J Plant Res (2015) 128:747–761
DOI 10.1007/s10265-015-0739-2

REGULAR PAPER

# First occurrence of *Cedrelospermum* (Ulmaceae) in Asia and its biogeographic implications

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Received: 26 February 2015 / Accepted: 16 May 2015 / Published online: 4 July 2015


**Abstract** *Cedrelospermum* (Ulmaceae) is an extinct genus with extensive fossil records in Europe and North America. However, no fossil of the genus has been reported from Asia. Here we describe *Cedrelospermum asiaticum* L.B. Jia, Y.J. Huang et Z.K. Zhou sp. nov. based on compressed fruits from the late Miocene of Yunnan, southwestern China. The fossil fruits are characterized by an ovate fruit body adjoined by double wings, with the veins on the primary wing converging toward a stigmatic area. According to the historical geographic distribution of the genus, we hypothesize that *Cedrelospermum* originated in North America where both single-winged and double-winged fruits were reported. The single-winged form subsequently spread into Europe via the North Atlantic land bridge and the double-winged form dispersed into Asia via the Bering land bridge. From the Eocene to Oligocene, a southward retreat of the genus distribution probably took place, which coincided with the global surface cooling initiated during the Eocene–Oligocene transition. The extinction of *Cedrelospermum* from Asia may be related to the intensification of the East Asian monsoon.

**Keywords** Asia · Biogeography · *Cedrelospermum* · Miocene · Monsoon · Ulmaceae

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## Introduction

*Cedrelospermum* Saporta is an extinct genus in the elm family (Ulmaceae), showing a close affinity to the extant genera *Phyllostylon*, *Holoptelea* and *Hemiptelea* (Manchester 1987, 1989; Manchester and Tiffney 2001) (Fig. 1). Fossils of *Cedrelospermum* have been reported from the Paleogene and Neogene of Europe and North America (Manchester 1987, 1989; Magallón-Puebla and Cevallos-Ferriz 1994; Hably and Thiébaut 2002; Wilde and Manchester 2003; Kovar-Eder et al. 2004; Paraschiv 2008; Kvaček 2011) (Fig. 2; Tables 1, 2). They are represented by twigs with attached leaves, fruits and flowers, as well as detached leaves and fruits (Manchester 1989). In many cases, detached fossil leaves of this group are difficult in genus assignment due to morphological overlap among leaves of *Cedrelospermum*, *Zelkova*, and *Ulmus* (Kovar-Eder et al. 2004; Denk and Grimm 2005). However, fossil fruits of *Cedrelospermum* are distinctive, because they are characterized by an ovate fruit body adjoined by one or two wings with the veins on the wing or primary converging toward a stigmatic area (Manchester 1987).

The fossil fruits from an Early Eocene locality, Lewis Rach, Lincoln country, Wyoming, USA constitute the earliest reliable fossil record of *Cedrelospermum* (Grande 2013) (Table 1). So far, six species of *Cedrelospermum*

have been described based on fruit compressions. They are *C. leptospermum* (Ettingshausen) Manchester, *C. aquense* (Saporta) Saporta, and *C. stiriacum* (Ettingshausen) Kovar-Eder & Kvaček from the Middle Eocene to Late Miocene Europe (Manchester 1987, 1989; Wilde and Manchester 2003; Kovar-Eder et al. 2004; Kvaček 2011), and *C. nervosum* (New.) Manchester, *C. lineatum* (Lesq.) Manchester, and *C. manchesteri* Magallón-Puebla et Cevallos-Ferriz from the Early Eocene to Early Oligocene North America (Manchester 1987, 1989; Magallón-Puebla and Cevallos-Ferriz 1994). Based on wing morphology, these fossil fruits can be divided into two forms, viz., single-winged form and double-winged form (Manchester and Tiffney 2001) (Fig. 3). The single-winged form has a single lateral wing and a distal stigmatic notch, while the double-winged form has two wings and a stigmatic area confined to the distal portion of the lateral margin and/or apex of the larger wing (Manchester and Tiffney 2001) (Fig. 3). Based on these criteria, *C. leptospermum*, *C. aquense*, *C. stiriacum*, and some specimens of *C. nervosum* belong to the single-winged form, while *C. lineatum*, *C. manchesteri*, and the remaining specimens of *C. nervosum* belong to the double-winged form (Table 3). Generally, only the single-winged form fruits are found in Europe, while both forms are documented in North America (Manchester and Tiffney 2001). Despite its abundant fossil records in Europe and North America, no fossil of *Cedrelospermum* has ever been found in Asia.

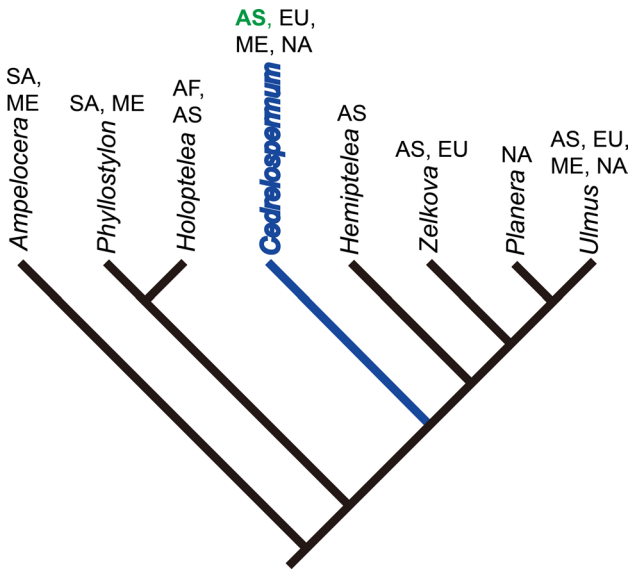



**Fig. 1** Phylogenetic tree of Ulmaceae including *Cedrelospermum* and the distribution of each genus Adapted from Manchester and Tiffney (2001), the tree was based on 17 morphological characters with *Ampelocera* as outgroup. *AF* Africa; *AS* Asia (India for *Holoptelea*, East Asia for *Zelkova* and *Hemiptelea*); *EU* Europe; *SA* South America; *ME* Mexico; *NA* North America

Recently, plenty of *Cedrelospermum* fossil fruits, characterized by double wings and a stigmatic area on the larger wing, were found from the late Miocene Yunnan, southwestern China. They constitute the first recognition of this genus in Asia. In this study, we characterized the

