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Oligocene *Koelreuteria* (Sapindaceae) from the Lunpola Basin in central Tibet and its implication for early diversification of the genus

Hui Jiang[a,e], Tao Su[b], William Oki Wong[c,a], Feixiang Wu[d], Jian Huang[b], Gongle Shi[a,*]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China
[b] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China
[c] State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
[d] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[e] University of Science and Technology of China, Hefei 230026, China

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ABSTRACT

Fossils are critical for understanding the uplift history of the Tibetan Plateau and its impact on the diversity and diversification of living organisms in Eurasia. However, well-preserved fossils, especially plant megafossils are rare in the plateau. In this paper, we describe two species of *Koelreuteria*, namely *K. lunpolaensis* sp. nov. and *K. miointegrifoliola*, based on exquisitely preserved capsular valves from the late Oligocene of the Lunpola Basin, central Tibet. *Koelreuteria lunpolaensis* is distinguishable from all extant and fossil species of the genus in the strongly asymmetric form of the capsular valves, the emarginate or lobed apex of the valves, and zigzag lateral veins that are tapering towards the margin of the valves, and is considered to represent an extinct lineage of the genus. *Koelreuteria miointegrifoliola* is most similar to *K. bipinnata*-type group of extant *Koelreuteria*. The diverse *Koelreuteria* confirms a warm and humid environment with a low elevation in central Tibet during the late Oligocene based on their modern distributions. Fossil evidence indicates that the Tibetan Plateau was a center for diversity and diversification of *Koelreuteria* in the Oligocene/Miocene. It also suggests that Tibet might also serve as a refugium for the *K. bipinnata*-type group in the late Oligocene.

1. Introduction

Understanding the uplift history of the Tibetan Plateau and the role it played in the diversification of plants and animals has long been one of the most important scientific issues in geology, evolutionary biology and biogeography (Deng and Ding, 2015; Favre et al., 2015; Renner, 2016). Recent studies based on geological evidence have increasingly suggested that the Tibetan Plateau had almost attained its present heights by the middle Eocene (e.g. Rowley and Currie, 2006; Wang et al., 2008; Ding et al., 2014). In contrast, paleontological evidence indicates that the elevations of the plateau were significantly lower in the Paleogene than estimated by geological studies, and the establishment of its present elevation had occurred in the Miocene or later (Spicer et al., 2003; Wang and Wu, 2015; Wang et al., 2015; Wei et al., 2016; Ding et al., 2017). The molecular-clock studies appear to favor more the inferences based on paleontological evidence. In most cases, molecular studies indicate a young divergence time for organisms that are exclusively or partly endemic to Tibet today and link the diversification to a recent, mostly Miocene or Pliocene, uplift of the plateau (see a review in Renner, 2016).

Fossils can not only provide direct evidence for biodiversity change through geological time, but also serve as indicators of paleoenvironment and paleoclimate. Therefore, fossils, especially Cenozoic fossils from the Tibetan Plateau, are critical for understanding the timing and scenarios of the uplift of the plateau, as well as its impact on the diversity and diversification of extant plants and animals (Deng and Ding, 2015). However, well-documented fossils, especially plant megafossils are rare in Tibet, partly due to the difficulty of field work on the plateau. In a recent publication, Wu et al. (2017) reported a fossil biota including exquisitely preserved climbing perch (anabantid fish) and diverse angiosperms from the late Oligocene Dingqing Formation of Lunpola and Nyima (Nima) basins in central Tibet (Fig. 1). Our recent fieldwork in the same region has also yielded new and diverse plant fossils, among which the capsular valves of *Koelreuteria* Laxmann are particularly of interest since they are rich in fossil specimens and show different morphology.

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* Corresponding author.
E-mail address: glshi@nigpas.ac.cn (G. Shi).

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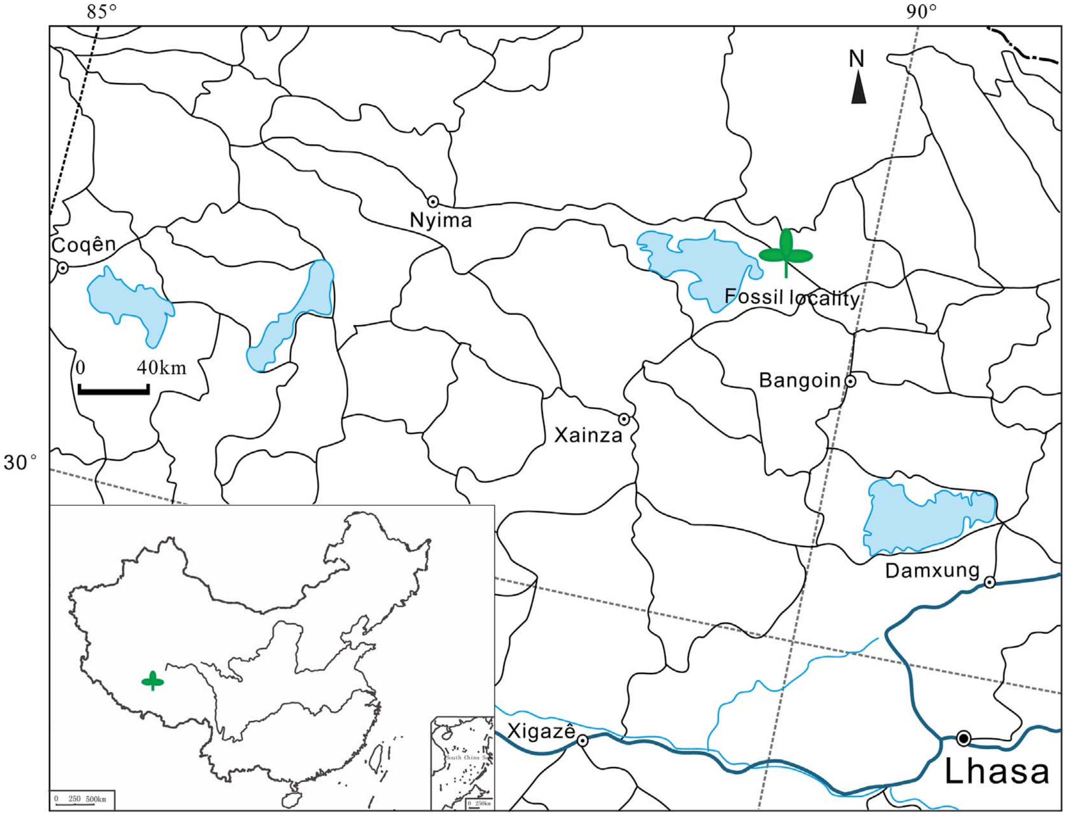

Fig. 1. Map showing the location of the Lunpola Basin, Tibet, indicated by green trifoliate leaf symbol.

