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Research Article

# First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai–Tibetan Plateau: Implications for morphological evolution and biogeography

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**Abstract** *Cedrelospermum* Saporta is an extinct genus in the Ulmaceae with abundant fossil records in North America and Europe. However, so far, fossil records of this genus from Asia are sparse, which limits the interpretations of the morphological evolution and biogeographical history of the genus. Here we report well-preserved fruits (*Cedrelospermum tibeticum* sp. nov.) and a leaf (*Cedrelospermum* sp.) of *Cedrelospermum* from the upper Oligocene Lunpola and Nyima basins in the Qinghai–Tibetan Plateau (QTP). This is the first fossil record of *Cedrelospermum* in the QTP, showing that this genus grew in this region during the late Oligocene. *Cedrelospermum tibeticum* fruits are double-winged, morphologically similar to the Eocene and Oligocene double-winged *Cedrelospermum* species from North America. This supports the hypothesis that *Cedrelospermum* migrated to Asia from North America by way of the Bering Land Bridge. Given that *Cedrelospermum* was a typical element of Northern Hemispheric flora in the Paleogene and Neogene, the presence of this genus indicates that the central region of the QTP was phytogeographically linked with other parts of the Northern Hemisphere during the late Oligocene. The morphological observations of *C. tibeticum* fruits and other double-winged *Cedrelospermum* fruits suggest an evolutionary trend from obtuse to acute apex for the primary wing. *Cedrelospermum tibeticum* likely had warm and wet climatic requirements. This type of an environment possibly existed in the central QTP in the late Oligocene, thereby supporting the survival of *C. tibeticum*.

**Key words:** extinct plants, paleobotany, phytogeography, Tibet.

## 1 Introduction

The morphological evolution and biogeographical history of plants can be understood mainly by three lines of evidence: genetic material, morphology, and fossils (Manchester, 1999; Hunt & Slater, 2016; Grímsson et al., 2017). However, for the case of extinct taxa, fossils are the only evidence. *Cedrelospermum* Saporta is an extinct genus in the elm family (Ulmaceae), morphologically the closest to the extant genera *Phyllostylon* Capan. ex Benth. & Hook. f. and *Hemiptelea* Planch. (Manchester, 1987, 1989; Manchester & Tiffney, 2001). Fossil fruits and leaves of *Cedrelospermum* have been extensively reported from the early Eocene to the early Oligocene of North America (Manchester, 1987, 1989; Magallón-Puebla & Cevallos-Ferriz, 1994) and the middle Eocene to the middle Miocene of Europe (Hably & Thiébaut, 2002; Wilde & Manchester, 2003; Kovar-Eder et al., 2004; Paraschiv & Sebe, 2007, Paraschiv, 2008; Kvaček & Teodoridis, 2011). However, so far, its fossil records in Asia are sparse with only one occurrence from the Miocene of southwestern China (Jia et al., 2015; Huang et al., 2016) (Fig. 1). This hampers a satisfactory elucidation of the morphological evolution and biogeographic history of the genus.

The fruit of *Cedrelospermum* is very distinctive and characterized by an ovate fruit body laterally adjoined by one or two wing(s) (Manchester, 1987, 1989). According to the number of wings, *Cedrelospermum* fruits have been divided into two types, single and double-winged (Manchester & Tiffney, 2001). The single-winged type has a single wing and a stigmatic notch, whereas the double-winged type has one large wing with a stigmatic surface on one side, and a much smaller wing in the same plane (Manchester & Tiffney, 2001). Geographically, only the single-winged type has been

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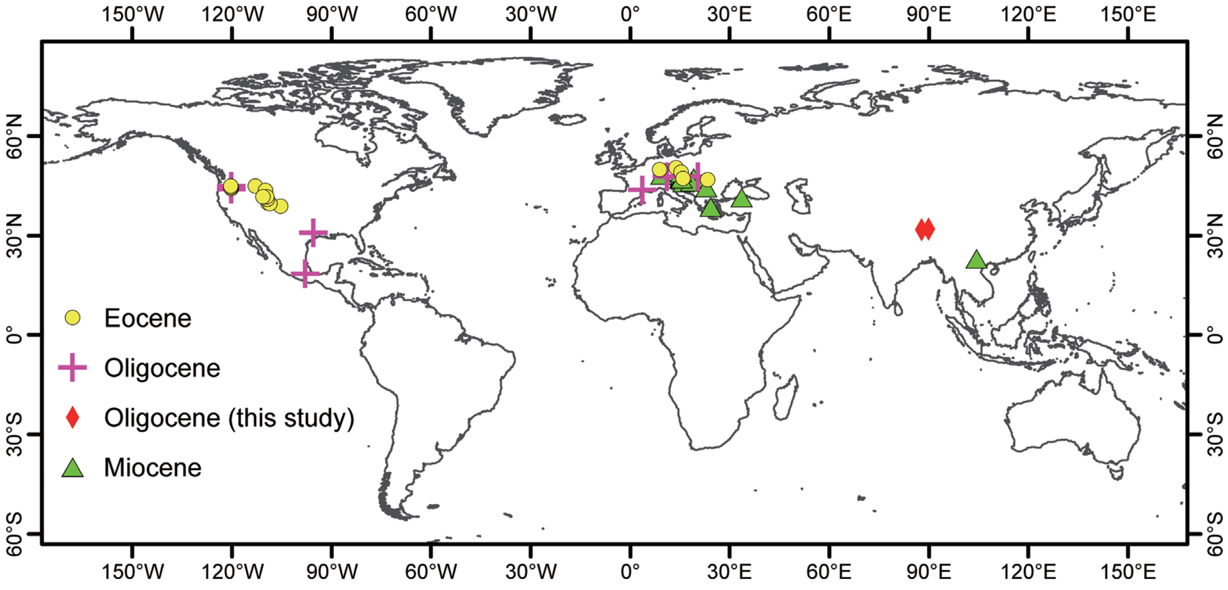

**Fig. 1.** Map showing the fossil records of *Cedrelospermum*. The base map was downloaded from the website of DIVA-GIS (http://www.diva-gis.org/).

found in Europe and only the double-winged type has been found in Asia, whereas both types have been found co-occurring at sites in western North America (Manchester & Tiffney, 2001; Jia et al., 2015). Because of their distinctive features and abundant fossil records, *Cedrelospermum* fruit fossils provide important evidence for understanding the morphological evolution and biogeographic history of the genus.