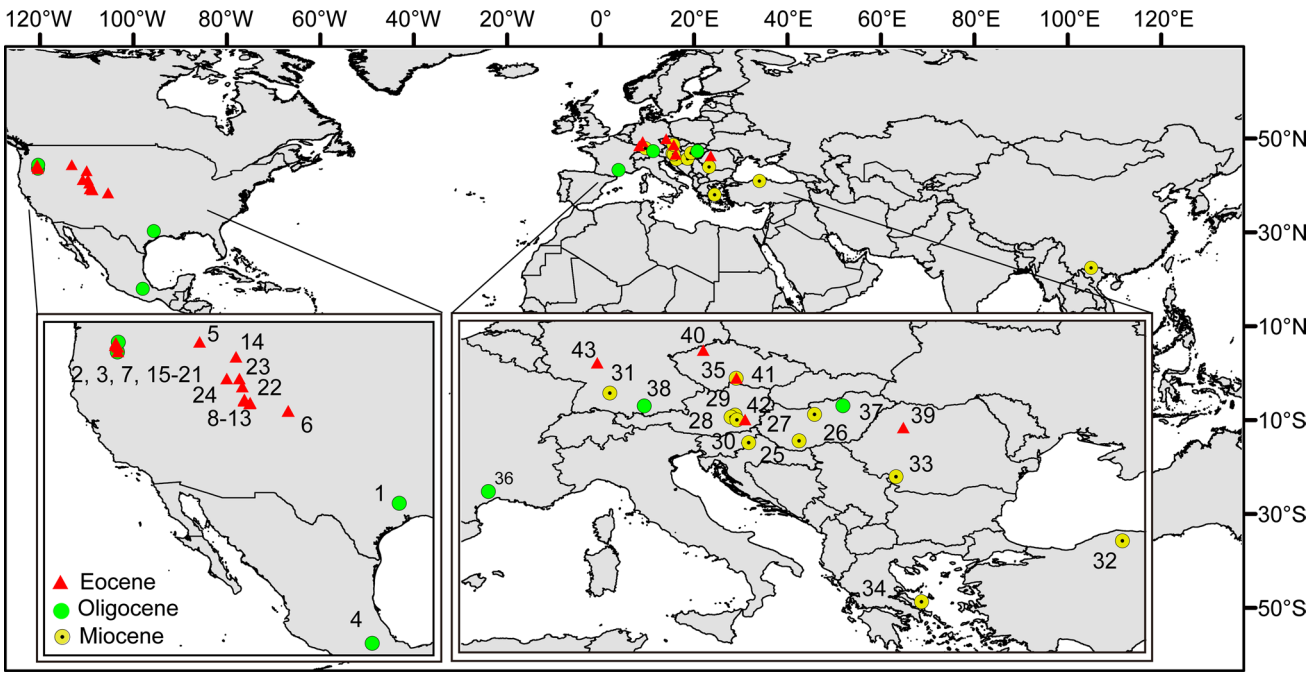



**Fig. 2** Fossil records of *Cedrelospermum* based on fruit remains. Numbers on the map correspond to the occurrences indicated in Table 1

**Table 1** Occurrences of *Cedrelospermum* fruits in North America in approximate stratigraphic order respectively

| Position on map | Species | Age | Formation name | Place name | Latitude/lontitude | References |
|---|---|---|---|---|---|---|
| 1 | *C. lineatum* | Early Oligocene | Catahoula Fm. | Huntsville Texas, Walker County, Texas, USA | 30°51′56.81″N 95°32′36.36″W | Daghlian et al. (1980); Manchester (1989) |
| 2 | *C. lineatum* | Early Oligocene | John Day Fm. | Crooked River, Crook County, Oregon, USA | 44°08.093′N 120°16.977′W | Meyer and Manchester (1997) |
| 3 | *C. lineatum* | Early Oligocene | John Day Fm. | Fossil/Wheeler High School, Jefferson County, Oregon, USA | 45°00.169′N 120°12.676′W | Meyer and Manchester (1997) |
| 4 | *C. manchesteri* | Early Oligocene (personal correspond-ence with Dr. Cevallos-Ferriz SRS 2014) | Pie' de Vaca Fm. | Puebla, Mexico | 18°35′N 97°55′W | Magallón-Puebla and Cevallos-Ferriz (1994) |
| 5 | *C. lineatum* | Late Eocene | | Beaverhead Basin, Beaverhead County, Montana, USA | 45°00′31″N 113°03′58″W | Becker (1969) |
| 6 | *C. lineatum* | Late Eocene | | Florissant, Teller County, Colorado, USA | 38°57.17′N 105°18.71′W | MacGinitie (1953) |
| 7 | *C. lineatum* | Late Eocene | John Day Fm. | Teater Road, Jefferson County, Oregon, USA | 44°10.039′N 120°14.856′W | Manchester (1987) (Pl. 2, Figs. 8, 10) |
| 8 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | Bonanza, Uintah County, Utah, USA | 39°56′24.19″N 109° 7′57.61″W | Kvaček (1995); MacGinitie (1969) |
| 9 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | Watson, Uintah County, Utah, USA | 39°53′40.76″N 109° 8′42.31″W | MacGinitie (1969) |
| 10 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | Head of Roan Creek, Garfield County, Colorado, USA | 39° 36.517′N 108° 40.023′W | MacGinitie (1969) |
| 11 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | Douglas Creek, Rio Blanco County, Colorado, USA | 39°41.014′N 108° 38.418′W | MacGinitie (1969) |
| 12 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | White River, Uintah County, Utah, USA | 39°57′10.50″N 109° 8′59.21″W | MacGinitie (1969) |
| 13 | *C. nervosum* | Middle Eocene | Green River Fm., Parachute Creek Member | Wardell Ranch, Rio Blanco County, Colorado, USA | 39°39′8.37″N 108°38′26.67″W | MacGinitie (1969) |
| 14 | *Cedrelospermum* sp. | Middle Eocene | Aycross Fm. | Kisinger Lakes, Fremont County, Wyoming, USA | 43° 42′01.9″N 109°52′44.9″W | MacGinitie (1974) |
| 15 | *C. nervosum* | Middle Eocene | Clarno Fm. | Alex Canyon,Wheeler County, Oregon, USA | 44°34′53.40″N 120°15′57.31″W | Bestland et al. (1999) |
| 16 | *C. nervosum* | Middle Eocene | Clarno Fm. | West Branch Creek, Wheeler County, Oregon, USA | 44°35′25.31″N 120°15′27.83″W | Bestland et al. (1999) |
| 17 | *C. nervosum* | Middle Eocene | Clarno Fm. | Gosner Road, Jefferson County, Oregon, USA | 44°43.861′N 120°27.594′W | Bestland et al. (1999) |
| 18 | *C. nervosum* | Middle Eocene | Clarno Fm. | Red Gap, Jefferson County, Oregon, USA | 44°44.324′N 120°24.953′W | Bestland et al. (1999) |
| 19 | *C. nervosum* | Middle Eocene | Clarno Fm. | White Cliffs Sr., Jefferson County, Oregon, USA | 44°44.302′N 120°28.376′W | Bestland et al. (1999) |

**Table 1** continued

| Position on map | Species | Age | Formation name | Place name | Latitude/lontitude | References |
|---|---|---|---|---|---|---|
| 20 | *C. nervosum* | Middle Eocene | Clarno Fm. | John Day Gulch East, Wheeler County, Oregon, USA | 44°42.358′N 120°22.618′W | Bestland and Retallack (1994) |
| 21 | *C. lineatum* | Middle Eocene | Clarno Fm. | Clarno Nut Beds, Wheeler County, Oregon, USA | 44°55′23.60″N 120°25′53.84″W | Manchester (1994) |
| 22 | *C. nervosum* | Early Middle Eocene | Green River Fm., Laney Member | Little Mountain, Sweetwater County, Wyoming, USA | 41° 05.55′N 109°19.52′W | Wilf (2000) |
| 23 | *Cedrelospermum* sp. | Early Middle Eocene | Bridger Fm. | Blue Rim, Sweetwater County, Wyoming, USA | 41°47.920′N 109°35.019′W | Manchester and Zavada (1987) |
| 24 | *C. nervosum* | Early Eocene | Green River Fm., Fossil Butte Member | Lewis Ranch, Lincoln County, Wyoming, USA | 41°47′38.12″N 110°42′5.76″W | Grande (2013) |

morphology of these fossil fruits and compared them with the European and North American species. We also summarized fossil records of *Cedrelospermum* and discussed its historical biogeography incorporating with this Asian occurrence.

## Materials and methods

### Geologic setting

Fossil fruits were collected from Maguan County, southeastern Yunnan Province, southwestern China (23°1′N, 104°23′E, 1320 m a.s.l.) (Fig. 4). The Cenozoic sediments in Maguan are composed of the Paleogene Yanshan Group, Neogene Xiaolongtan Formation, and Quaternary deposits (Zhang 1976; Bureau of Geology and Mineral Resources of Yunnan Province 1996; Zhang et al. 2015). The basal Paleogene Yanshan Group is composed of coarse breccias and lacks fossils (Zhang 1976). Sitting unconformably on the Paleogene deposits, the Xiaolongtan Formation in Maguan is a fluvio-lacustrine deposit, composed of laminated sedimentary strata, and bears abundant plant and animal fossils (Zhang 1976; Zhang et al. 2015). The Quaternary deposit overlies unconformably on the Xiaolongtan Formation (Zhang 1976; Zhang et al. 2015).