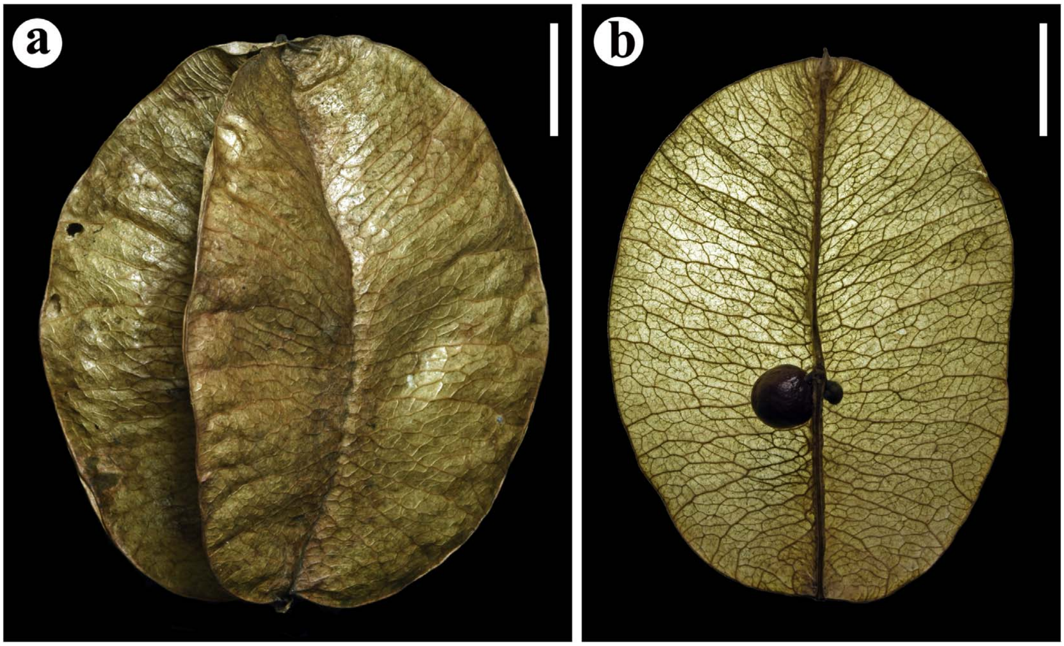

Fig. 2. *Koelreuteria bipinnata* Franchet. Extant material for comparison. All scale bars = 1 cm. (a) Balloon-like, three-angled capsule with three ovate membranous valves. (b) Individual capsular valve showing craspedodromous lateral veins.

Koelreuteria, commonly known as the golden rain tree, is a small sapindaceous genus consisting of four extant species: *K. paniculata* Laxmann widely distributed in Anhui, Gansu, Hebei, Henan, Liaoning, Shaanxi, Shandong, Sichuan and Yunnan of China, and in Korea and Japan; *K. bipinnata* Franchet in southern and southwestern China; *K. henryi* Dümmer (=*K. elegans* subsp. *formosana* (Hayata) F.G. Mey.) native to the island of Taiwan, China; and *K. elegans* (Seemann) A.C. Smith native to Vanua Levu and Viti Levu islands of Fiji (Acevedo-Rodríguez et al., 2011; Wang et al., 2013). The precise position of *Koelreuteria* within Sapindaceae is still controversial. Traditionally, *Koelreuteria* is placed in the subfamily Dodonaeoideae based on its loculicidal, inflated capsules with two ovules per locule (Radlkofer, 1890, 1931; Fig. 2a). However, only one of the two ovules in each locule matures fully in *Koelreuteria* (Fig. 2b), suggesting that the genus may represent an intermediate form between the states found in the subfamilies Dodonaeoideae and Sapindoideae (Ronse Decraene et al., 2000). Molecular phylogenetic studies resolve *Koelreuteria* as an early diverging lineage within the subfamily Sapindoideae and exclude it from Dodonaeoideae (Harrington et al., 2005), and estimate that the stem group of *Koelreuteria* diverged at a minimum age of 37.2 Ma (late Eocene) (Buerki et al., 2011).

Reports of fossil *Koelreuteria* preserved as pollen, leaves, wood and capsules/capsular valves are relatively common in the strata of the Northern Hemisphere in comparison with most other sapindaceous genera (see a review in Wang et al., 2013). Reliably identified fossil fruits reveal that *Koelreuteria* was widely distributed in Europe, East Asia and western North America in the Paleogene, with the earliest known occurrence from the early Eocene (ca. 52 Ma) of western North America, based on a fossil capsular valve of *K. allenii* from Wyoming, US (Smith et al., 2008; Wang et al., 2013).

In this paper, we describe two species of *Koelreuteria* based on excellently preserved capsular valves from the late Oligocene of the Lunpola Basin, central Tibet. The discovery of diverse *Koelreuteria* in the late Oligocene of central Tibet provides new evidence for the paleoenvironmental conditions in central Tibet during the late Paleogene.

2. Material and methods

2.1. Geological setting

The fossil capsular valves of *Koelreuteria* studied in this paper were collected from the Dingqing Formation of Dayu (32°01′29″N, 89°46′19″E) (Elevation 4683 m asl), Lunpola Basin, central Tibet, China (Fig. 1; Wu et al., 2017). The Cenozoic deposits in the Lunpola Basin are up to 4000 m in thickness and mainly consist of the Niubao Formation and Dingqing Formation from the bottom upwards (Deng et al., 2012; Sun et al., 2014). The Dingqing Formation is ca. 1000 m thick and mainly composed of lacustrine deposits including fine-grained greyish mudstone, fine siltstone and limestone. The age of the Dingqing Formation has been controversial (Rowley and Currie, 2006; DeCelles et al., 2007; Deng et al., 2012); recent U-Pb isotopic analysis suggests a late Oligocene to early Miocene age (He et al., 2012). The fossiliferous bed in Dayu, Lunpola Basin, belongs to the middle to upper part of the Dingqing Formation, and mainly consists of greyish green and red mudstones interbedded with limestones and shales (Wu et al., 2017). These beds have been considered most likely 26–23.5 Ma in age based on biostratigraphical correlations (Kapp et al., 2007; Wu et al., 2017), corresponding to the Chattian Stage (late Oligocene).

The Dingqing Formation in Dayu, Lunpola Basin yields well-preserved insects, fishes (Wu et al., 2017), mammals (Deng et al., 2012) and diverse plants (Wu et al., 2017). The plant fossils consist of leaves of 16 dicots and 7 monocots and 5 types of fruits. Recognizable taxa include *Koelreuteria*, *Cedrelospermum* Saporta (Ulmaceae), *Handeliodendron* Rehder (Hippocastanaceae), *Pistacia* L. (Anacardiaceae), *Exbucklandia* R.W. Brown (Hamamelidaceae), *Limnobiophyllum* Krassilov (Lemnoideae, Araceae), *Typha* L. (Typhaceae), Araliaceae, Bignoniaceae and Lauraceae. The plant fossil assemblage together with fish fossils of *Eoanabas* suggest a warm and humid subtropical climate and a paleoelevation of ca. 1000 m in central Tibet during the late Oligocene (Wu et al., 2017).

2.2. Fossil preparation, photography

Fossil specimens were prepared manually with a fine needle to remove extraneous matrix, and photographed using a Nikon D810 digital camera with 90 mm Nikkor macrolens under oblique illumination. Some specimens were immersed in water to enhance contrast. The figured specimens are deposited partly at the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS), and partly at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), CAS. The illustrated extant material of *Koelreuteria* was collected in Nanjing in November 2016.