Morphologically, two evolutionary patterns of *Cedrelospermum* fruits have been observed (Manchester & Tiffney, 2001). First, the size of *Cedrelospermum* fruits increased gradually from the early Eocene to the Miocene (Manchester & Tiffney, 2001). Second, the earliest fossil record of *Cedrelospermum* was exclusively of the single-winged type from North America (Grande, 2013), and subsequently, in the early Middle Eocene, the double-winged type appeared, although they were only occasionally found (Manchester & Tiffney, 2001). In the late middle Eocene, the double-winged type became predominant and by the late Eocene and early Oligocene, only the double-winged type has been observed (Manchester & Tiffney, 2001). This scenario indicated that the single-winged fruit was the ancestral type, and the double-winged type evolved later (Magallón-Puebla & Cevallos-Ferriz, 1994; Manchester & Tiffney, 2001; Jia et al., 2015).

Biogeographically, *Cedrelospermum* was suggested to have originated in North America where the earliest fossil record of the genus was uncovered (Jia et al., 2015). Because the single-winged type was only found in North America and Europe, this type was suggested to have migrated from North America to Europe by the North Atlantic Land Bridge (Manchester, 1987). Later the double-winged type originated in North America (Jia et al., 2015). As all *Cedrelospermum* fruits from Asia are double-winged, this type was inferred to have migrated to Asia by way of the Bering Land Bridge (Jia et al., 2015).

However, above observations or hypotheses are more or less based on the premise that the morphology of *Cedrelospermum* fruits in the Northern Hemisphere was well understood. Unfortunately, the morphology of *Cedrelospermum* fruits in Asia is still less well recognized due to the relatively few available fossil records to date.

Recently, well-preserved fruits and a leaf of *Cedrelospermum* were uncovered from the upper Oligocene of Lunpola and Nyima basins, central Qinghai–Tibetan Plateau (QTP), China. This is the first *Cedrelospermum* fossil record from the QTP and the earliest *Cedrelospermum* fossil record known from Asia. In this study, we characterized the morphology of these fossil fruits and leaf and compared them with other *Cedrelospermum* species. Incorporating with previous fossil records, we discussed the significance of the new fossil findings for the morphological evolution and biogeographical history of the genus.

## 2 Material and Methods

### 2.1 Geological setting

Fruit and leaf fossils were collected from the Lunpola basin and Nyima basin in the central QTP (Fig. 2). Abundant fish fossils, that is, climbing perch fossils, *Eoanabas thibetana*, were reported from the same layers in the Lunpola and Nyima basins (Wu et al., 2017).

The Cenozoic sediments in the Lunpola basin are segregated into two stratigraphic units, the Niubao Formation in the lower part of the sequence and the Dingqing Formation in the upper part of the sequence (Deng et al., 2012; He et al., 2012). The Niubao Formation is approximately 3000 m thick and is characterized by reddish clastic deposits mainly consisting of mudstone, sandstone, and gravel, mostly representing a fluvial to marginal lacustrine environment (He et al., 2012). This formation bears relatively fewer fossils, and plant megafossils have not yet been reported from this formation (Deng et al., 2012). The Dingqing Formation is approximately 1000 m thick and represents lacustrine deposits composed of fine-grained gray mudstone, fine siltstone,

**Fig. 2.** Map showing the position of the two localities where the fossils were collected from the Qinghai–Tibetan Plateau, China. The base map was downloaded from the website of DIVA-GIS (http://www.diva-gis.org/).

and limestone (Deng et al., 2012). It bears abundant plant fossils, and animal fossils such as insects and fishes (Deng et al., 2012). The age of the Dingqing Formation is late Oligocene to early Miocene based on mammalian fossils (Deng et al., 2012) and SIMS U–Pb zircon dating (He et al., 2012; Sun et al., 2014). The layers yielding the fossil materials in this study are characterized by grayish green and red mudstones, which are interbedded with limestone and shale belonging to the lower part of the Dingqing Formation according to stratigraphic correlations. Therefore, the age of the layers bearing fossil materials of this study is probably the late Oligocene, as also suggested by Wu et al. (2017).

The Nyima basin is a Cenozoic east–west trending rift basin resting on a Jurassic–Cretaceous marine succession, which contains deformed flysch and mélange (DeCelles et al., 2007). The Cenozoic lithological unit in the Nyima basin includes fossiliferous strata of the Nyima Redbed unit (DeCelles et al., 2007). The layer where our fossil fruits were collected consists of sheet-like calcareous shale interbedded with mudstone, sandstone, and limestone. It belongs to the Nyima Redbed unit based on stratigraphic correlations. The Nyima Redbed unit yielded a biotite $Ar^{40}/Ar^{39}$ age of 26–23.5 Ma (DeCelles et al., 2007; Kapp et al., 2007), indicating an age of the Late Oligocene. Detailed geological background and lithological facies of the two localities were elaborated in detail by Wu et al. (2017).

### 2.2 Morphological study

A total of nine fossil fruits and one fossil leaf of *Cedrelospermum* were collected from the Lunpola basin, and one fossil fruit was collected from the Nyima basin. These specimens were photographed using a Nikon D700 digital camera (Nikon, Kanagawa, Japan). Morphological details of some specimens were further observed and photographed under a stereomicroscope (S8APO; Leica, Wetzlar, Germany). Measurements were taken using ImageJ 1.47 (http://rsb.info.nih.gov.ig/). The fossil record of *Cedrelospermum* was compiled from published sources and plotted on a map by using ArcGIS 10.2 (ESRI, Redlands, CA, USA). The terminology for fruit and leaf morphology follows Manchester (1987, 1989) and Ellis et al. (2009), respectively.

## 3 Systematics

**Family** Ulmaceae Mirbel

**Genus** *Cedrelospermum* Saporta

**Fruits**

***Cedrelospermum tibeticum*** **L. B. Jia, T. Su & Z. K. Zhou sp. nov.**

**Specific diagnosis** Samara 15.2–20.2 mm long and 4.7–8.1 mm wide (Fig. 3). Fruit body ovate, laterally adjoined by two wings (Fig. 3). One wing prominent, vascularized with 8–13 subparallel veins, possessing a stigmatic area at the distal end (Figs. 3, 4A, 4B); veins converging towards the stigmatic area (Figs. 3, 4A, 4B), or occasionally minority veins dichotomizing near the apex of the primary wing and converging with the external-marginal vein of the primary wing (Fig. 3D). The other wing minute, sometimes vestigial (Fig. 3C), subtriangular (Figs. 4C, 4D), or falcate (Fig. 4E) in shape, occasionally with venation (Fig. 4C).