The sediments bearing the present fossil fruits are characterized by cyclic deposits of light-yellow or light-grey pelitic laminated mudstone and siltstone (Fig. 5). They belong to the Xiaolongtan Formation according to stratigraphic correlations (Zhang 1976; Bureau of Geology and Mineral Resources of Yunnan Province 1996; Zheng et al. 1999). A detailed lithological facies of the outcrop have been described by Zhang (1976) and recently reconstructed by Zhang et al. (2015). The Xiaolongtan Formation was assigned to the late Miocene based on various evidence, such as stratigraphy (Bureau of Geology and Mineral Resources of Yunnan Province 1996), pollen analysis (Wang 1996), mammal fossils (Dong 2001), and floristic comparisons (Xia et al. 2009; Xing et al. 2013; Meng et al. 2014).

Besides fruits of *Cedrelospermum*, the sediments yielded abundant plant macrofossils of many other taxa such as *Sequoia* Endl. (Zhang et al. 2015), *Engelhardia* Lesch. ex Blume, *Craigia* W.W. Sm. & W.E. Evans, *Burretiodendron* Rehder (Lebreton-Anberrée et al. 2015, in press), *Ailanthus* Desf., *Ulmus* L., *Acer* L., *Koelreuteria* Laxm., *Bauhinia* L. and *Podocarpium* (A. Braun ex Braun) Herendeen, as well as animal fossils such as fishes and insects.

### Morphological study

A total of 98 fossil fruits of *Cedrelospermum* were collected. These specimens were photographed with a digital

**Table 2** Occurrences of *Cedrelospermum* fruits in Europe in approximate stratigraphic order respectively

| Position on map | Species | Age | Place name | Latitude/lontitude | References |
|---|---|---|---|---|---|
| 25 | *C. aquense* | Miocene | Radoboj, Croatia | 46°9′56.31″N 15°55′15.16″E | Unger (1861) |
| 26 | *Cedrelospermum* sp. | Miocene | Budapest, Hungary | 47°29′52.48″N 19°2′24.85″E | Hably and Thiébaut (2002) |
| 27 | *C. stiriacum* | Miocene | Magyaregregy, Hungary | 46°14′59.15″N 18°18′29.13″E | Hably and Thiébaut (2002); Kovar-Eder et al. (2004) |
| 28 | *C. stiriacum* | Miocene | Leoben, Austria | 47°22′35.00″N 15°5′28.07″E | Hably and Thiébaut (2002); Kovar-Eder et al. (2004) |
| 29 | *Cedrelospermum* sp. | Miocene | Parschlug, Styria, Austria | 47°28′N 15°17′E | Kovar-Eder et al. (2004) |
| 30 | *C. stiriacum* | Miocene | Schönegg, Austria | 47°14′39.28″N 15°22′10.81″E | Ettingshausen (1890); Kovar-Eder et al. (2004) |
| 31 | *C. stiriacum* | Miocene | Randecker Maar, Germany | 48°30′50.05″N 9°20′53.97″E | Rüffle (1963); Kovar-Eder et al. (2004) |
| 32 | *Cedrelospermum* sp. | Late Miocene | Gorj district, Romania | 41°31′N 33°37′E | Paraschiv (2008) |
| 33 | *Cedrelospermum* sp. | Late Miocene | Mehedinti district, Romania | 44°33′N 22°54′E | Paraschiv (2008) |
| 34 | *Cedrelospermum* sp. | Early Miocene | Kimi, Greece | 38°38′10.07″N 24°6′9.99″E | Unger (1867) |
| 35 | *Cedrelospermum* sp. | Early Miocene | Bohemia, Telč, Czech Republic | 49°12′47.85″N 15°19′40.15″E | Bůžek et al. (1996) |
| 36 | *C. aquense* | Oligocene | Aix, Bonnieux, Céreste, France | 43°51′18.04″N 3°35′35.73″E | Saporta (1889); Hably and Thiébaut (2002) |
| 37 | *C. aquense* | Oligocene | Eger-Kiseged, Hungary | 47°54′38.7″N 20°23′00.19″E | Hably and Thiébaut (2002) |
| 38 | *C. aquense* | Late Oligocene | Rott, Germany | 47°54′17.93″N 10°58′22.04″E | Weyland (1938) and Figs. 46, 47 in Manchester (1989) |
| 39 | *Cedrelospermum* sp. | Eocene | Jegenye, Leghia, Romania | 46°52′21″N 23°14′30″E | Andrèanszky and Mészáros (1959) |
| 40 | *C. leptospermum* | Late Eocene | Kučlín, North Bohemia | 50°32′N 13°46′E | Kvaček (2011) |
| 41 | *Cedrelospermum* sp. | Late Eocene | Telč, Czech Republik | 49°13′5.29″N 15°20′29.43″E | Knobloch (1969) |
| 42 | *C. leptospermum* | Late Eocene | Häring, Austria | 47°14′55.82″N 15°44′56.11″E | Ettingshausen (1853) and Fig. 45 in Manchester (1989) |
| 43 | *C. leptospermum* | Middle Eocene | Messel, near Darmstadt, Germany | 49° 55.029′N 8° 44.983′E | Wilde and Manchester (2003); Collinson et al. (2012) |

camera (Nikon D700, Kanagawa, Japan). Morphological details of some specimens were observed and photographed with a stereo microscope (Leica S8APO, Wetzlar, Germany). The morphometric study was conducted using Image J 1.47 (http://rsb.info.nih.gov.ig/). Fossil records of *Cedrelospermum* were compiled from published sources and plotted on map using ArcGIS 10.1 (ESRI, USA). The terminology for fruit morphology follows Manchester (1987, 1989) and Magallón-Puebla and Cevallos-Ferriz (1994).

## Results

### Systematics

Family: Ulmaceae Mirbel

Genus: *Cedrelospermum* Saporta

Species: *Cedrelospermum asiaticum* L.B. Jia, Y.J. Huang et Z.K. Zhou sp. nov.

Holotype: MG0002 (Fig. 6a) (designated here)

Paratypes: MG0001, MG0014 (Fig. 6b, c) (designated here)

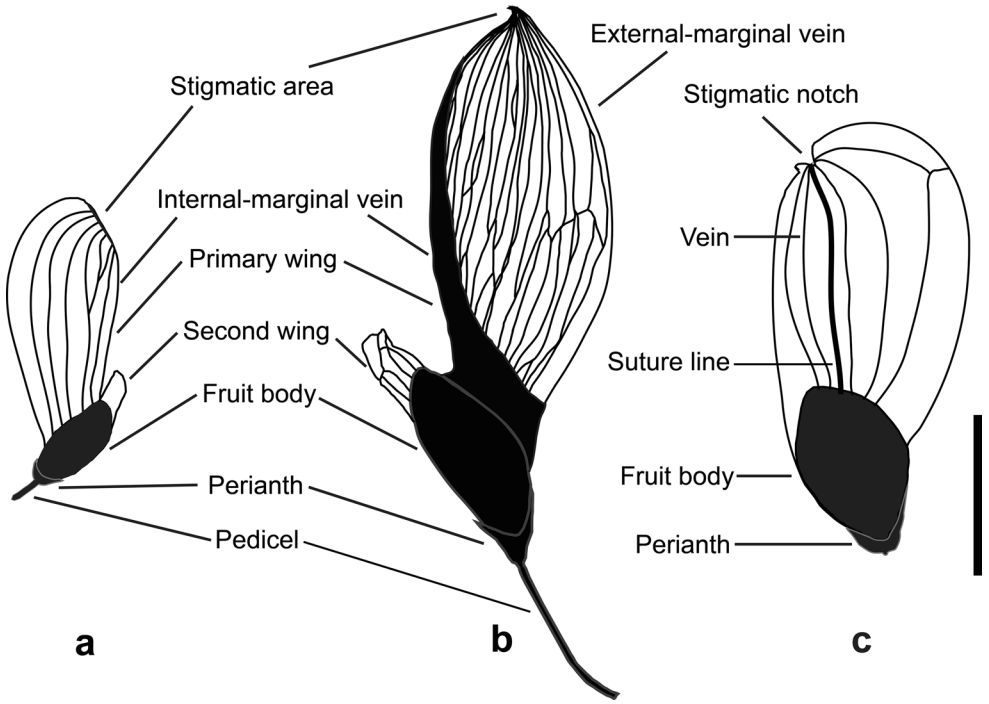



**Fig. 3** Morphology of *Cedrelospermum* fruits and corresponding terms. **a** Illustration of the general morphology of *Cedrelospermum* double-winged samaras from North America. The drawing of panel "**a**" is based on specimens from North America, i.e., UCMP 3665 (University of California Museum of Paleontology) and Fig. 24 in Manchester (1989). **b** Illustration of the general morphology of *Cedrelospermum* double-winged samaras from Asia. The drawing of panel "**b**" is based on a specimen from Asia, i.e., MG0002 (Kunming Institute of Botany). **c** Illustration of the general morphology of single-winged samaras from Europe and North America. The drawing of panel "**c**" is based on European specimen, i.e., V56922A (Natural History Museum, London) and North American specimens, i.e., Figs. 46, 47 in Manchester (1989). *Scale bar* 5 mm

Repository: All fossil specimens are stored at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Type locality: the upper Miocene Xiaolongtan Formation, Maguan County, southeastern Yunnan, China (23°1′N, 104°23′E).

