

Fossil leaves of *Berhamniphyllum* (Rhamnaceae) from Markam, Tibet and their biogeographic implications

Zhekun ZHOU^{1,2*†}, Tengxiang WANG^{1,3†}, Jian HUANG¹, Jia LIU¹, Weiyudong DENG^{1,3},
Shihu LI^{4,5}, Chenglong DENG⁴ & Tao SU^{1,3§}

¹ Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna 666303, China;

² Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China;

³ University of Chinese Academy of Sciences, Beijing 100049, China;

⁴ State Key Laboratory of Lithospheric Evolution, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing 100029, China;

⁵ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

Received May 7, 2019; revised August 16, 2019; accepted August 23, 2019; published online November 22, 2019

Abstract A new occurrence of buckthorn fossil leaves is reported from the upper Eocene strata of Markam Basin, southeastern Tibet, China. The leaf margin is either entire or slightly sinuous. Secondary veins are regularly spaced, forming eu-campitodromous venation. These secondaries exist as straight lines from midvein to near margin and then arch abruptly upward and enter into a margin vein. The tertiary veins are densely spaced and parallel, and are percurrent to secondary veins. This leaf architecture conforms with *Berhamniphyllum* Jones and Dilcher, an extinct fossil genus reported from America. Our fossils are characterized by their dense secondaries, with secondary veins on the upper half portion of the blade accounting for over 40% of all secondaries. A new species, *Berhamniphyllum junrongiae* Z. K. Zhou, T. X. Wang et J. Huang sp. nov., is proposed. Further analysis shows that confident assignment among *Rhamnidium*, *Berchemia*, and *Karwinskia* cannot be made based on leaf characters alone. *Berhamniphyllum* might represent an extinct common ancestor of these genera. In this study, several fossil *Berchemia* from Yunnan and Shandong are emended and reassigned to *Berhamniphyllum*. A new complex, namely the *Berchemia* Complex, is proposed based on morphology, molecular evidence, and the fossil record. This complex contains the fossil leaves of *Rhamnidium*, *Karwinskia*, *Berchemia*, and *Berhamniphyllum*. The historical biogeography of the *Berchemia* Complex is also discussed in this paper. This complex might have originated in the late Cretaceous in Colombia, South America, and dispersed to North America via Central America during the Eocene. Subsequently, the complex moved from North America to East Asia via the Bering Land Bridge no later than the late Eocene. Besides, the complex migrated from North America to Europe via the North Atlantic Land Bridge and then migrated further to Africa. In East Asia, it first appeared in Markam on the Qinghai-Tibetan Plateau, and then dispersed to other regions of Asia.

Keywords *Berchemia* complex, *Berhamniphyllum*, Cenozoic, Qinghai-Tibetan Plateau, Biogeography

Citation: Zhou Z, Wang T, Huang J, Liu J, Deng W, Li S, Deng C, Su T. 2020. Fossil leaves of *Berhamniphyllum* (Rhamnaceae) from Markam, Tibet and their biogeographic implications. *Science China Earth Sciences*, 63: 224–234, <https://doi.org/10.1007/s11430-019-9477-8>

† Contributed equally to this work

* Corresponding author (email: zhouzk@xtbg.ac.cn)

§ Corresponding author (email: sutao@xtbg.org.cn)

1. Introduction

The modern distribution pattern of a taxon may be closely related to its dispersal history in the geological past. This can be reconstructed by studying the fossil record of the taxon. In this way, fossil material plays a critical role in biogeography research (Taylor et al., 2008). Tracing back the fossil history of a certain taxon can provide a glimpse into how its distribution pattern has evolved throughout geological time. Therefore, studying a taxon's fossil history has become an important component in biogeography research.

The uplift of the Qinghai-Tibetan Plateau (QTP) is one of the most important geological events during the Cenozoic. This event significantly altered the topography of Asia and reshaped Asian atmospheric circulation, thereby having a significant impact on the biodiversity of Asia. Many studies, in both Earth sciences and life sciences, have focused on how the uplift of the plateau and the corresponding environmental effects influenced the biodiversity in this area. In recent years, an increasing number of new fossil taxa have been discovered and reported, and they have increased our understanding of the topographical history of the QTP; furthermore, these discoveries have also provided a novel insight into the evolution of the biodiversity of the QTP (Ding et al., 2017; Spicer, 2017; Wu et al., 2017; Ai et al., 2019; Deng et al., 2019; Jia et al., 2019; Jiang et al., 2019; Liu et al., 2019; Su et al., 2019a, 2019b; Tang et al., 2019; Xu C L et al., 2019; Xu H et al., 2019).