**Holotype** KUNPC-XZDY2-101B (Fig. 3A)

**Paratypes** KUNPC-XZDY2-0105 (Fig. 3D), KUNPC-XZDY2-0107 (Fig. 3E)

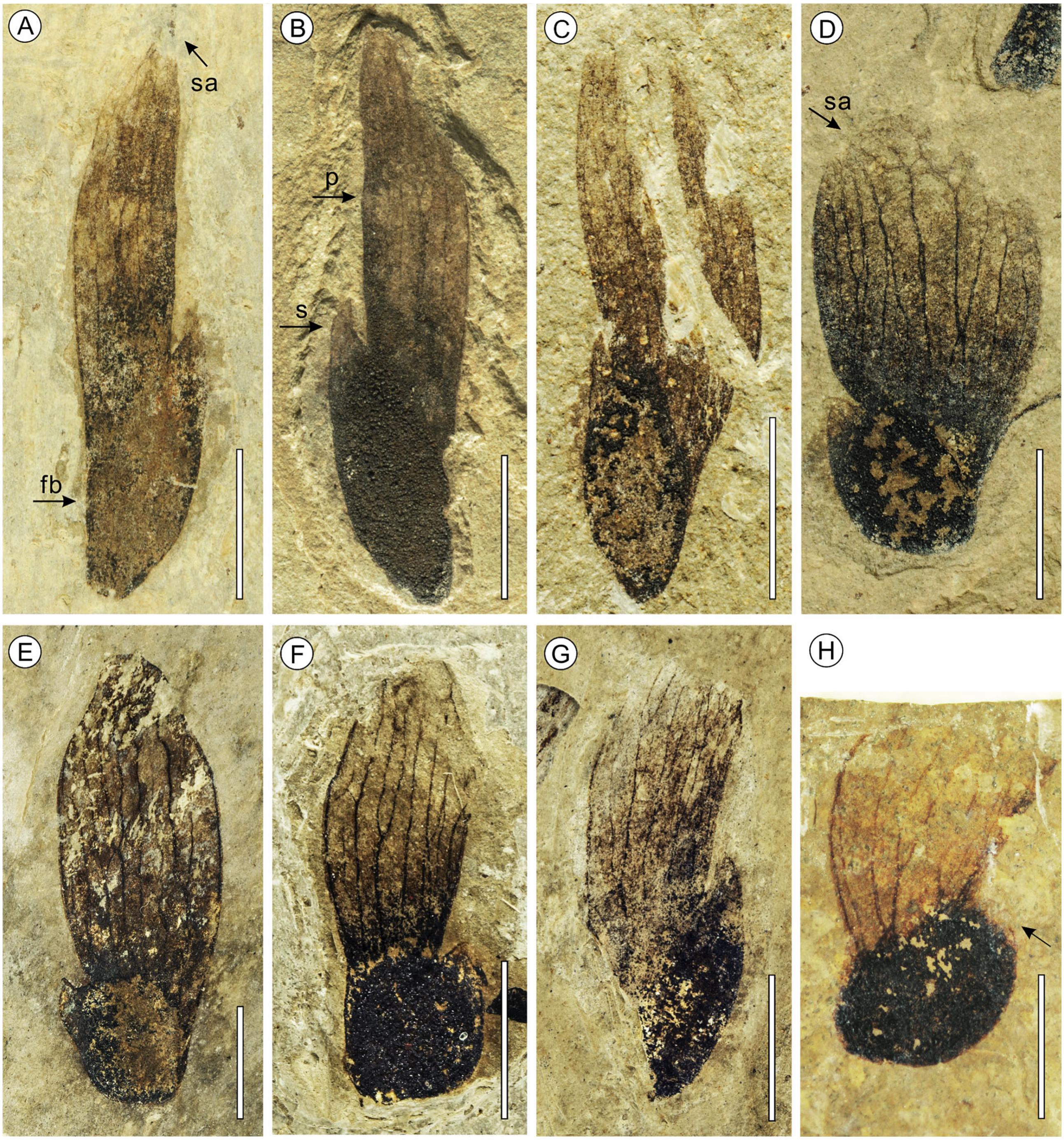

**Fig. 3.** Fossil fruits of *Cedrelospermum tibeticum* sp. nov. **A**–**G,** *Cedrelospermum* fruits from Lunpola basin. **H,** *Cedrelospermum* fruits from Nyima basin. **A,** Fruit showing ovate fruit body (fb), small angle between the primary wing and secondary wing, and acute apex of the primary wing, KUNPC-XZDY2-0101B (Holotype). sa, stigmatic area. **B,** Fruit showing hooked secondary wing (s), XZDY2-0101A (counterpart of image A). p, primary wing. **C,** Fruit showing minute secondary wing, and the small angle between the primary wing and secondary wing, XZDY2-0102. **D,** Fruit showing triangular secondary wing, obtuse apex of the primary wing, and the stigmatic area situated at the side of the primary wing near the secondary wing, KUNPC-XZDY2-0105 (Paratype). **E,** Fruit showing obtuse apex of the primary wing, KUNPC-XZDY2-0107 (Paratype). **F,** Fruit showing round fruit body and dichotomous veins, XZDY2-0103. **G,** Fruit showing elliptical fruit body and hooked secondary wing, XZDY2-0112. **H,** Fruit showing oval fruit body and faint impression of secondary wing (arrow), KUN-XZNM3-0001A. Scale bar = 5 mm.