Etymology: The specific epithet "*asiaticum*" means of Asia and refers to status of the species as the first fossil record of *Cedrelospermum* in Asia.

*Diagnosis*

Fruit samara, borne on pedicel, sometimes with persistent perianth. Fruit body ovate and adjoined by two lateral wings. One wing prominent with subparallel veins and a stigmatic area at the distal end; veins converging towards the stigmatic area. The other wing minute or sometimes vestigial, subtriangular, hooked, or rectangular. Fruit body surface reticulate.

*Description*

Samaras 12.1–22.1 mm long and 4.2–7.9 mm wide (Table 3), borne on pedicel (Figs. 6a–c, g, 7b–d), occasionally with persistent perianth (Figs. 6a, 7c–e, 8f), are formed by two unequally developed carpels (Figs. 3, 6). Proximal ends of the two carpels fuse to form a fruit body (Figs. 3, 6). The fruit body is prolate spheroidal to ovate-oblong in profile (Figs. 6, 7a–f), 4.4–6.3 mm long and 1.7–2.8 mm wide (Table 3). The surface of the fruit body reticulates with vascular bundles (Fig. 8e). These vascular bundles originate from the pedicel (Fig. 8e). The distal ends of the two carpels remain separate, each becoming a wing on the fruit body (Figs. 6, 7a–f). Primary wing is elongated, 7.9–15.2 mm long and 3.0–6.3 mm wide, with a stigmatic area on the wing apex (Figs. 6, 7a–f). External flank of the primary wing is cambered (Figs. 6, 7a–f). Internal flank of the primary wing is straight to slightly cambered, gradually increasing concavity near the apex of wing (Figs. 6, 7a–f). The primary wing is vascularized with 9–17 subparallel veins (Table 3). These veins connect with the vascular bundles on the fruit body and eventually converge toward the stigmatic area (Figs. 6, 7a–f, 8e). Secondary wing is minute, 0.7–2.6 mm long, subtriangular (Figs. 6b; 7a), hooked (Figs. 6c, d, f; 8d), sometimes rectangular (Fig. 8c) in profile. It is parallel to the long axis of the fruit body (Fig. 6a, b, e) or sometimes curves towards

**Table 3** Comparison of *Cedrelospermum* fruits

| | *C. nervosum* | *C. lineatum* | *C. manchesteri* | *C. leptospermum* | *C. aquense* | *C. stiriacum* | *C. asiaticum* |
|---|---|---|---|---|---|---|---|
| Number of wings | 2, occasionally 1 | 2 | 2 | 1 | 1 | 1 | 2 |
| Stigmatic configuration | Stigmatic area, occasionally stigmatic notch | Stigmatic area | Stigmatic area | Stigmatic notch | Stigmatic notch | Stigmatic notch | Stigmatic area |
| Primary apex shape | Usually wide and obtuse | Usually wide and obtuse | Usually wide and obtuse | – | – | – | Acute |
| Angle between primary wing and second wing | 16.3°–31.8° | 15.3°–22.8° | 9.4°–35.9° | – | – | – | 36.9°–85.2° |
| Fruit length (mm) | 4.4–11.0 | 9.0–14.5 | 13.0–16.0 | 9.0–11.0 | 6.5–14.0 | 14.0–23.0 | 12.1–22.1 |
| Fruit width (mm) | 1.9–4.0 | 2.2–5.5 | 3.8–7.8 | 4.0–5.0 | Unknown | 5.0–8.0 | 4.2–7.9 |
| Endocarp length (mm) | 1.5–4.0 | 3.2–5.0 | 4.0–7.0 | 2.5 | Unknown | Unknown | 4.4–6.3 |
| Endocarp width (mm) | 1.0–2.6 | 2.0–3.8 | 1.6–3.6 | 1.5–2.0 | Unknown | Unknown | 1.7–2.8 |
| Pedicel length (mm) | 0.5–1.2 | 2.0–3.0 | Unknown | 0 (sessile) | 0 (sessile) | Unknown | 4.6–5.1 |
| Continent | North America | North America | North America | Europe | Europe | Europe | Asia |
| Reference | Manchester (1989) | Manchester (1989) | Magallón-Puebla and Cevallos-Ferriz (1994) | Kvaček (2011) | Manchester (1989) | Kovar-Eder et al. (2004) | This study |

In some cases, the second wing in the double-winged fruits is too minute to measure the angle between the primary wing and second wing. Paraschiv (2008) reported two specimens of *Cedrelospermum* fruits with single wing from the Miocene of Romania with open nomenclature, namely *Cedrelospermum* sp. 1 (16.5 mm long and 6 mm wide) and *Cedrelospermum* sp. 2 (20 mm long and 6 mm wide)