2.3. Terminology

In order to interpret the studied Tibetan fossils accurately, it is necessary to clearly understand the structure of the capsule of extant *Koelreuteria*. Capsules of *Koelreuteria* are loculicidal, inflated and three-angled, consisting of three elliptical to ovate membranous valves that adhere to each other along their margins (Meyer, 1976; Lo and Chen, 1985; Manchester and O'leary, 2010; Acevedo-Rodríguez et al., 2011; Fig. 2a). The ovary is three-carpellate, with two ovules per carpel, and the septa are incomplete in the distal portion; the stigma is entire or trifid. The capsular valves split apart at maturity, each with one or two seeds on both sides of the incomplete septum (Manchester and O'leary, 2010; Fig. 2b). Each valve has a distinct longitudinal suture in the middle aligned to the incomplete septum, and straight to slightly sinuous lateral veins spread from the suture (Manchester and O'leary, 2010; Fig. 2b). Lateral veins are craspedodromous and end at the distinct fimbrial veins. Intervening veins between the lateral veins form a polygonal reticulum (Manchester and O'leary, 2010; Fig. 2b). The terms used here to describe the form and venation of the fossil capsular valves are based on standard terminology for leaf architecture (Ellis et al., 2009), and also follows the terms for capsules and capsular valves of *Koelreuteria* (Wang et al., 2013). The classification of fossils follows the phylogenetic treatment of the Angiosperm Phylogeny Group (APG III, 2009)

3. Results

3.1. Systematic paleontology

Order: Sapindales Jussieu ex Berchtold et J. Presl
Family: Sapindaceae Jussieu
Genus: *Koelreuteria* Laxmann
Species: *Koelreuteria lunpolaensis* Jiang, Su, Wong, Wu et Shi, sp. nov. (Figs. 3 and 4)
Holotype: XZDY2-0128 (Fig. 3a and b, part and counterpart).
Paratype: XZDY2-0127 (Fig. 4a and b, part and counterpart).
Repository: Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China.
Type locality: Dayu, Lunpola Basin, Central Tibet, China.
Stratigraphy: Middle-upper part of the Dingqing Formation, late Oligocene (Chattian) (ca. 26–23.5 Ma).
Etymology: The specific epithet "*lunpolaensis*" refers to the Lunpola Basin, Tibet, China, where the studied fossils were collected.
Diagnosis: Capsular valves strongly asymmetric, elliptical to orbicular in outline. Base rounded, strongly asymmetric, margin entire, apex emarginate to lobed with a mucro in the middle between two apical lobes. Each valve with a longitudinal middle carpellary suture and a septum along the proximal region of the suture. Septum extending almost to the distal point of valve between two apical lobes. Lateral veins irregularly zigzag, tapering gradually towards the margin. Intervening veins between lateral veins anastomose, areoles commonly 3–6 sided, relatively consistent in size and form.

Description:

Koelreuteria lunpolaensis sp. nov. is represented by individual capsular valves that are preserved as part and counterpart of impressions. The material includes two complete valves with form and venation excellently preserved (Figs. 3 and 4). The capsular valves are strongly asymmetric, elliptical to orbiculate in outline, measuring 4.66 cm × 3.48 cm (Fig. 3a and b) and 4.34 cm × 4.20 cm (Fig. 4a and b), respectively. The base of the valve is rounded and strongly asymmetric, the margin is entire in the holotype (Fig. 3a and b), but appear

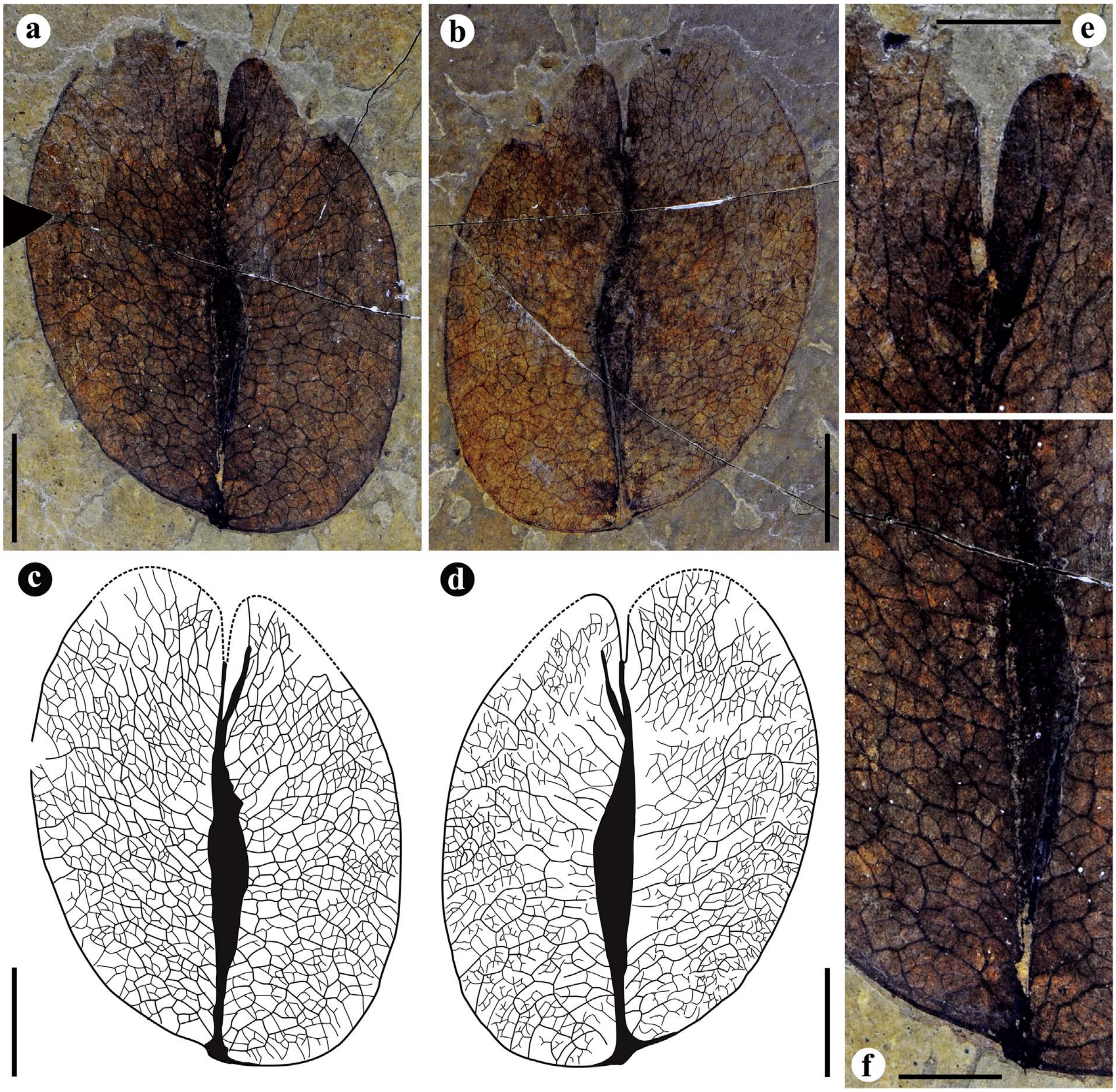

Fig. 3. *Koelreuteria lunpolaensis* sp. nov. XZDY2-0128 (XTBG). Holotype. Scale bars in (a)–(d) = 1 cm. (a) Individual capsular valve with strongly asymmetric form and emarginate apex. XZDY2-0128-a. (b) Counterpart of specimen in (a). XZDY2-0128-b. (c) Line drawing of (a). (d) Line drawing of (b). (e) Detail of apical region of capsular valve, enlarged from (a), showing the emarginate apex with a mucro. Scale bar = 5 mm. (f) Detail of middle region of capsular valve, enlarged from (a), showing detailed venation. Scale bar = 5 mm.

