Miocene U. fossil fruits from Southwest China and their evolutionary and biogeographic implications

Qiu-Yue Zhang\textsuperscript{a,c}, Jian Huang\textsuperscript{a}, Lin-Bo Jia\textsuperscript{b}, Tao Su\textsuperscript{a}, Zhe-Kun Zhou\textsuperscript{a,b}, Yao-Wu Xing\textsuperscript{a,*}

\textsuperscript{a} Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China
\textsuperscript{b} Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, China
\textsuperscript{c} University of Chinese Academy of Sciences, Beijing, 100049, China

ARTICLE INFO

Article history:
Received 29 May 2018
Received in revised form 15 October 2018
Accepted 16 October 2018
Available online 17 October 2018

Keywords:
Ulmaceae
Neogene
Winged fruits
Diversification
Dispersal
Karst vegetation

ABSTRACT

The genus U. (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 U. are still scarce. In this study, we report two new species of the section U. 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. U. prelanceaefolia represents the only unequivocal record of the ser. Lanceaefolia in the world and U. maguanensis represents the earliest unequivocal record of the ser. Nitenes in East Asia. The evolutionary and biogeographic histories of U. 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 U. and have diversified since the Eocene. The Oligocene was an important epoch for the rapid diversification of broad-winged lineages of U., 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 U. during the Cenozoic.

© 2018 Elsevier B.V. All rights reserved.

1. Introduction

U. is the most diverse genus in the elm family (Ulmaceae Mirr.), comprising approximately 45 tree or shrub species (Sherman-Broyles et al. 1997; Fu et al. 2003). Most species of U. 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 U. is of great interest in respect of floristic evolution in the Northern Hemisphere. U. has abundant Cenozoic megafossil records across North America and Eurasia in forms of fruits and leaves (Wolf 1977; Iliinskaja 1982; Manchester 1989; Xing et al. 2016), which are essential for reconstructing its evolutionary and biogeographic histories. The oldest fossil records of U. are represented by fossil leaves dating back to the Paleocene of Asia (Kodru 1999; Feng et al. 2003), Europe (Kvaček et al. 1994) and North America (Brown 1962). However, as most lineages (sections) of U. 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, U. 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 U. could provide vital information for the evolutionary history within the genus. The earliest unequivocal fruit fossils of U. 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. U. 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; Iliinskaja 1982; Burnham 1986), fruit fossils of U. 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

https://doi.org/10.1016/j.revpalbo.2018.10.007
0034-6667/© 2018 Elsevier B.V. All rights reserved.
the lower part of the section (Meng et al. 2014; Zhang et al. 2015; other two specimens (KUNPC DMS-3709A and its counterpart KUNPC

Huazhige Formation in Wenshan is 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 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 (Lebreton-Anberrée et al. 2016). 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 (Amarynodontidae) from the bottom of this section (Qi 1992). Gigantamynodon existed 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 including Cedrelaspermum and Divacerv (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 Cedrelaspermum from different ages suggests that Cedrelaspermum 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 lithologic facies represented in the outcrop have been described by Jia (2017). Some other fossils have been previously reported from this outcrop, such as Cedrelaspredum 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 Axios Imager A2; equipped with microscope Zeiss AxiosCam 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.](image)
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 Fl.
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 Ul. 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, oblique, with 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 reticulate 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. Blepharocarpus 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;...
Moreover, our fossils differ from samaras of the above sections by having narrow and deep perigynous tubes (Plate I, 1, 3). 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 example, 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.