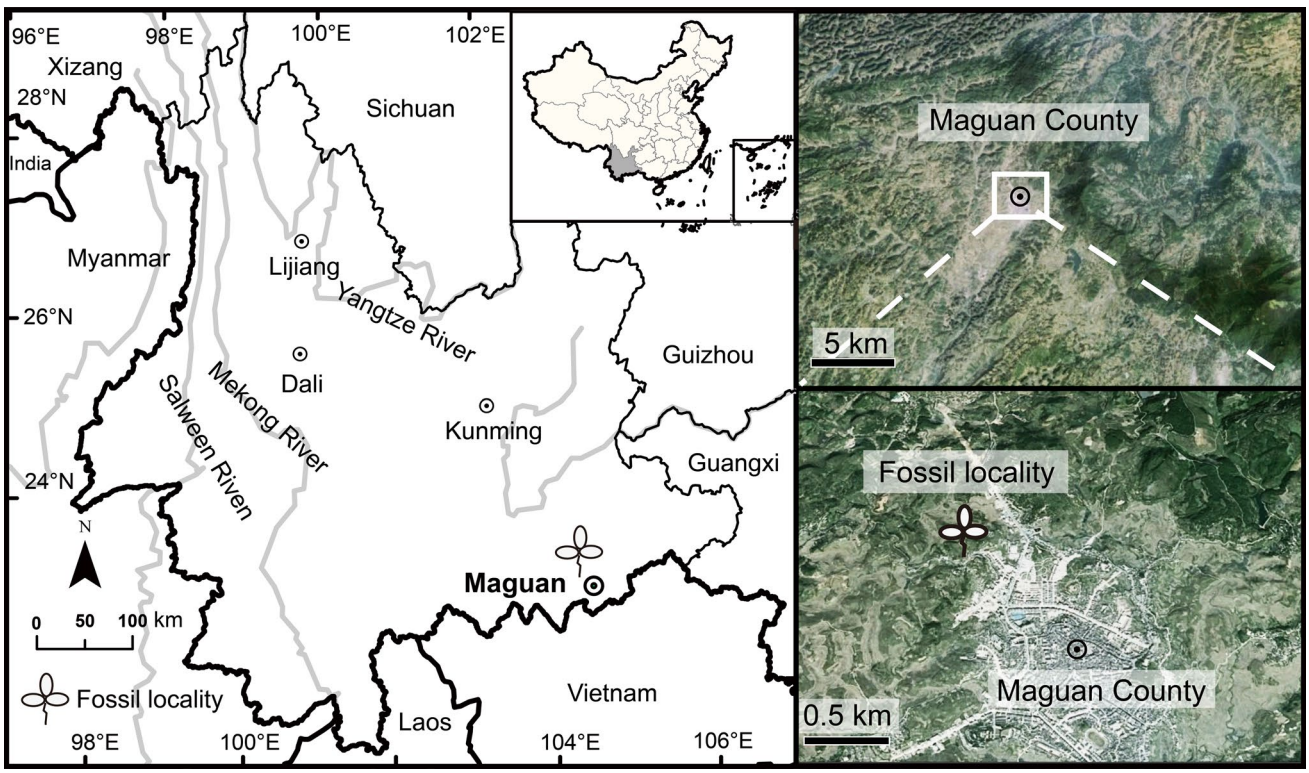



**Fig. 4** The fossil locality in Maguan County, southeastern Yunnan Province, China

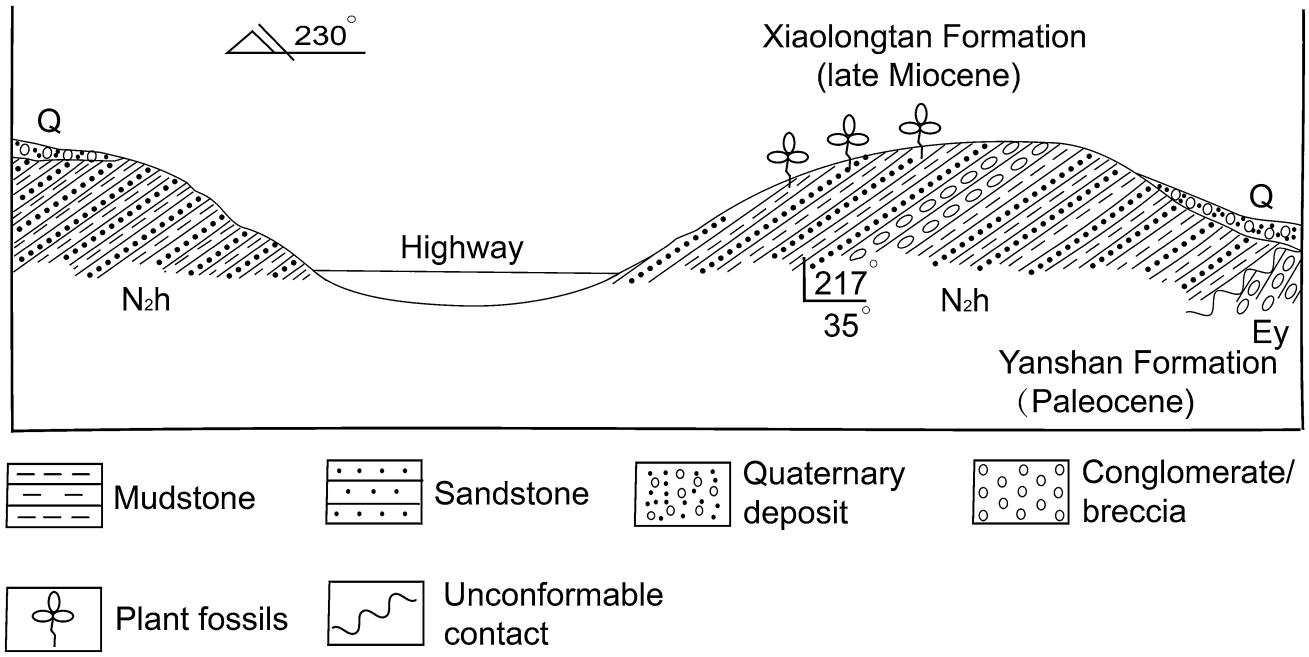



**Fig. 5** Cross section of fossil locality in Maguan County, southeastern Yunnan Province, China

the primary wing (Fig. 6d, h). Some vascular bundles on the fruit body extend into the second wing (Fig. 8e).

## Discussion

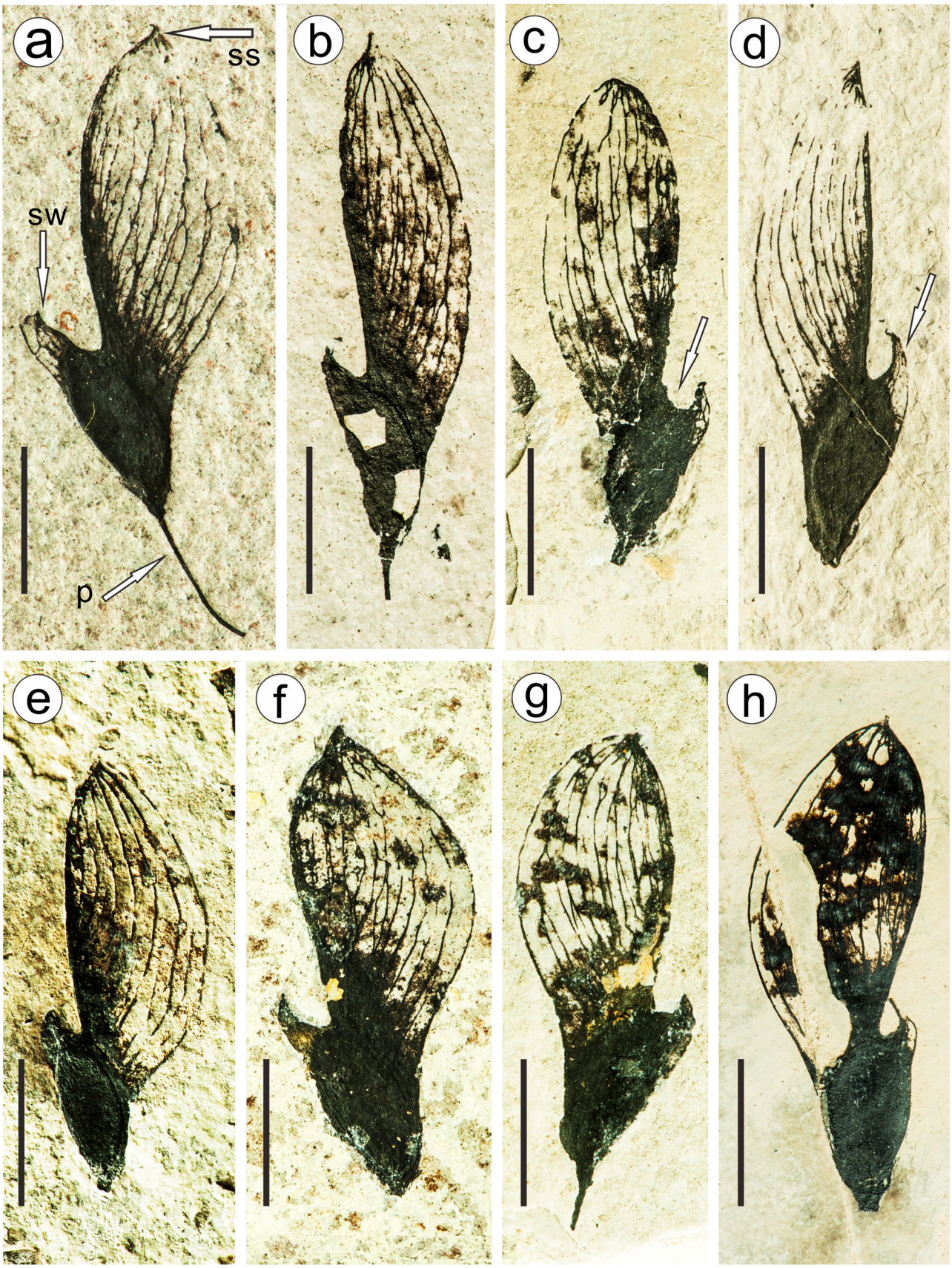
### Morphological comparison

Fossil fruits of *Cedrelospermum* were formerly assigned to various families, *e.g.* Proteaceae (Unger 1861), Sapindaceae (Weyland 1938), Aceraceae (Andrèanszky and Mészáros 1959) and Polygalaceae (MacGinitie 1974). The generic name, *Cedrelospermum*, was established for these distinctive disseminules by Saporta (1889), who considered them similar to seeds of *Cedrela* in the Meliaceae. In recent studies (Manchester 1987, 1989), the fruits were unambiguously transferred into the Ulmaceae based on well preserved twigs with attached leaves, fruits and flowers with in situ pollen (Manchester 1989). Our fossil fruits can be unequivocally assigned to *Cedrelospermum* by having the following diagnostic characters: (1) an ovate fruit body adjoined by two separated wings, a large primary wing and a diminutive secondary wing; (2) a stigmatic area at the distal end of the primary wing; and (3) veins on the primary wing converging toward the stigmatic area (Figs. 3, 6, 8).