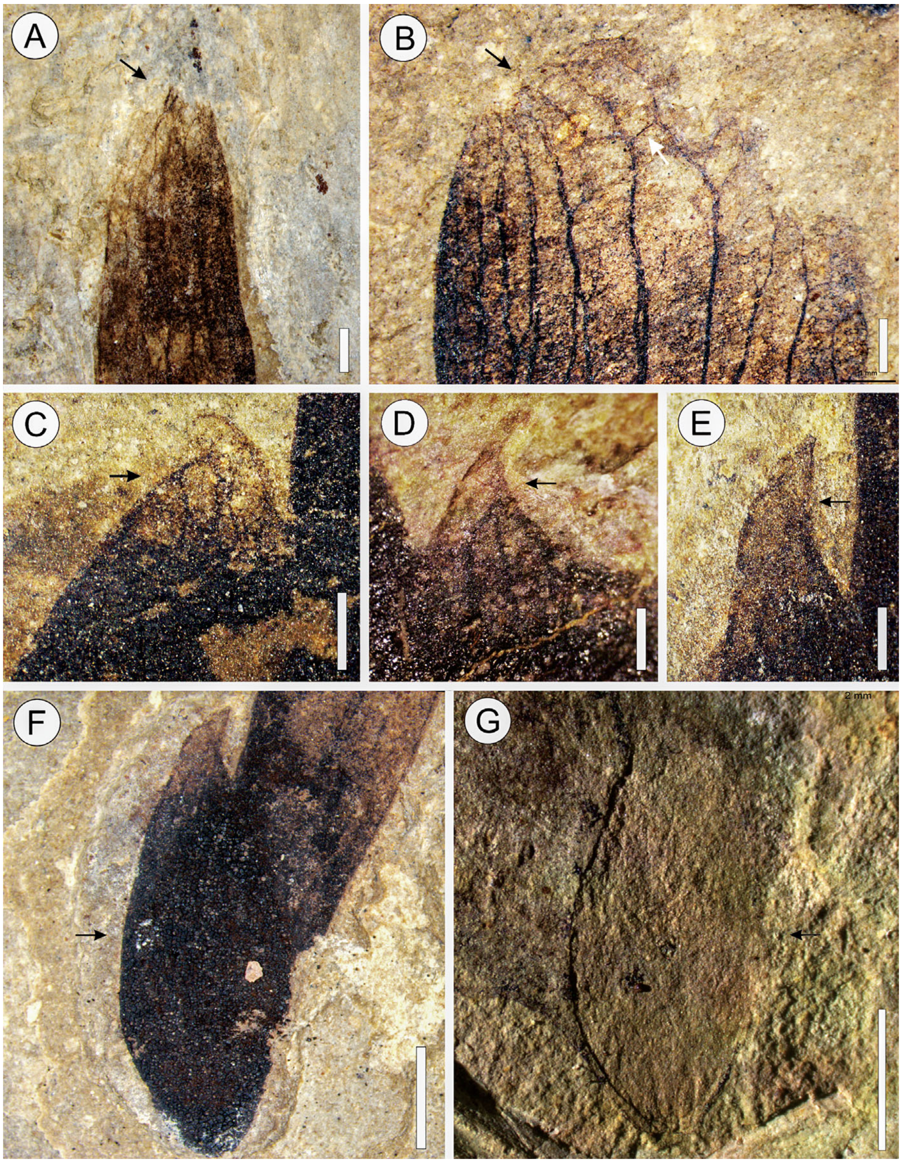

**Fig. 4.** Amplification of *Cedrelospermum tibeticum* sp. nov. showing fruits in detail. **A,** All veins on the primary wing converging towards the stigmatic area (arrow), XZDY2-0101B. **B,** Most veins on the primary wing converging towards the stigmatic area (upper arrow); minority veins dichotomizing near the apex of the primary wing and converging with the external–marginal vein (lower arrow), XZDY2-0105. **C,** Obtuse second wing (arrow), XZDY2-0105. **D,** Vestigial second wing (arrow), XZDY2-0077. **E,** Falcate second wing (arrow), XZDY2-0101A. **F,** Elliptical fruit body (arrow), XZDY2-0070b. **G,** Elliptical fruit body with clear outline (arrow), XZDY2-0101A. Scale bar = 1 mm (A, B, E–G) or 400 μm (C, D).

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

**Locality** The upper Oligocene of Dingqing Formation, Shuanghu County (32°02′N, 89°46′E; 4655 m a.s.l.; type locality), and the Upper Oligocene of Nyima Redbed unit, Nyima County (31°48′N, 87°46′E; 4615 m a.s.l.), Tibet, China (Fig. 2).

**Etymology** The specific epithet "*tibeticum*" means Tibet where the present fossils were collected.

**Description** Samara 15.2–20.2 mm long and 4.7–8.1 mm wide, formed by an ovate fruit body and two lateral wings (Fig. 3; Table 1). The fruit body 5.6–6.9 mm long, 3.1–4.1 mm wide, ovate to prolate in profile (Figs. 3, 4F, 4G; Table 1). The primary wing 10.5–14.3 mm long and 3.1–4.1 mm wide, elongated (Fig. 3; Table 1) with obtuse to acute apex; external flank convex (Fig. 3); internal flank straight to convex (Fig. 3); vascularized with 8–13 subparallel veins, originating from different points along the internal flank of the endocarp (Fig. 3). The veins extending along the long axes of the primary wing, finally converging to the stigmatic area (Figs. 3, 4A, 4B), or occasionally minority vein dichotomizing near the apex of the primary wing and converging with the external-marginal vein of the primary wing (Figs. 3D, 4B). Secondary wing minute (Figs. 3C–3E, 4), 1.2–2.7 mm long, subtriangular (Fig. 4C) or falcate (Fig. 4E) in shape, occasionally vascularized