slightly sinuous in the paratype (Fig. 4a and b), probably due to the shrinkage of the membranous valve before it was buried. The apex is emarginate or lobed (Figs. 3e and 4b), with the length of the lobed part accounting for 20–30% of the valve length. Each apical lobe is rounded and between the two lobes the apex of the valve has a mucro that represents part of the stigma (Figs. 3e and 4b). The middle vein of the valve that represents the longitudinal carpellary suture is thick with a prominent septum in the proximal region (Figs. 3a, c, d and 4a, c). The lateral veins are sub-opposite, diverging from the suture at an angle of 30–120° (Figs. 3c, d and 4d). They are craspedodromous, irregularly zigzag, taper gradually towards the valve margin and terminate at the thick fimbrial veins (Figs. 3a, c, d and 4d). Intervening veins between lateral veins are similar to the lateral veins in thickness near the suture, and are thinner than the lateral veins near the valve margin (Fig. 3a, c and f). Intervening veins are anastomose with each other or lateral veins to form a reticulum with areoles that are relatively consistent in size and form and generally with 3–6 sides (Fig. 3c and f). The septa are 3.34 mm and 3.14 mm in length respectively in the two individual fossil valves, extending almost to the distal point of the valves between the two apical lobes (Figs. 3a, c, d and 4a, c). The septa account for approximately 2/3 of the whole valve length. Seeds are not preserved.

3.2. Comparison of *Koelreuteria lunpolaensis* sp. nov. with extant and fossil *Koelreuteria*

The studied Tibetan capsular valves closely resemble those of extant *Koelreuteria* (Fig. 2b) in not only the gross morphology including form and size, but also the detailed morphology, such as a distinct longitudinal suture in the middle, a septum aligned to the suture, craspedodromous lateral veins ending at the thick fimbrial vein, and reticulate thinner veins. The seeds are not preserved on the capsular valves in the Tibetan Oligocene materials, but it is not surprising since in extant species the seeds are often detached from the capsular valves when maturity. *Craigia* W.W. Smith et W.E. Evans (Malvaceae) and *Ptelea* L. (Rutaceae) bear resemblance to the studied fossils in the general shape and venation of the capsular valves, but clearly differ in having a smaller size and a well-defined locular region in the center of the valve (Kvaček et al., 2002, 2005; Manchester and O’Leary, 2010). Some other

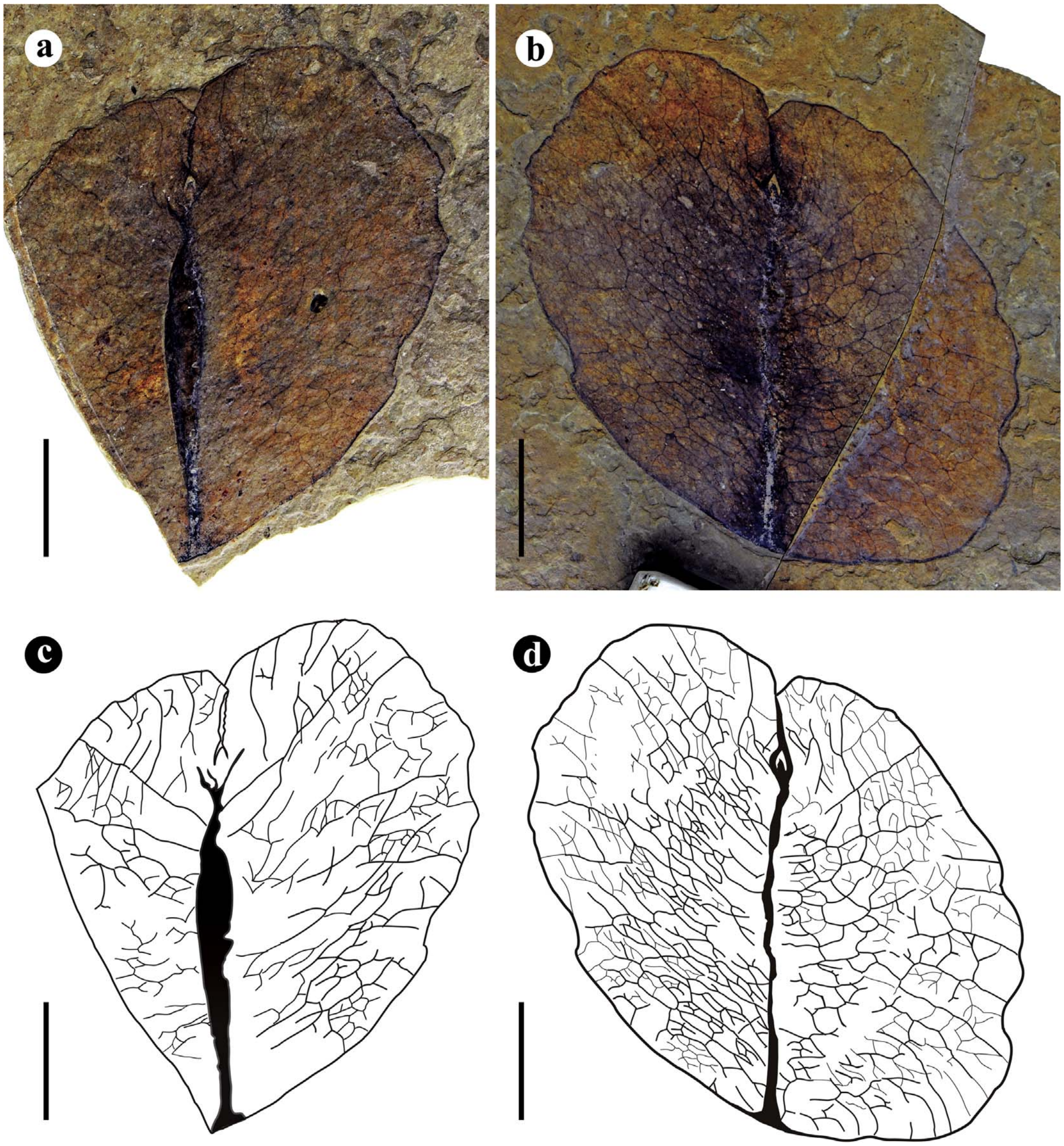

Fig. 4. *Koelreuteria lunpolaensis* sp. nov. XZDY2-0127 (XTBG). Paratype. Scale bars in (a)–(d) = 1 cm. (a) Individual capsular valve. Note that the septum that almost extends to the apical point of the capsular valve. XZDY2-0127-a. (b) Counterpart of specimen in (a). XZDY2-0127-b. (c) Line drawing of (a). (d) Line drawing of (b).