*Cedrelospermum asiaticum* fruits have two wings and a distal stigmatic area on the larger wing and thus should be assigned to the double-winged form (Figs. 6, 8). They are similar to those of the North American double-winged species, *C. nervosum, C. lineatum* and *C. manchesteri* in

**Fig. 6** Samaras of *Cedrelospermum asiaticum* sp. nov. **a** General view of samara showing a long pedicel (*p*), rectangular second wing (*sw*), dichotomous venation and stigmatic surface (*ss*). MG0002 (Holotype). **b** Specimen showing a long and narrow fruit with veins on the primary wing converging toward the stigmatic surface. MG0001 (paratype). **c** Specimen showing a clear constriction at the joint between the fruit body and primary wing. MG0298. **d** Specimen showing a pointed primary wing and a hooked secondary wing. MG0304. **e** Specimen showing an ovate fruit body. MG0014 (paratype). **f** Specimen showing a broad primary wing. MG0292. **g** Specimen showing the general view of the fruit. MG0299. **h** Specimen showing that the *long axis* of the fruit body and primary wing are nearly parallel. MG0301. *Scale bars* 5 mm

morphology (Fig. 7). Despite sharing basic fruit architecture, *C. asiaticum* fruits are distinguishable from these North American double-winged fruits in the following ways: (1) *Cedrelospermum asiaticum* fruits differ from those of *C. nervosum* and *C. lineatum* by having a larger angle between the primary wing and secondary wing. The range of angles between the primary wing and second wing in *C. asiaticum* fruits are 36.9°–85.2°, while they are 9.4°–35.9° in *C. nervosum*, *C. lineatum*, and *C. manchesteri* (Table 3). (2) *Cedrelospermum asiaticum* fruits are distinguishable from *C. nervosum*, *C. lineatum* and *C. manchesteri* fruits by having more veins on the primary wing. The number of veins on the primary wings of *C. asiaticum* is 9–17, while it is 5–8 in *C. nervosum*, *C. lineatum*, and *C. manchesteri* (Table 3). Besides, veins on the primary wing of *C. asiaticum* are more dichotomous than those of *C. nervosum*, *C. lineatum*, and *C. manchesteri* fruits (Figs. 3, 7). (3) *Cedrelospermum asiaticum* fruits bearing an acute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primary wing apex are different from *C. nervosum*, *C. lineatum*, and *C. manchesteri* fruits with a wide and obtuse primary wing apex (Figs. 3, 7). Finally, *C. asiaticum* fruits differ from *C. nervosum*, *C. lineatum*, and *C. manchesteri* fruits by having a larger size although the range of fruit size overlaps among these four species (Table 3).

Therefore, our fossil fruits cannot be assigned to any of the North American species. They differ more obviously from the European species of *Cedrelospermum* which have only one wing and a distal stigmatic notch. We thus designate these fossil fruits to a new species, *C. asiaticum*.

## Biogeographic implication

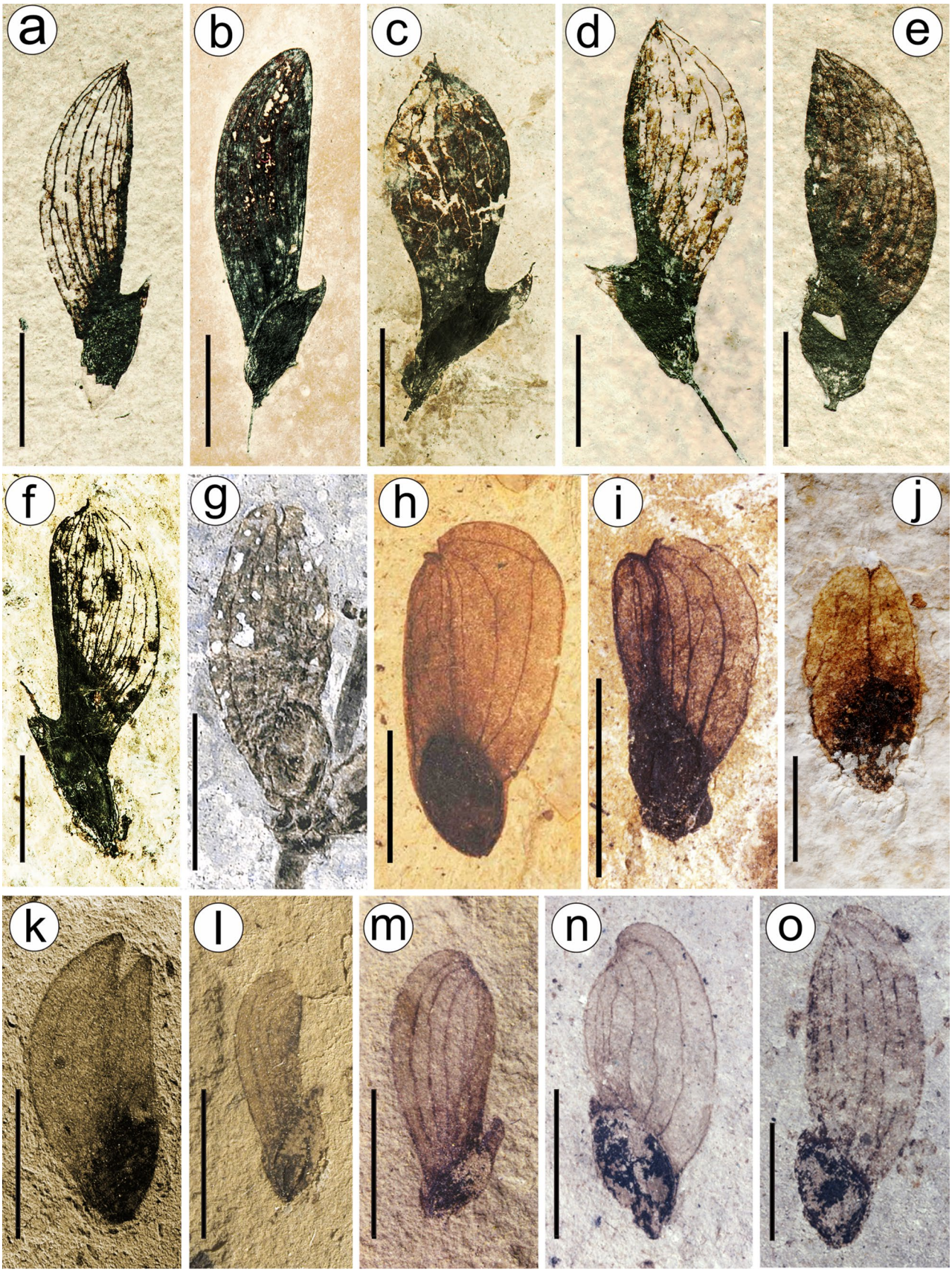
With the present fossil record considered, the distribution of *Cedrelospermum* includes three regions in the Northern Hemisphere: Europe, North America, and Asia. The earliest fossils of *Cedrelospermum* were found from the Early Eocene of North America, probably suggesting a North American origin of the genus (Tables 1, 2). The single-winged form of *Cedrelospermum* was predominant in the early Middle Eocene, while by the late Middle Eocene, the double-winged form became predominant with the single-winged form being only occasionally found (Manchester and Tiffney, 2001) (Fig. 9). Later in the Late Eocene and Oligocene, only the double-winged form was observed in North America (Manchester and Tiffney 2001) (Fig. 9). This scenario suggests that the single-winged form might be ancestral and later the double-winged form appeared and prevailed, as proposed by Magallón-Puebla and Cevallos-Ferriz (1994).