**Table 1** Morphological comparison of *Cedrelospermum* fruits

| | *C. nervosum* | *C. lineatum* | *C. manchesteri* | *C. leptospermum* | *C. aquense* | *C. stiriacum* | *C. asiaticum* | *C. tibeticum* |
|---|---|---|---|---|---|---|---|---|
| Number of wings | 2, occasionally 1 | 2 | 2 | 1 | 1 | 1 | 2 | 2 |
| Stigmatic configuration | Stigmatic area, occasionally stigmatic notch | Stigmatic area | Stigmatic area | Stigmatic notch | Stigmatic notch | Stigmatic notch | Stigmatic area | Stigmatic area |
| Primary apex shape | Usually wide and obtuse | Usually wide and obtuse | Usually wide and obtuse | – | – | – | Acute | Acute or obtuse |
| Angle between primary wing and second wing | 16.3°–31.8° | 15.3°–22.8° | 9.4°–35.9° | – | – | – | 36.9°–85.2° | 6.7°–38.3° |
| Fruit length (mm) | 4.4–11.0 | 9.0–14.5 | 13.0–16.0 | 5.0–11.0 | ? | 14.0–23.0 | 12.1–22.1 | 15.2–20.2 |
| Fruit width (mm) | 1.9–4.0 | 2.2–5.5 | 3.8–7.8 | 3.2–5.0 | ? | 5.0–8.0 | 4.2–7.9 | 4.7–8.1 |
| Endocarp length (mm) | 1.5–4.0 | 3.2–5.0 | 4.0–7.0 | 2.5 | ? | ? | 4.4–6.3 | 5.6–6.9 |
| Endocarp width (mm) | 1.0–2.6 | 2.0–3.8 | 1.6–3.6 | 1.5–2.0 | ? | ? | 1.7–2.8 | 3.1–4.1 |
| Pedicel length (mm) | 0.5–1.2 | 2.0–3.0 | ? | 0 (sessile) | 0 (sessile) | ? | 4.6–5.1 | ? |
| Continent | North America | North America | North America | Europe | Europe | Europe | Asia | Asia |
| Reference | Manchester (1989) | Manchester (1989) | Magallón-Puebla & Cevallos-Ferriz (1994) | Wilde & Manchester (2003); Kvaček & Teodoridis (2011) | Manchester (1989) | Kovar-Eder et al. (2004) | Jia et al. (2015) | This study |

–, Character does not apply to the corresponding species; ?, State of the character for the corresponding species not reported in published works.

with faint and reticulate veins (Figs. 4C, 4D). Long axis of the secondary wing parallel to that of the fruit body (Fig. 3). Apex of the secondary wing occasionally curving towards the primary wing (Figs. 4D, 4E).

**Leaf**

***Cedrelospermum* sp.**

**Locality** The upper Oligocene of Dingqing Formation, Shuanghu County (32°02′N, 89°46′E; 4655 m a.s.l.), Tibet, China (Fig. 2).

**Repository** Specimen is stored at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

**Description** Leaf narrow elliptical with its apex and base missing (Figs. 5A, 5E), the remaining part 39.3 mm long and 6.4 mm wide (Figs. 5A, 5E). Primary vein framework pinnate (Figs. 5A, 5E). Secondaries craspedodromous (Figs. 5B, 5D), occasionally semicraspedodromous, spaced regularly, and excurrently attached to the midvein (Fig. 5D). Semicraspedodromous secondaries dichotomizing near the leaf margin, either terminating into two adjacent teeth (Fig. 5D) or forming one or more sets of loops in a festooned semicraspedodromous pattern (Fig. 5D). The angle between the secondary and midvein 27.8°–35.5°. Tertiaries percurrent or reticulate (Figs. 5C, 5D). Quaternary veins forming polygons, sometimes orthogonal meshes (Fig. 5D). Leaf margin prominently serrate with simple teeth, spaced regularly (Figs. 5A, 5D). Number of teeth per centimeter 6–7 (Figs. 5A, 5E). Sinus shape angular (Figs. 5B–5D). Distal flank of the tooth concave to flexuous (Figs. 5B–5D). Proximal flank of the tooth concave (Figs. 5B–5D). Tooth principal vein present, terminating at the apex of the tooth (Figs. 5B, 5C). Tooth apex mucronate (Figs. 5B, 5C).

# 4 Discussion

## 4.1 Morphological comparisons

Fossils representing fruits and leaves of *Cedrelospermum* were first reported in the late 19th century (e.g., Unger, 1861). However, for nearly a century, their systematic position remained poorly understood. Manchester (1987) convincingly assigned these fossils to Ulmaceae by studying the intact twigs of the genus with organically attached fruits, flowers, and leaves. Manchester (1989) further carried out a whole-plant reconstruction of *Cedrelospermum* with a complete description of fruits, leaves, and flowers with pollen *in situ*, based on these twigs. This provides a solid basis for identifying other detached *Cedrelospermum* fossil fruits and leaves.

The new fossil fruits can be unambiguously assigned to *Cedrelospermum* based on the following characters: (i) an ovate fruit body laterally adjoined by a primary and a secondary wing; (ii) the presence of a stigmatic area on the distal ends of the primary wing; and (iii) the convergence of nearly all the veins on the primary wing towards the stigmatic area (Figs. 3, 4). Within *Cedrelospermum*, seven species currently have been documented based on fruit remains (Jia et al., 2015) (Fig. 6). They are *C. leptospermum* (Ettingshausen) Manchester, *C. aquense* (Saporta) Saporta, and *C. stiriacum* (Ettingshausen) Kovar-Eder & Kvaček from Europe (Manchester, 1987, 1989; Wilde & Manchester, 2003; Kovar-Eder et al., 2004), *C. nervosum* (New.) Manchester,