genera of Sapindaceae also have inflated capsules with membranous capsular valves more or less similar to the Tibetan Oligocene fossils and extant *Koelreuteria*. As noted by Manchester and O'Leary (2010) and Wang et al. (2013), these sapindaceous genera include *Arfeuillea* Pierre ex Radlk., *Boniodendron* Gagnepain (= *Sinoradlkofera* F. Meyer), *Cardiospermum* L., *Conchopetalum* Radlk., *Erythrophysa* E. Meyer ex Arnold, *Stocksia* Bentham. *Arfeuillea arborescens* Pierre ex Radlk., the single species of *Arfeuillea*, is similar to the studied fossils in venation of capsular valves, but its capsular valve differs in having a rounded apex and a complete septum accounting for the whole length of the valve (Bůzek et al., 1989). The studied fossil capsular valves, however, have an emarginate to lobed apex and an incomplete septum accounting for approximately 2/3 of the whole valve length. The capsular valves of *Boniodendron*, *Cardiospermum* and *Stocksia* (Wang et al., 2013) are smaller than the studied fossils. The capsules of *Erythrophysa* and *Conchopetalum* bear a prominently elongated style (Acevedo-Rodríguez et al., 2011). In contrast, the Tibetan fossil capsular valves only have a mucro at the tip, indicating a very short style.

Extant species of *Koelreuteria* are divided into two groups based on the morphology of the capsular valves as well as the development of septa (Table 1; Wang et al., 2013). The *K. paniculata*-type including a single species, namely *K. paniculata*, has ovate capsular valves with acute or slightly acuminate apex and an incomplete septum extending ca. 1/3 of the valve length from the base. The *K. bipinnata*-type, consisting of *K. bipinnata*, *K. henryi* and *K. elegans*, has elliptical, ovate-elliptical to sub-rounded capsular valves with rounded or obtuse apex and relatively longer septa extending more than 1/3 of the valve length. The Tibetan Oligocene materials are distinct from both types of extant *Koelreuteria* in the strongly asymmetric form of the capsular valves, the emarginate or lobed apex of the valves, with the length of the lobed part accounting for 20–30% of the valve length, and zigzag lateral veins that taper towards the margin of the valves (Table 1). In contrast, the capsular valves of extant *Koelreuteria* have straight to slightly sinuous lateral veins that are even in thickness throughout their whole length (Fig. 2b). We consider the strongly asymmetric form of *K. lunpolaensis* as an original characteristic, rather than the result of taphonomy, since the two specimens are similarly asymmetric. The septum of *K. lunpolaensis* accounts for approximately 2/3 of the whole valve length, but it extends nearly to the apical tip of the valve between the two apical lobes, indicating that the septum is nearly complete. In most cases, the septum of *Koelreuteria* is incomplete, which distinguishes it from other genera of Sapindaceae. However, in a few cases, *K. bipinnata* has a

Table 1
Comparison of *Koelreuteria lunpolaensis* sp. nov. with extant (indicated by *) and fossil species of *Koelreuteria*. Only fossils species represented by capsules/capsular valves are listed. Data are based on Wang et al. (2013), Li et al. (2016), and observation and examination on extant material or published figures.

Species	Capsular valves					
	Shape	Size (cm)	Apex	Base	Lateral veins	Septum
K. lunpolaensis sp. nov.	Elliptical to orbiculate, strongly asymmetric	4.66 × 3.48, 4.34 × 4.20	Emarginate or lobed	Rounded and strongly asymmetric	Irregularly zigzag, taper gradually towards the margin, diverging at 30–120°	ca. 2/3 of valve length from the base
K. paniculata Laxm.*	Ovate	2.2–7.2 × 2–4	Acute to acuminate	Rounded, slightly convex	Sinuous, sparse, diverging at about 50–90°	1/3 of valve length
K. bipinnata Franch.*	Elliptic to rounded	3.7–6.6 × 3–5	Short acuminate, mucronate	Rounded, slightly convex	Sinuous, sparse, diverging at about 30–120°	1/3 to 1/2 of valve length, or occasionally complete
K. henryi Dümmer*	Suborbicular	4–5 × 3–4.5	Short acuminate, mucronate	Rounded	Straight, dense, diverging at about 40–110°	1/2 of valve length
K. elegans A.C. Sm.*	Suborbicular	3.4–5 × 3.1–4.6	Short acuminate, mucronate	Rounded	Sinuous, sparse, diverging at about 40–110°	1/2 of valve length
K. allenii (Lesq.) W.N. Edwards	Obvate, obovoid-elliptic	3–5.5 × 1.8–2.4	Rounded, slightly emarginate, or mucronate	Narrowly cuneate or decurrent, slightly asymmetrical	Sinuous, diverging at about 30–90°	1/2 (or slightly more) of valve length
K. dilcheri Wang, Manchester, Gregor, Shen & Li	Oblong or oblong-elliptic	3.5–5.8 × 2.8–3.6	Rounded	Rounded	Sinuous, diverging at 30–100°	Incomplete
K. macroptera (Kováts) W.N. Edwards	Oblong-ovate, widely or narrowly ovate	3.4–5 × 2.5–4	Rounded, acute, slightly emarginate, or mucronate	Rounded, slightly truncate, cordate or concave-convex	Straight or sinuous, diverging at ca. 30–90° or even 110° near the base	1/3 (or slightly more) of valve length
K. miointegrifoliola Hu & Chaney	Widely ovate, oblong, elliptic, or suborbicular	3.2–5.2 × 3.0–4.2	Rounded, slightly emarginated, or mucronate	Rounded, slightly truncate or cordate	Sinuous, radiating at 30–150° from the carpellary suture	Ca. 1/2 of valve length
K. quasipaniculata Li, Xiao & He	Narrowly ovate or elliptic-ovate	3.7–4.3 × 1.9–2.7	Acute or slight acuminate	Rounded to slightly convex	Straight to somewhat sinuous, diverging at ca. 50–80°	1/3 of valve length
K. taoana Wang, Manchester, Gregor, Shen & Li	Elliptic or ovoid-elliptic	2.4–2.5 × 1.6–1.7	Rounded	Rounded or slightly truncate	Sinuous, diverging at 30–90° or even 120° near the base	Ca. 1/2 of valve length

nearly complete septum and in this respect, it is similar to *K. lunpolaensis*.