*Cedrelospermum* subsequently colonized Europe and Asia (Figs. 2, 9). Between Europe and North America, a dispersal of *Cedrelospermum* across the North Atlantic land bridge was previously proposed by Manchester (1987) (Fig. 9). This hypothesis is consistent with the presence of the single-winged form of this genus in both the European and North American Eocene and the absence of the single-winged form in Asia. Moreover, the absence of the double-winged form in Europe may indicate that the dispersal of *Cedrelospermum* between North America and Europe might have occurred in the Early Eocene before the emergence of the double-winged form. At that time, the North Atlantic land bridge was available for the floristic exchanges between the two continents (Tiffney and Manchester 2001). After that, a vicariance should have occurred between North America and Europe as the North Atlantic land bridge became increasingly uncertain after the early Eocene (Tiffney 1985; Hably et al. 2000; Tiffney and Manchester 2001; Denk et al. 2010, 2011) (Fig. 9). This probably resulted in a biogeographic separation of the European and North American lineages. The European lineage remained the single-winged form in its course, while the double-winged form appeared and replaced the single-winged form in North America (Fig. 9).

The presence of double-winged form of samara in both Asia and North America and its absence in Europe, suggests that *Cedrelospermum* might have spread directly from North America to Asia via the Bering land bridge (Fig. 9). The Bering land bridge physically connected Asia and North America and allowed for migration of terrestrial organisms at least from the early Paleogene to Late Miocene (Marincovich and Gladenkov 1999; Tiffney and Manchester 2001; Ickert-Bond et al. 2009). Being a deciduous taxon (Manchester 1989), *Cedrelospermum* in all likelihood could have crossed the Bering land bridge. The absence of the single-winged form of *Cedrelospermum* in Asia indicates that the transpacific floristic exchange possibly occurred after the disappearance of the single-winged form in North America.

Fossils of *Cedrelospermum* were common from the Eocene of the middle latitudes in North America, while in the Oligocene they were found only in northwestern Gulf of Mexico and northwestern United States (Fig. 2). This suggests an overall southward retreat of the genus distribution in this continent from the Eocene to Oligocene, probably in response to the global cooling initiated during in the Eocene–Oligocene transition (Tiffney 1985; Graham 1999; Xiang and Soltis 2001; Zachos et al. 2008) (Fig. 2). Similar to the situation in North America, the genus also underwent an overall southward retreat from the Eocene to Oligocene in Europe, and even reached more southern latitudes in the

**Fig. 7** *Cedrelospermum* fruits from Asia, Europe and North America for comparison. **a–f** Asian fruits, *Cedrelospermum asiaticum* sp. nov. They have a primary and a secondary wing, with a stigmatic surface at the apex of the primary wing (double-winged type). **a** MG0294 l; **b** MG0300; **c** MG0297; **d** MG0293; **e** MG0295; **f** MG0296. **g–i** European fruits for comparison. They have a single wing and a distal stigmatic notch (single-winged form). **g** Fruit of *C. leptospermum* sessile on a twig from the middle Eocene Messel, Germany (stored at Senckenberg Museum, Germany, complete specimen figured in Collinson et al. (2012), plate 41, fig. c, f). **h** Fruit of *C. aquense* from late Oligocene of Rott, Germany, showing the typical single wing with a distal stigmatic notch. V56922A (Natural History Museum, London). **i** Fruit of *C. aquense* from late Oligocene of Rott, Germany (University of Bonn, Bonn, Germany). **j–o** North American fruits. They vary from single-winged type to double-winged type. **j** Fruit of *C. nervosum* with a single wing and prominent distal stigmatic notch, from the Fossil Butte Member of the Green River Formation, the early Eocene. UMNH-PB157 (Utah Museum of Natural History, USA). **k** Fruit of *C. nervosum* from the White Cliffs locality, the middle Eocene Clarno Formation, Oregon, USA. UF 262–17883. **l** Fruit of *C. nervosum* with two wings present. The middle Eocene Clarno Formation Gosner Road locality, Oregon, USA. UF 238–5472. **m** Fruit of *C. lineatum* showing the obtuse primary wing from the middle Eocene Green River Formation of Uintah County, Utah, USA. lU15751–5294. **n** Fruit of *C. lineatum* from the late Eocene of Florissant, Colorado, USA. UCMP3665 (University of California Museum of Paleontology, USA). **o** Larger fruit of *C. lineatum* from the late Eocene Florissant flora, Colorado, USA. UCMP3667. *Scale bars* 5 mm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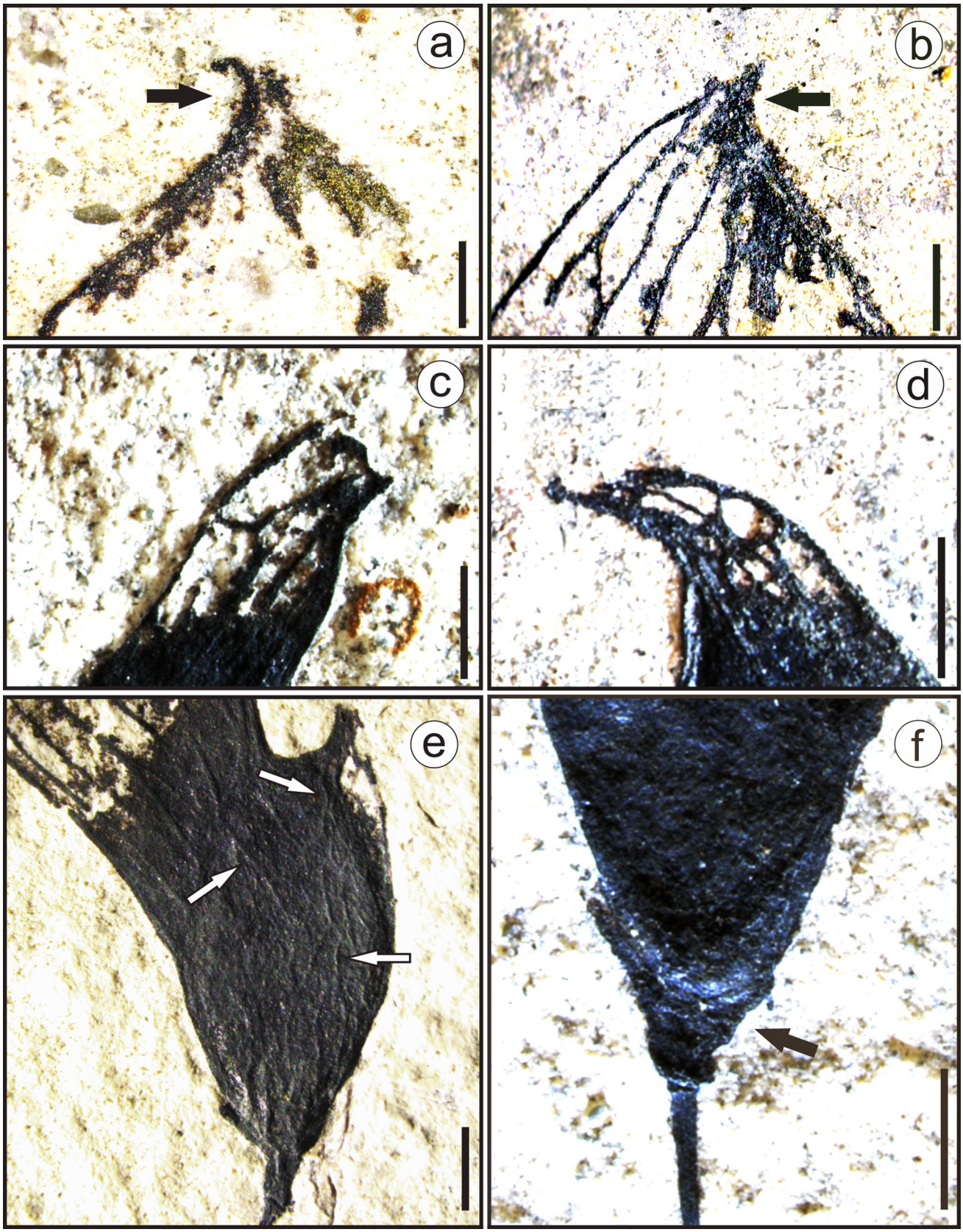
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◀ **Fig. 8** Details of *Cedrelospermum asiaticum* sp. nov. samaras. **a** Magnification of the primary wing showing the curved stigmatic area. MG0002. *Scale bar* 500 μm. **b** The distal end of primary wing showing veins converging toward the stigmatic area. MG0014. *Scale bar* 500 μm. **c** Rectangular secondary wing with clear veins. MG0002. *Scale bar* 500 μm. **d** Hooked secondary wing. MG0014. *Scale bar* 500 μm. **e** Reticulation on the surface of the fruit body. MG0424. *Scale bar* 1 mm. **f** Magnification of receptacle and perianth. MG0002. *Scale bar* 1 mm

Miocene (Fig. 2). The late Miocene Asia occurrence of *Cedrelospermum* is among the southernmost fossil records of the genus (Fig. 2). This is in agreement with the inferred historical southward retreat of *Cedrelospermum* in the North Hemisphere.