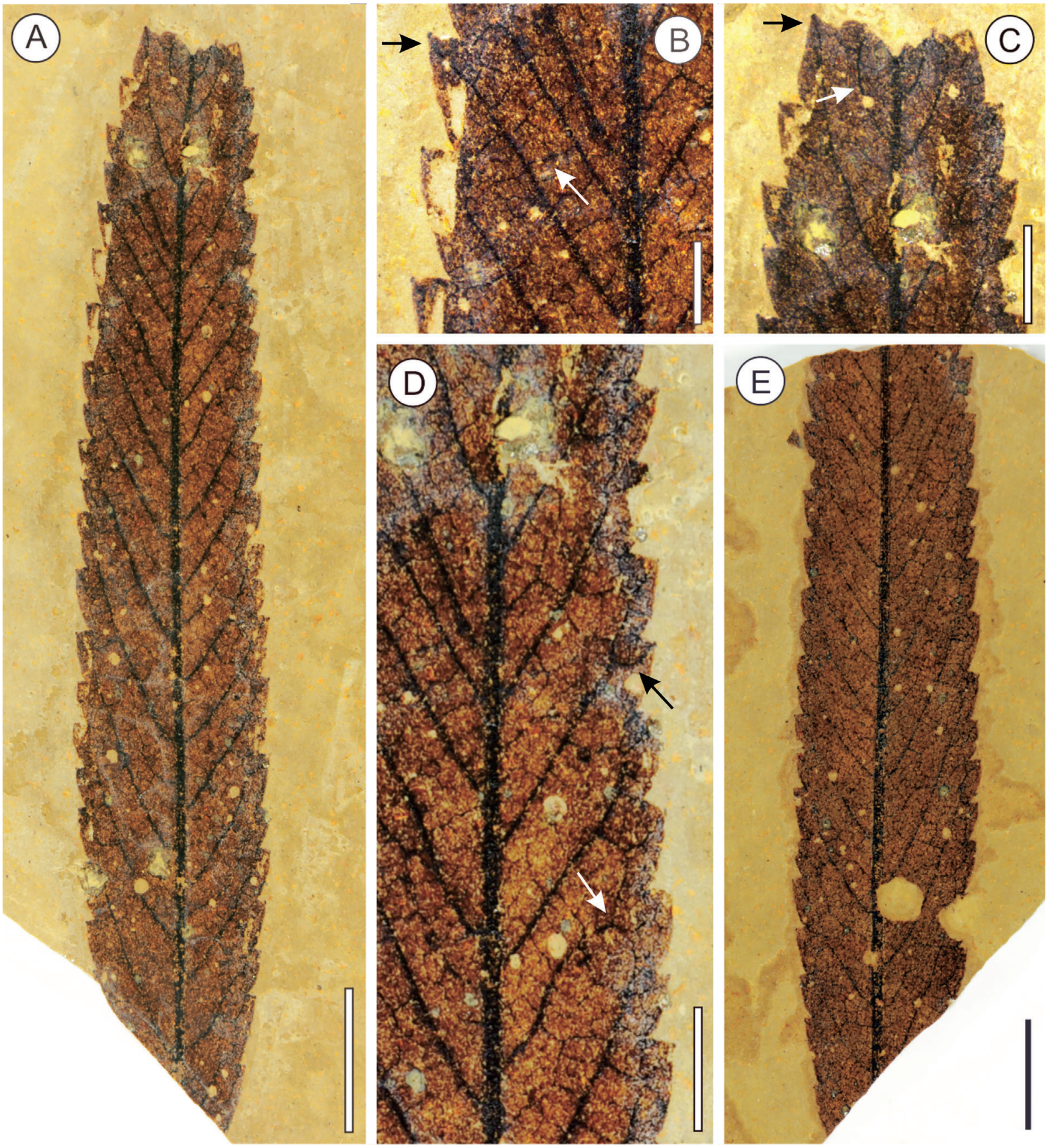

**Fig. 5.** Leaf of *Cedrelospermum* sp. **A,** Overall leaf features, XZDY1-0060B. **B,** Amplification of XZDY1-0060B, showing secondary terminating into tooth (upper arrow) and percurrent tertiary (lower arrow). **C,** Magnified image of XZDY1-0060B, showing mucronate teeth apexes (upper arrow) and the secondaries at the upper part curving towards the direction of the apex of the leaf (lower arrow). **D,** Amplification of XZDY1-0060B, showing semicraspedodromous secondaries dichotomizing near the leaf margin, either terminating into two adjacent teeth (arrow) or forming one or more sets of loops in a festooned semicraspedodromous pattern (arrow). **E,** XZDY1-0060A, counterpart of XZDY1-0060B. Scale bar = 5 mm (A, E), 1 mm (B, D), or 2 mm (C).

*C. lineatum* (Lesq.) Manchester, and *C. manchesteri* Magallón-Puebla & Cevallos-Ferriz from North America (Manchester, 1987, 1989; Magallón-Puebla & Cevallos-Ferriz, 1994), and *C. asiaticum* L. B. Jia, Y. J. Huang & Z. K. Zhou from Asia (Jia et al., 2015). Three species, *C. leptospermum*, *C. aquense*, and *C. stiriacum*, which have one wing, are obviously distinguished from *C. tibeticum*, which possesses two wings (Fig. 6; Table 1). Two species, *C. nervosum* (4.4–11.0 mm long, 1.0–4.0 mm wide) and *C. lineatum* (9.9–14.5 mm long, 2.2–5.5 mm wide), have a fruit size smaller than that of *C. tibeticum* (15.0–20.2 mm long, 4.7–8.1 mm wide) (Table 1). *Cedrelospermum manchesteri* and *C. tibeticum* overlap in size. However, the apex of the primary wing of *C. manchesteri* severely curls towards the direction of the secondary wing, in contrast to the straight apex of *C. tibeticum*. Moreover, the primary wing of the three species *C. nervosum*, *C. manchesteri*, and *C. lineatum* is vascularized with 5–8 subparallel veins, whereas that of *C. tibeticum* is vascularized with 8–13 subparallel veins. The gross fruit morphology of *C. tibeticum* is the most similar to that of *C. asiaticum*. However, the veins on the primary wing of *C. asiaticum* originate from both the internal flank of the endocarp and the internal-marginal vein of the primary wing, but those of *C. tibeticum* only originate from the internal flank of the endocarp. In addition, the apex of the primary wing of *C. asiaticum* is exclusively acute, whereas *C. tibeticum* fruits have both obtuse and acute apices. Notably, the apex of the primary wing of one *C. tibeticum* specimen (Fig. 3E) is clearly constricted but the distal apex point was more or less obtuse, representing a transitional morphology between an obtuse and acute apex. Evidently, *C. tibeticum* is morphologically distinct from the other species of *Cedrelospermum*. We here thus assign our fossil fruits to a new species, *C. tibeticum* sp. nov.

The new fossil leaf has pinnate venation, craspedodromous secondaries, percurrent or reticulate tertiaries, and simple teeth, resembling *Zelkova* Spach and *Cedrelospermum* in leaf architecture. However, the leaves of *Zelkova* are generally ovate to elliptical (Denk & Grimm, 2005), whereas the new fossil leaf is considerably narrower and slender. It is morphologically consistent with *Cedrelospermum*, which typically has narrow elliptical leaves. Thus the new fossil leaf should represent *Cedrelospermum* rather than *Zelkova*.