On the basis of careful reinvestigation of previously published *Koelreuteria* fossils, Wang et al. (2013) regarded five species as reliable fossil records of capsules or capsular valves of the genus. Recently, another species, *K. quasipaniculata* X. Li, L. Xiao et W. He was described from the early–middle Miocene Garang Formation of Zeku, Qinghai (Li et al., 2016). Among these six fossil species of *Koelreuteria*, *K. macroptera* (Kováts) W.N. Edwards (Edwards, 1927; Wang et al., 2013) and *K. quasipaniculata* (Li et al., 2016) have been referred to the *K. paniculata*-type. They are clearly different from *K. lunpolaensis* in having acute or slightly acuminate apex, symmetric or slightly asymmetric form, and septa that account for only about 1/3 of the valve length. *Koelreutera allenii* (Lesquereux) W.N. Edwards, *K. dilcheri* Q. Wang, Manchester, H.-J. Gregor, S. Shen et Z.Y. Li, *K. taoana* Q. Wang, Manchester, H.-J. Gregor, S. Shen et Z.Y. Li, and *K. miointegrifoliola* Hu et R.W. Chaney have been considered to belong to the *K. bipinnata*-type (Wang et al., 2013). They are readily distinguishable from *K. lunpolaensis* by the rounded, unlobed or nearly unlobed apex, symmetric or nearly symmetric form, and septum accounting for about half of the valve length.

3.3. Description of *Koelreuteria miointegrifoliola*

Species: *Koelreuteria miointegrifoliola* Hu et R.W. Chaney (Fig. 5)
Materials: IVPP B 2505 (Fig. 5a and b), XZDY2-0125 (Fig. 5k), XZDY2-0126 (Fig. 5f and g).

Description:

Fossils are preserved as part and counterpart of individual capsular valve impressions (Fig. 5a, b, g, h and i). The studied materials include one complete, excellently preserved valve (Fig. 5a and b) and two incomplete valves (Fig. 5f, g and k). The capsular valves are elliptical in outline. The complete valve is 2.92 cm long and 2.31 cm wide (Fig. 5a and b); the two incomplete valves are 2.22 cm (Fig. 5f and g) and 3.30 cm (Fig. 5k) wide respectively. The base of the valve is rounded, symmetric (Fig. 5a, b, f and g) or slightly asymmetric (Fig. 5k), the margins are entire, the apex is emarginate with a mucro representing part of the stigma (Fig. 5e). The middle vein of the valve representing the longitudinal carpellary suture is thick with a prominent septum in the proximal region (Fig. 5a and c). The lateral veins are craspedodromous, alternate to sub-opposite, diverging from the suture at an angle of 50–140° (Fig. 5c, d, h and i). They are slightly sinuous to nearly straight, running towards the valve margin and not tapering, terminate at the thick fimbrial veins (Fig. 5j). Intervening veins between the lateral veins in most cases are thinner than the lateral veins (Fig. 5j). Intervening veins anastomose with each other or lateral veins to form a reticulum with areoles that are relatively consistent in size and form, and generally with 3–6 sides (Fig. 5c, d, h, i, j and l). The septum is distally incomplete, extending approximately 50% of the valve length from the base of the valve. Seeds are not preserved.

Comments:

The Tibetan Oligocene material is well within the range of *Koelreuteria miointegrifoliola* Hu et R.W. Chaney that was originally proposed for compressed individual capsular valve and leaflet from the Miocene Shanwang Formation of Linqu, Shandong, East China (Hu and Chaney, 1938). The characteristics of the species include a rounded, slightly truncate or cordate base; a rounded, slightly emarginate, or mucronate apex, and an incomplete septum extending ca. half of the valve length based on recent revision of the species (Wang et al., 2013). *Koelreuteria miointegrifoliola* belongs to the *K. bipinnata*-type group and is the most similar to extant *K. bipinnata* that is distributed in South and Southwest China today. The fossil species has been also known from the Miocene of Honshu, Japan (see a review in Wang et al., 2013). The present discovery extends the fossil distribution of *K. miointegrifoliola* to central Tibet, and also extend its geological range to the late Oligocene.

4. Discussion

4.1. Diversity and diversification of *Koelreuteria* during the Oligocene/Miocene in the Tibetan Plateau

In recent years, more and more discoveries from the fossil record have provided important evidence for the biodiversity history in the Tibetan Plateau. The two species of *Koelreuteria* capsular valves from the late Oligocene of the Lunpola Basin, central Tibet (Fig. 6a and b), together with *K. quasipaniculata* recently reported from the early middle Miocene of Qinghai (Li et al., 2016; Fig. 6c), provide unequivocal evidence for the diversity of *Koelreuteria* in the Tibetan Plateau during the Oligocene and Miocene. *Koelreuteria miointegrifoliola* from the Lunpola Basin belongs to the *K. bipinnata*-type (Fig. 6b), while *K. quasipaniculata* from Qinghai belongs to the *K. paniculata*-type (Fig. 6c), suggesting that both groups of extant *Koelreuteria* were established in the plateau by the Oligocene/Miocene. *Koelreuteria lunpolaensis* (Fig. 6a) clearly differs from the two groups of extant *Koelreuteria* and other known fossil species of the genus in the form of the capsular valves and thus might represent a third group of *Koelreuteria* that had become extinct.

Therefore, the available fossil evidence suggests that the Tibetan Plateau was an important centers for diversity and diversification of *Koelreuteria* in the Oligocene/Miocene. The genus is hardly diverse in Cenozoic floras of other regions of the world. Fossils of the *K. paniculata*-type are exclusively known from the Europe except for *K. quasipaniculata* from Qinghai, while fossils of *K. bipinnata* type are only present in Asia and North America. It is of interest to note that tricolporate, spheroidal pollen grains (*Talisiipites megorites* Song and Li), being similar to those of extant *Koelreuteria*, have been reported from the Santonian–Maastrichtian (late Late Cretaceous) of the Xigaze Region, Tibet (Song et al., 2004; Li et al., 2008), although these pollen grains could be also produced by other plants within or outside the family Sapindaceae. Today *Koelreuteria* is absent in Tibetan Plateau, but present and diverse in neighboring regions (Sichuan and Yunnan Provinces of China) with both *K. paniculata* and *K. bipinnata* (Xia and Luo, 1995; Xia and Gadek, 2007). *Koelreuteria lunpolaensis* is very similar to *K. bipinnata* that occurs in Sichuan and Yunnan today in morphology of capsular valves, suggesting a close relationship of the two species. The extinction of *K. lunpolaensis* is very likely related to the continued uplift of the Tibetan Plateau after the Oligocene and subsequently dramatic climatic changes (Spicer et al., 2003; Deng and Ding, 2015; Ding et al., 2017).