### Possible causes of the disappearance of *Cedrelospermum*

*Cedrelospermum* disappeared from North America after the Oligocene and from Europe and Asia after the Miocene. In North America, the genus was confined to the northwestern Gulf of Mexico and northwestern United States in the Oligocene (Fig. 2). Extinction of the genus in North America might be related to the cooling initiated during the Eocene–Oligocene transition and drying due to the uplift of Rocky Mountains (Manchester 1987; Graham 1993; Retallack et al. 2004; Mix et al. 2011; Fan et al. 2014). In Europe, the genus remained prevalent during the Miocene, despite its apparent southward retreat following the Eocene (Fig. 2). The disappearance of *Cedrelospermum* from Europe might be related to the cooling in the late Neogene (Manchester 1987).

The Maguan fossil flora also yielded fossil remains of several other plant taxa, including *Sequoia* (Zhang et al. 2015), *Engelhardia*, *Craigia*, *Burretiodendron*, *Bauhinia*, *Ailanthus*, *Ulmus*, *Acer* and *Koelreuteria*. The co-occurrence of these taxa suggests warm and wet climatic conditions in Maguan, southeastern Yunnan, during the late Miocene. This is in line with the results of palaeoclimatic reconstruction of the Xiaolongtan flora, a contemporary flora nearby (Xia et al. 2009). After the late Miocene, drastic environmental changes took place in Yunnan, such as the southeastern extrusion of the Tibetan Plateau (Jacques et al. 2014 and references therein), intensification of the East Asian monsoon (An et al. 2001; Su et al. 2013a; Tang et al. 2015), along with the overall global cooling (Zachos et al. 2008). Among these factors, the

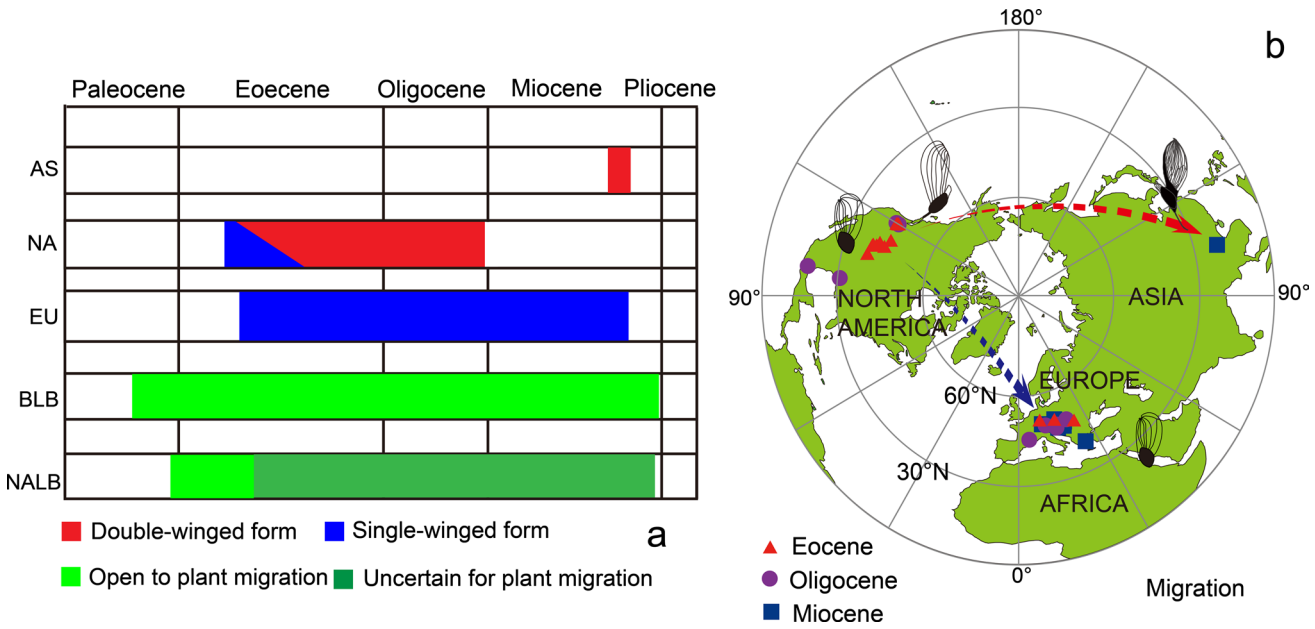


**Fig. 9** Hypothesized migration of *Cedrelospermum* between Asia, Europe and North America. **a** Occurrences of the two types of *Cedrelospermum* fruits in Asia (*AS*), Europe (*EU*) and North America (*NA*) (Manchester and Tiffney 2001) and the availiablity of the Bering land bridge (*BLB*) and the North Atlantic land bridge (*NALB*) in the Paleogene and Neogene The BLB physically connected Asia and North America and allowed for plant dispersal at least from the early Paleogene to 5.5–4.8 Ma (Tiffney and Manchester 2001; Marincovich and Gladenkov 2001; Ickert-Bond et al. 2009). Geological, paleozoological, and botanical data supported that the NALB was emergent and open to land migration from the late Paleocene to early Eocece (Tiffney 1985; Marincovich et al. 1990; Tiffney 2000; Tiffney and Manchester 2001). For the timing of subsidence of different part of NALB, geological studies have arrived at different dates including Early Eocene (Marincovich et al. 1990), the early Oligocene (Davies et al. 2001; Poore 2008), prior to the Middle Miocene (Ramsay et al. 1998). However, recent paleobotanical and phylogenetic studies suggest that the NALB may have served as a effective corridor (possible island hopping) until the latest Miocene (Hably et al. 2000; Tiffney2008; Denk et al. 2010, 2011). **b** Hypothesized migration routes

intensification of the East Asian monsoon amplified the seasonality of precipitation, resulting in the decrease of winter and spring precipitations (Su et al. 2013a; Tang et al. 2015). The associated winter and spring drying has been interpreted to be responsible for the extinction of some other plant taxa, e.g. *Cedrus* (Su et al. 2013b) and *Sequoia* (Zhang et al. 2015) by hindering their seed germination. *Cedrelospermum* may have also experienced the same fate.

**Acknowledgments** The authors thank Dr. Hongshan Wang for compiling the North American fossil records; Dr. Shitao Zhang for study on geological horizon; Dr. Frédéric M.B. Jacques for improving the figures; Dr. Jianwei Zhang, Shufeng Li, He Xu and Honghu Meng for technical assistance with software; Julie Lebreton-Anberrée for giving comments on the geological setting and polishing the manuscript; Dr. Sergio R.S. Cevallos-Ferriz for providing the isotope dating age for the flora of the Pié de Vaca Formation, Puebla, Mexico; Dr. Arata Momohara and Dr. Sergei Vikulin for providing references; members of the Paleoecology Research Group in Kunming institute of Botany, CAS for help with field work; the two anonymous reviewers for improving the manuscript. This work was supported by the National Natural Science Foundation of China (No. 41372035) and the National Key Basic Research Project ("973" Project, No. 2012CB821900). This work is a contribution to NECLIME (Neogene Climate Evolution in Eurasia).

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