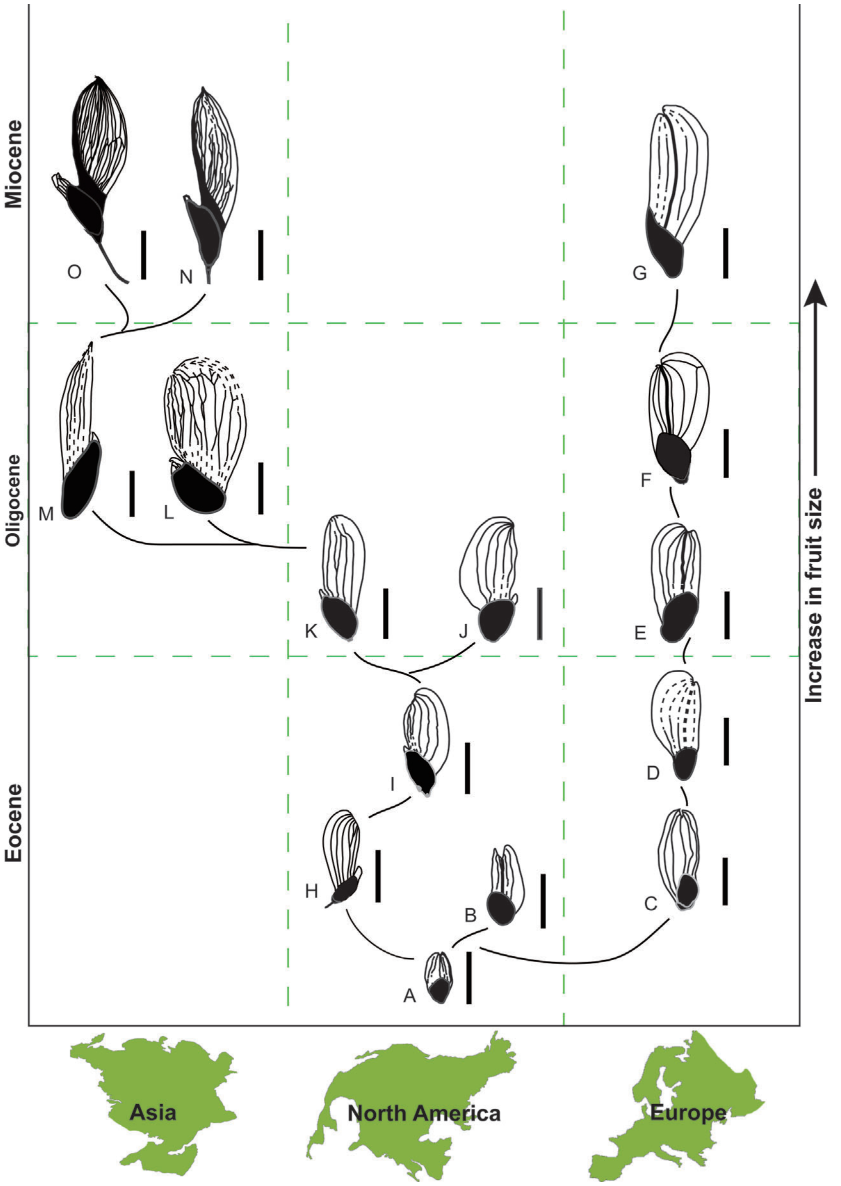

**Fig. 6.** Continued.

Among the six *Cedrelospermum* species mentioned above, *C. nervosum*, *C. lineatum*, and *C. leptospermum* were erected based on twigs with descriptions of leaves (Manchester, 1989; Wilde & Manchester, 2003). In addition, two other species of *Cedrelospermum* were erected based on fossil leaves, *C. flichei* (Saporta) (Hably & Thiébaut, 2002) and *C. ulmifolium* (Unger) Kovar-Eder & Kvaček (Kovar-Eder et al., 2004). The new fossil leaf is narrow elliptical in shape, different from the leaves of *C. flichei* and *C. ulmifolium*, which are usually ovate, narrow ovate, or lanceolate. It is more similar to *C. nervosum*, *C. lineatum*, and *C. leptospermum*, which typically have narrow elliptical to narrow ovate leaves. However, because the apex and base of the new fossil leaf is not preserved and just one specimen was found, comparing it with the three leaf taxa in more detail is difficult. For the same reason, we also did not further compare the new fossil leaf with other detached leaves that were assigned to other fossil genera, including *Tremophyllum* (e.g., Kvaček & Teodoridis, 2011) and *Magdalenophyllum* (Magallón-Puebla & Cevallos-Ferriz, 1994), which possibly represent these of *Cedrelospermum*. Although there is a high possibility that the new fossil leaf and fossil fruits, that is, *C. tibeticum*, represent the same species, we refrained from assigning them to one species because the two types of organs were not found in organic connection.

### 4.2 Significance for fruit morphological evolution

As mentioned above, the size of *Cedrelospermum* fruits was suggested to have increased gradually through time (Manchester & Tiffney, 2001). The fruits of *C. tibeticum* from the late Oligocene of central QTP are 15.2–20.2 mm long and 4.7–8.1 mm wide (Table 1). They are larger than the North American Eocene species, *C. nervosum*, and the Early Oligocene species, *C. lineatum* (Manchester, 1989) (Table 1). They are also larger than the European Eocene species, *C. leptospermum* (Wilde & Manchester, 2003), and the Oligocene species, *C. aquense* (Manchester, 1989), but slightly smaller than the European Miocene species, *C. stiriacum* (Kovar-Eder et al., 2004). Generally, the size of *C. tibeticum* is consistent with the tendency of increased size of *Cedrelospermum* fruits through time. However, the size of *C. tibeticum* is similar to that of the Asian middle Miocene species, *C. asiaticum* (Jia et al., 2015; Lebreton-Anberrée et al., 2016) (Table 1). This probably indicates that *Cedrelospermum* fruit size did not increase significantly from the late Oligocene to the middle Miocene in Asia.