4.2. Biogeographic implications

Paleobotanical evidence demonstrates that *Koelreuteria* with capsule/capsular valves similar to the extant *K. bipinnata*-type had been well established in the mid-latitude regions of the Russian Far East, northeastern China and western North America by the middle Eocene (see a review in Wang et al., 2013; Fig. 7). However, *K. bipinnata*-type fossil capsules or capsular valves are absent from the Oligocene deposits throughout the world except for *K. miointegrifoliola* from central Tibet, although *K. paniculata*-type fossils are known from the Oligocene of Europe (Fig. 7). This appears to suggest that the Lunpola Basin was not only a center for diversity and diversification of *Koelreuteria* during the late Oligocene, but also served as a refugium for the *K. bipinnata*-type group in the late Oligocene. Oligocene floras are quite rare in China. Until now, *Koelreuteria* is not present in the extensively collected, highly diverse Oligocene Ningming flora from Guangxi, South China (Shi et al., 2012, 2014) nor in the late Oligocene Santang flora from Guangxi (Quan et al., 2016). Therefore, *K. bipinnata*-type fossils (*Koelreuteria miointegrifoliola*) from the middle Miocene of Shanwang, Shangdong, East China (Hu and Chaney, 1938), and from the late Miocene of

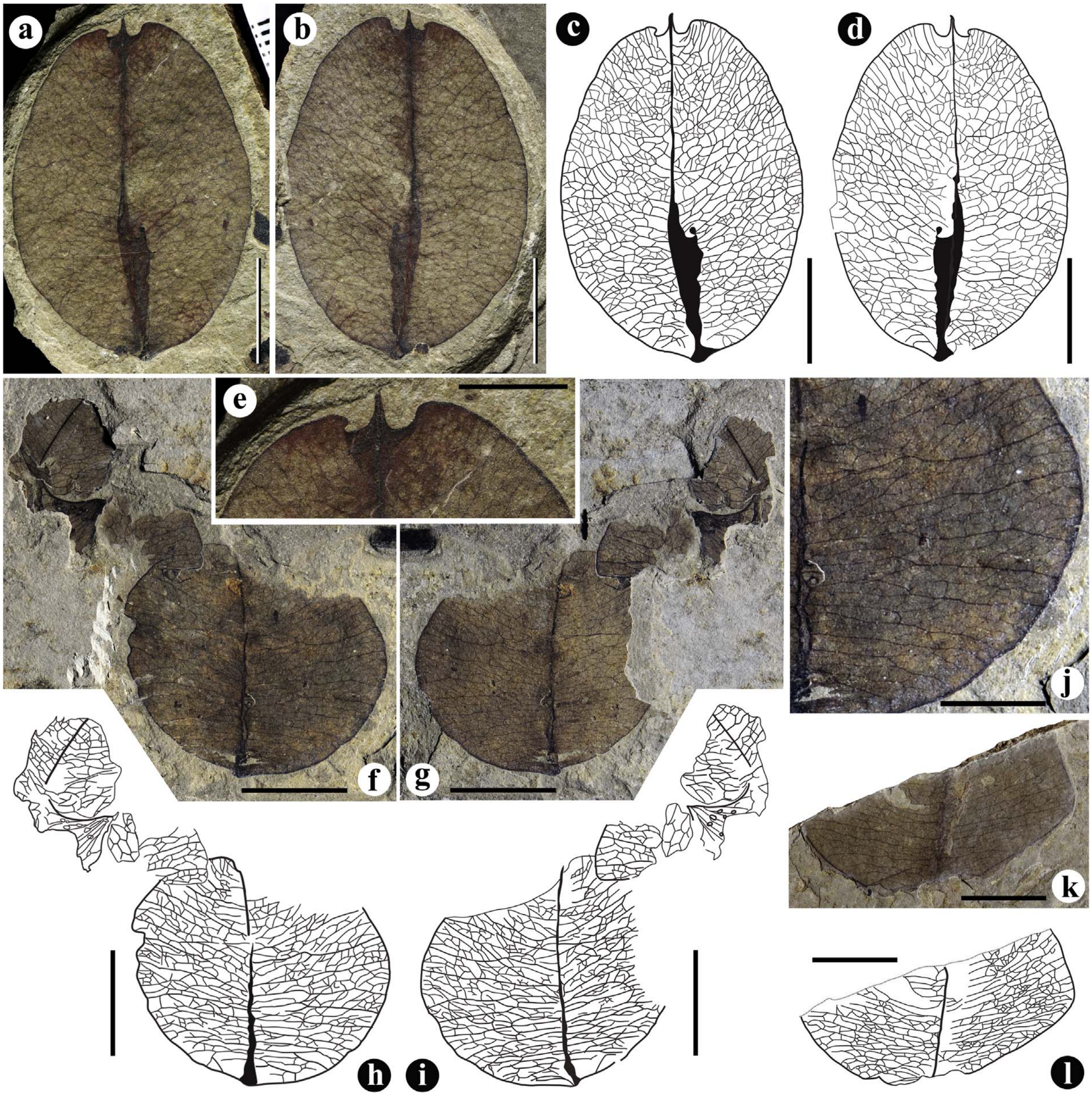

Fig. 5. *Koelreuteria miointegrifoliola* Hu et R.W. Chaney. Scale bars in (a)–(d), (f)–(i), (k), (l) = 1 cm. (a) Individual capsular valve. Note that the septum extends approximately half of valve length from base of valve. IVPP B 2505-a. (b) Counterpart of specimen in (a). IVPP B 2505-b. (c) Line drawing of (a). (d) Line drawing of (b). (e) Detail of apical region of capsular valve, enlarged from (a), showing the emarginate apex with a mucro. Scale bar = 5 mm. (f) Individual capsular valve. XZDY2-0126-a. (g) Counterpart of specimen in (f). XZDY2-0126-b. (h) Line drawing of (f). (i) Line drawing of (g). (j) Detail of middle region of capsular valve, enlarged from (f), showing detailed venation. Scale bar = 5 mm. (k) Incompletely preserved capsular valve. XZDY2-0125. (l) Line drawing of (k).

Ninghai, Zhejiang, East China (Li and Guo, 1982; Li, 1984) might have migrated from Tibet after the Oligocene.

4.3. Paleoenvironmental implication

The extant species of *Koelreuteria bipinnata*-type (*K. bipinnata*, *K. henryi*, and *K. elegans*), which *K. miointegrifoliola* from the late Oligocene of central Tibet closely resembles, produce deciduous trees up to 20 m high, inhabiting subtropical to tropical forests at altitudes of up to 2500 m (Xia and Luo, 1995; Xia and Gadek, 2007). It is very likely that *K. miointegrifoliola* inhabited a similar environment in the late Oligocene of central Tibet, as its living relatives. Other fossil plant assemblages containing *K. miointegrifoliola* in China, e.g. the middle Miocene Shanwang flora (Hu and Chaney, 1938) and the late Miocene Xia'nanshan flora (Li and Guo, 1982; Li, 1984) in East China, also represent a subtropical lowland vegetation in a warm and humid climate. The fossil anabantid fish *Eoanabas* (Anabantidae) (climing perch) from the same bed of the Dingqing Formation, as well as the plant megafossil assemblage of the formation including palms, suggest a warm and humid environment with an elevation of ca. 1000 m in the Lunpola Basin during the late Oligocene, in stark contrast to the vegetation of alpine meadow in the Lunpola Basin with an elevation of ca. 4500 m today (Wu et al., 2017). It is consistent with a recent cyclostratigraphic study, which reveals that the regional uplift of the Lunpola Basin occurred at the latest Oligocene (23.7 Ma) (Ma et al., 2017).