<table>
<thead>
<tr>
<th>Section/series</th>
<th>Wing</th>
<th>Fruit surface and margin</th>
<th>Perigynous tube shape</th>
<th>Calyx lobes depth</th>
<th>Seed position</th>
<th>Gynophore</th>
<th>The ratio of fruit stalk/perianth length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blepharocarpa</td>
<td>Broad, symmetric</td>
<td>Margin densely ciliate</td>
<td>Wide, shallow</td>
<td>Shallow</td>
<td>Toward the notch or not toward the notch</td>
<td>Invisible</td>
<td>2–4</td>
</tr>
<tr>
<td>Chaeoptelea</td>
<td>Narrow or broad, symmetric</td>
<td>Margin densely ciliate</td>
<td>Wide, shallow</td>
<td>Shallow</td>
<td>Not toward the notch or whole seed</td>
<td>Invisible</td>
<td>2–6</td>
</tr>
<tr>
<td>Trichoptelea</td>
<td>Narrow, symmetric</td>
<td>Surface pubescent, margin densely ciliate</td>
<td>Wide, shallow</td>
<td>Deep</td>
<td>Whole seed</td>
<td>Invisible</td>
<td>1</td>
</tr>
<tr>
<td>Microptelea</td>
<td>Broad, symmetric</td>
<td>Glabrous</td>
<td>Wide, shallow</td>
<td>Deep</td>
<td>Not toward the notch</td>
<td>Visible</td>
<td>1</td>
</tr>
<tr>
<td>Ulmus/Villosa</td>
<td>Broad, strongly oblique</td>
<td>Pubescent or glabrous</td>
<td>Narrow, deep</td>
<td>Shallow</td>
<td>Toward the notch</td>
<td>Invisible</td>
<td>2–3</td>
</tr>
<tr>
<td>Ulmus/Glabrae</td>
<td>Broad, symmetric</td>
<td>Glabrous</td>
<td>Narrow, deep</td>
<td>Shallow</td>
<td>Toward the notch</td>
<td>Invisible</td>
<td>1</td>
</tr>
<tr>
<td>Ulmus/Nitentes</td>
<td>Broad, strongly oblique</td>
<td>Glabrous</td>
<td>Narrow, deep</td>
<td>Shallow</td>
<td>Toward the notch</td>
<td>Invisible</td>
<td>7</td>
</tr>
<tr>
<td>U. maguanensis</td>
<td>Broad, symmetric</td>
<td>Glabrous</td>
<td>Narrow, deep</td>
<td>Shallow</td>
<td>Toward the notch</td>
<td>Invisible</td>
<td>1</td>
</tr>
</tbody>
</table>

Characteristics for comparisons are based on Wiegrefe et al. (1994) and Fu (1980) and described 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 Huazhig 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 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 2). The distance between seed base and samara base is usually more than 3 mm in extinct 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. protopajonica, was considered to belong to the ser. Nitentes, which resembles the extinct 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 longer 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...
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 sect. Glabrae of 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 from the Oligocene and no records were found in the Neogene (Table 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.

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.

Plate II. Samaras of Ulmus meganuensis 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.
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 zone (sect. Lanceaefolia), and late Oligocene fruits (sect. Lanceaefolia) have been found in Amytak, Kazakhstan (Zelkova and Wang et al. 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 sect. Nitenes (sect. Ulmus) in East Asia (Fig. 3). The Wenshan fossils represent the only unequivocal fossil record of the sect. Lanceaefolia (sect. Ulmus) 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 Ulmus.
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 Gladkov 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.

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).
Acknowledgment

The authors thank the central lab of Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences for providing the super depth microscope and fluorescence microscope; the Herbaria of Kunming Institute of Botany (KUN) and Institute of Botany (PE), Chinese Academy of Sciences for providing modern specimens for comparison; Ryan Fuller from Field Museum of Natural History (Chicago, U.S.) for English editing; Miss Congli Xu from XTBG for collecting the European fossil literature; Miss Wenna Ding from XTBG for technical assistance with the treatment of fossils. This work was financially supported by the National Natural Science Foundation of China (No. 31770226), the Pioneer Hundred Talents Program of the Chinese Academy of Sciences to Y.W. Xing and the Chinese Academy of Sciences 135 program (Nos. 2017XTBG-T03, 2017XTBG-F01), the Chinese Academy of Sciences “Light of West China” Program to J. Huang; Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (CAS-SEABRI, No. Y42X111B01).

References