As more double-winged *Cedrelospermum* fruit fossils were found, particularly the discovery of *C. tibeticum* fruits from the central QTP, another morphological evolutionary tendency could be presumed in the double-winged *Cedrelospermum* fruits. In North America, the double-winged *Cedrelospermum* fruits (*C. nervosum* and *C. lineatum*) were found from the strata ranging from the early middle Eocene to the early Oligocene (Manchester, 1989). Apices of the primary wings of these fruits are generally obtuse and curl towards the direction of the secondary wing. The stigmatic areas of these fruits are usually located at the side of primary wing near the secondary wing. Later in the late Oligocene, the apex morphology of the primary wings of *C. tibeticum* fruits found in the Lunpola and Nyima basins are of two types. The first type has an obtuse apex and the stigmatic area is situated at the side, near the secondary wing, similar to the North American double-winged fruits, whereas the second type has an acute and straight apex. In the middle Miocene, the apices of primary wings of *C. asiaticum* fruits from the Maguan basin are exclusively acute and straight, similar to the second type of *C. tibeticum* fruits from the Lunpola and Nyima basins. This morphology of *C. asiaticum* fruits is based on the observations of more than 100 specimens (Jia et al., 2015). Evidently, the primary wing of double-winged *Cedrelospermum* fruits possibly had a tendency of evolving from an obtuse apex to an acute one (Fig. 6). However, these observations regarding the evolution of fruit size and wing

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**Fig. 6.** Hypothesized fruit morphological evolution and biogeographic history of *Cedrelospermum*. Figure shows the earliest fossil record of *Cedrelospermum* is from North America, which exclusively belongs to the single winged type. Subsequently, this single-winged type dispersed to Europe. Later the double-winged type evolved in North America and dispersed to Asia. Morphologically, the size of *Cedrelospermum* fruits generally increased from the early Eocene to the Miocene. Note, however, that the late Oligocene *C. tibeticum* and *C. asiaticum* fruits are of similar size. It possibly indicates that the fruit size of *Cedrelospermum* did not increase significantly from the late Oligocene to the middle Miocene in Asia. The primary wing of the double-winged *Cedrelospermum* fruit might have an evolutionary tendency from obtuse to acute apex. The figure is drawn by Jia LB et al. **A,** *C. nervosum*, drawing based on specimen FMNH pp46003 from the early Eocene, Green River formation (UT, USA), fig. 190 in Grande (2013). **B,** *C. nervosum*, drawing based on specimen IU 15753-7337 from the middle Eocene, Green River formation near Watson (UT, USA), fig. 25 in Manchester (1989). **C,** *C. leptospermum*, drawing based on specimen SM.B Me 15974 from the middle Eocene, Messel, Germany, plate 41, fig. c, f in Collinson et al. (2012). **D,** *C. leptospermum*, drawing based on specimen KIN 192 from the Late Eocene Kučlín flora in North Bohemia, plate 6, fig. 15 in Kvaček & Teodoridis (2011). **E,** *C. aquence*, drawing based on specimen C-CED 14 from the early Oligocene, Céreste, France, plate 3, fig. 2 in Hably & Thiébaut (2002). **F,** *C. aquence*, drawing based on specimen from the late Oligocene, Rott, Germany, fig. 7h in Jia et al. (2015). **G,** *C. stiriacum*, drawing based on specimen IBUG Ett. coll. 2899 from the Miocene, Styria, Austria, plate 8, fig. 6 in Kovar-Eder et al. (2004). **H,** *C. lineatum*, drawing based on specimen UMNH-PB15751-5249 from the middle Eocene, Green River Formation near Uintah (UT, USA), fig. 7m in Jia et al. (2015). **I,** *C. lineatum*, drawing based on specimen UCMP3665 from the late Eocene, Florissant (CO, USA), fig. 7n in Jia et al. (2015). **J,** *C. lineatum*, drawing based on specimen IU 15880-7275 from the early Oligocene, Florissant (CO, USA), fig. 41 in Manchester (1989). **K,** *C. nervosum*, drawing based on specimen IU 15753-7334 from the middle Eocene, Green River formation (UT, USA), fig. 22 in Manchester (1989). **L,** *C. tibeticum*, drawing based on specimen KUNPC-XZDY2-0105 from the late Oligocene, Lunpola basin, Tibet, Fig. 3A in this study. **M,** *C. tibeticum*, drawing based on specimen KUNPC-XZDY2-0101B from the late Oligocene, Lunpola basin, Tibet, Fig. 3B in this study. **N,** *C. asiaticum*, drawing based on specimen MG0300 from the Miocene, Maguan, China, fig. 7b in Jia et al. (2015). **O,** *C. asiaticum*, drawing based on specimen MG0294 from the Miocene, Maguan, China, fig. 7a in Jia et al. (2015). Scale bar = 5 mm.

morphology appear to represent overall evolutionary tendencies, which will aid the identification of *Cedrelospermum* fruit fossils at the species level.

### 4.3 Significance for biogeographic history

Despite abundant fossil records of *Cedrelospermum* in North America and Europe (e.g., Manchester, 1987, 1989; Hably & Thiébaut, 2002), only one fossil record of the genus has been reported in Asia from the middle Miocene of Yunnan, southwestern China (Jia et al., 2015). Our discovery of *C. tibeticum* fruits and *Cedrelospermum* leaf from the Lunpola and Nyima basins is the first *Cedrelospermum* fossil record from the QTP and the earliest *Cedrelospermum* fossil record from Asia (Fig. 1). This indicates that the genus inhabited the QTP of Asia at least by the late Oligocene.

*Cedrelospermum tibeticum* fruits are exclusively double-winged and morphologically similar to the North American Eocene and Oligocene *Cedrelospermum* double-winged species. This supports the hypothesis proposed by Jia et al. (2015) that the Asian *Cedrelospermum* was the result of the dispersal of the genus from North America by way of the Bering Land Bridge (Fig. 6). Although the Lunpola and Nyima basins in the central QTP were considerably closer to the European localities that uncovered *Cedrelospermum* fruits than the North American ones, the morphological differences between the central QTP late Oligocene and European Eocene and Oligocene *Cedrelospermum* species are obvious. This possibly indicates that no exchange of *Cedrelospermum* between Europe and Asia has occurred, at least by the late Oligocene. The existence of the Turgai Sea Strait from the Paleocene to the late Oligocene (Tiffney & Manchester, 2001) was possibly responsible for the geographic isolation of *Cedrelospermum* between Asia and Europe.

Because *Cedrelospermum* was a typical element of the Northern Hemisphere, particularly in North America and Europe, the discovery of *Cedrelospermum* fossils herein might indicate that the central QTP was phytogeographically linked with other parts of the Northern Hemisphere during the late Oligocene.

*Cedrelospermum*, including *C. asiaticum*, which is perhaps the nearest relative of *C. tibeticum*, is generally inferred to have lived in warm and wet environments (Manchester, 1989; Jia et al., 2015). The occurrence of *C. tibeticum* in the Lunpola and Nyima basins therefore suggests a warm and wet climate in two regions during the late Oligocene. This is consistent with the inferences drawn based on pollen, fish, and mammal fossils (Deng et al., 2012; Sun et al., 2014; Wu et al., 2017).

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