The plant megafossil assemblage from the late Oligocene of Lunpola appears more comparable to the modern lowland subtropical vegetation in Zhejiang, East China in leaf physiognomy (Wu et al., 2017). The palynological evidence, however, suggests a mixed coniferous-broadleaved forest in the Lunpola Basin during the late Oligocene, with the coexistences of subtropical, temperate and mountain coniferous elements (Sun et al., 2014). This is not surprising considering the long

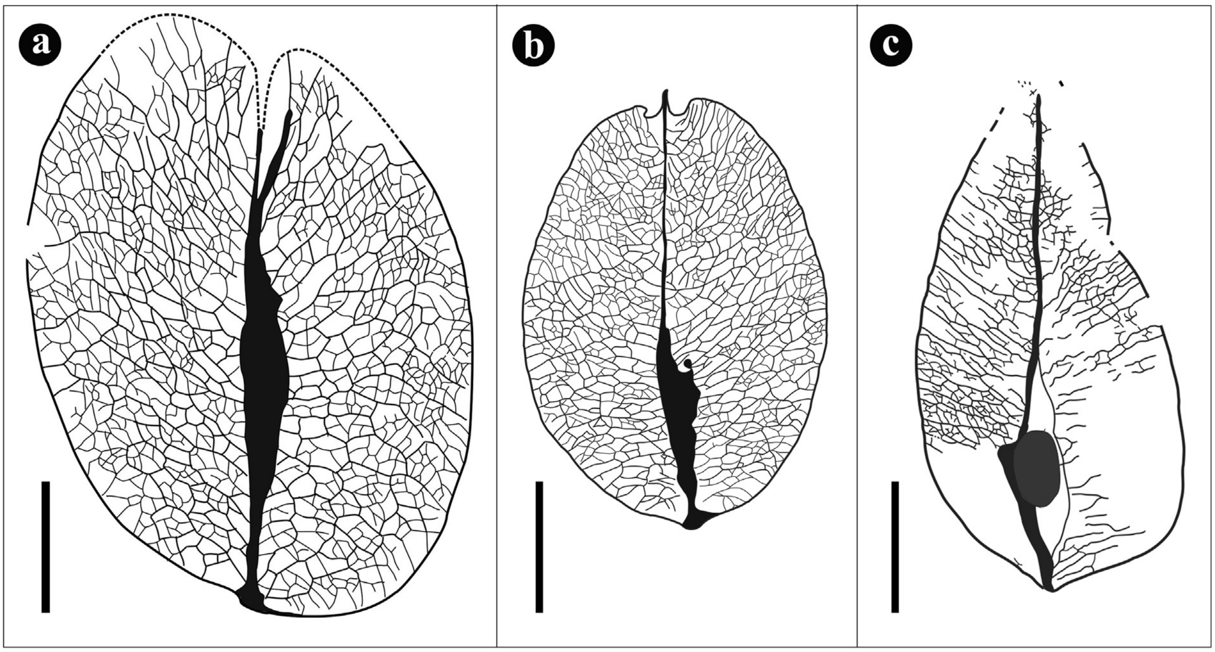

Fig. 6. Morphological diversity of *Koelreuteria* capsular valves in the Oligocene/Miocene of Tibetan Plateau. All scale bars = 1 cm. (a) *K. lunpolaensis* sp. nov. (b) *K. miointegrifoliola* Hu et R.W. Chaney. (c) *K. quasipaniculata* X. Li, L. Xiao et W. He, redrawn after Li et al. (2016).

distance of transportation of the bissacate pollen grains of certain conifers, especially alpine conifers including *Abies* and *Picea*, and indicates the complication of reconstructing the uplift history of the Tibetan Plateau. However, the plant megafossils and fish from the late Oligocene of the Lunpola Basin suggest a regional, lowland vegetation. The understanding of the evolution of the vegetation in the Tibetan Plateau on a large scale relies on more discoveries of fossils in this region.

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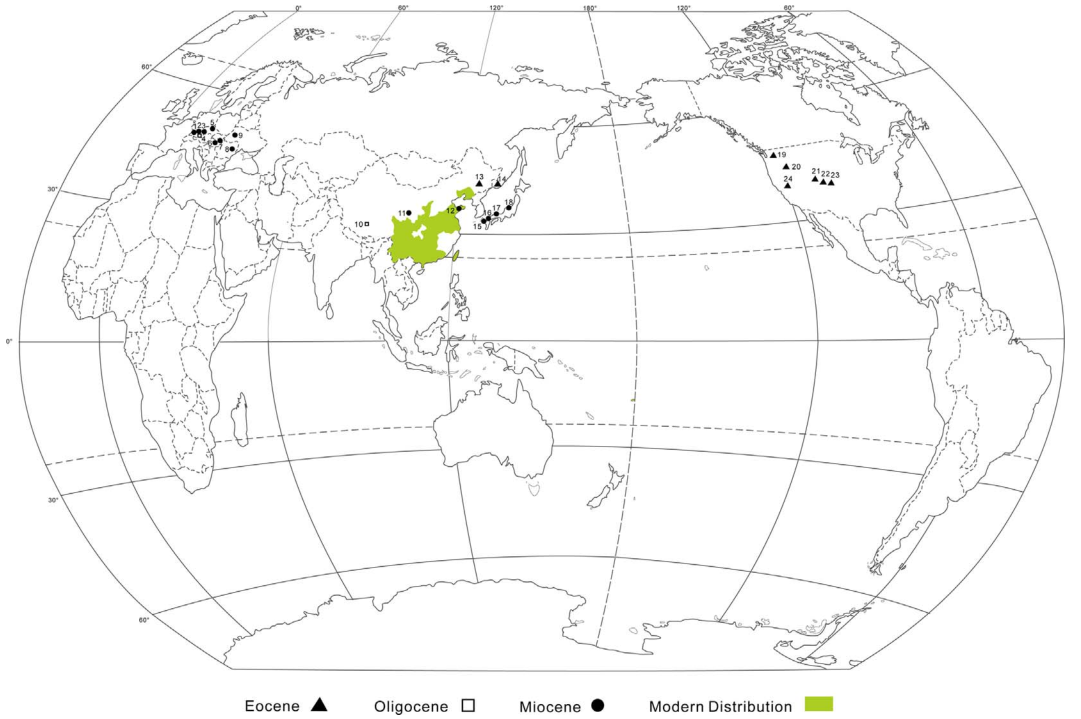

Fig. 7. Distribution of modern and fossil *Koelreuteria*, only fossil species represented by capsules/capsular valves are dotted. Data based on Wang et al. (2013). 1. Randecker Maar, Germany. 2. Burtenbach, Germany. 3. Geisenhausen, Germany. 4. Rott, Germay. 5. N. Bohemia, the Czech Republic. 6. Gomboska of Tállya, Hungary. 7. Déllő, Hungary. 8. Chiuzbaia, Romania. 9. Klepariv of L'viv City, Ukraine. 10. Lunpola, Tibet, China. 11. Zeku, Qinghai, China. 12. Shanwang, Shandong, China. 13. Huadian, Jilin, China. 14. Uglovsky (Uglovskaya) Basin, South Primorye, Russia. 15. Chōjabaru, Iki Island, Japan. 16. Shimonoseki, Southwest Honshu, Japan. 17. Tottori Prefecture, Southwest Honshu, Japan. 18. Ogumi-machi, Yamagata Prefecture, Japan. 19. Republic, Washington, USA. 20. Teater Road, Oregon, USA. 21. Fossil Butte, Wyoming, USA. 22. De Beque, Colorado, USA. 23. Florissant, Colorado, USA. 24. Independence Hill near Colfax, California, USA.

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