1994) and Fu (1980).

Ulmus, and samaras of *Cedrelospermum*, which suggest that the diversity of Ulmaceae has been relatively high since the Miocene (Jia et al. 2015; Huang 2017). Moreover, it is worth noting that the ser. *Lanceaefolia* is the only evergreen lineage in *Ulmus*. Our finding indicates that the evergreen type evolved in East Asia as early as the middle Miocene (Fig. 3). Furthermore, the plants of extant ser. *Lanceaefolia* grow in karst areas only, which may suggest that modern karst vegetation originated no later than the middle Miocene. This is consistent with the fossils *Burretiodendron* and *Ficus microtrivia*, which today only grow in limestone forests (Lebreton-Anberrée et al. 2015; Huang et al. 2018).

4.3. Biogeographic history of Ulmus based on fossil fruit records

The sect. *Chaetoptelea* is distributed in North America and Asia at present (Fig. 3). As mentioned above, the earliest fossil records of the sect. *Chaetoptelea* were from the early Eocene of both North America and East Asia (Table 3; Fig. 3). This suggests that floristic exchange of Ulmaceae between East Asia and North America already existed in the Eocene via the Bering land bridge that still presented in this epoch (Marincovich Jr. and Gladenkov 2001; Ickert-Bond et al. 2009). However, the geographic origin of the sect. *Chaetoptelea* cannot be deduced solely based on fruit fossil records. Furthermore, fruit fossils of the sect. *Chaetoptelea* were reported from the early Oligocene of North America (Meyer and Manchester 1997) and the late Miocene of Europe (Hantke 1954). These occurrences may be due either to dispersal from Asia or from North America via the North Atlantic land bridge. Extinction of the sect. *Chaetoptelea* in Europe must have occurred after the Miocene as no modern species exist there at present (Fig. 3).

The sect. *Microptelea* is currently distributed in North America and East Asia (Fig. 3). The earliest fossil record of this section is from the early Oligocene of North America (MacGinitie 1953). In addition, fossils had been uncovered from the late Oligocene of Europe (Bužek 1971) and the late Pliocene of East Asia (Miki 1937). We speculate that this section may have originated in North America and then dispersed to Europe during the Oligocene via the North Atlantic land bridge. Colonization of Asia from Europe or North America might be rather recent and accompanied by extinction in Europe (Fig. 3).

Sect. *Ulmus* is the most diverse lineage in the genus and is widely distributed across the Northern Hemisphere (Fig. 3). Within this section, the ser. *Nitentes* is the earliest divergent lineage according to the fruit fossil records (Fig. 3). The earliest fruit fossils were from the early Oligocene of North America (Meyer and Manchester 1997). Our Maguan fossils represent the earliest record from East Asia (Fig. 3). We deduce that this series may have originated in North America and dispersed to East Asia via the Bering land bridge during the Miocene. Our fossils from the Wenshan Basin represent the only unequivocal fossil record and are consistent with the modern distribution of ser. *Lanceaefolia*, suggesting that it may have originated in East Asia and persisted in situ since the middle Miocene (Fig. 3). We are aware that our biogeographic speculation may be biased due to the scarcity of the fruit fossil records. More information such as molecular evidence is needed to reconstruct a more comprehensive biogeographic history of this genus.

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