These recent studies indicate that a close link between flora on the QTP and other regions of the Northern Hemisphere was already established as early as the Paleogene, when the

QTP acted as a Floristic Hub for the exchange of floristic elements within the Northern Hemisphere. Some taxa, such as *Ailanthus*, entered the QTP from the Indian subcontinent (Liu et al., 2019), while some, such as *Cedrelospermum*, dispersed from North America to the QTP, after which they spread to other regions of East Asia (Jia et al., 2015, 2019). In addition, *Lagokarpus*, another extinct genus, has been found in Eocene strata in North America and Europe, and was recently discovered in Eocene strata on the QTP (Tang et al., 2019). However, our understanding of Cenozoic QTP floras is currently far from sufficient especially considering the tremendously vast area it covered. A more comprehensive study of Cenozoic QTP fossil flora is required to clarify how the QTP flora has exchanged and connected with floras in other parts of the Northern Hemisphere.

Berchemia is a genus of Rhamnaceae with about 32 living species. Most of *Berchemia* species are woody liana, rarely shrubs or small trees (Chen and Schirarend, 2007). This genus is distributed in temperate and tropical areas of East to Southeast Asia, while there is one species, *Berchemia scandens*, that is distributed in southeastern United States to Chiapas and Guatemala (Flora of North America Editorial Committee, 1993+). Two species are present in South Africa (Palgrave, 2015). Wu et al. (2006) classified the areal-type of *Berchemia* into areal-type 9, known as 'East Asia and North America disjuncted'. However, it is well documented that *Berchemia* also has an African distribution, indicating an areal-type closer to 'Tropical Asia-Tropical Africa-Tropical America (South America)' (areal-type 2-2) (Figure 1). In the tribal classification of Rhamnaceae proposed by Richardson et al. (2000), *Berchemia* was removed from the tribe Zizi-

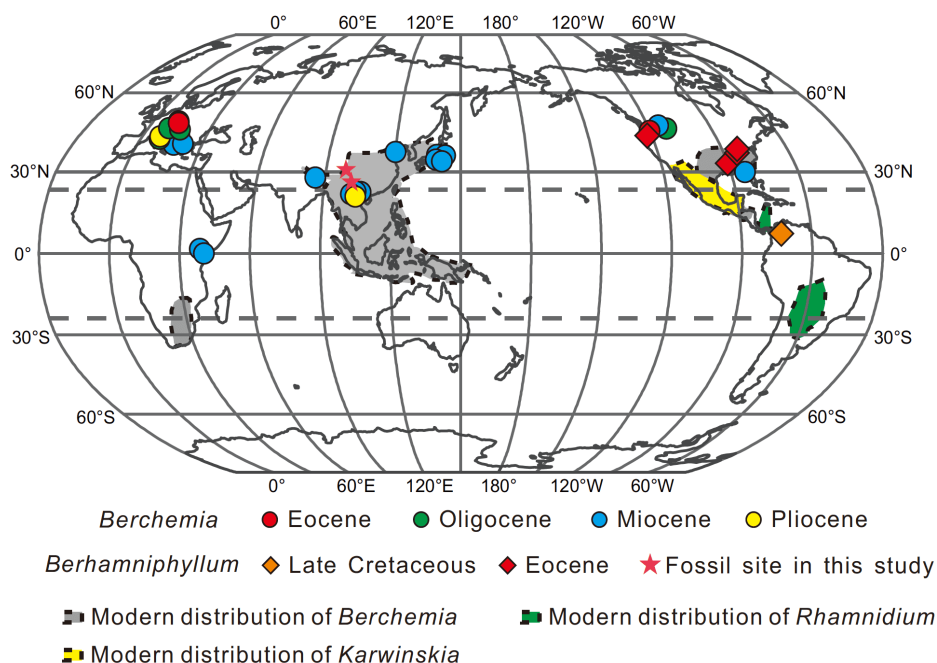


Figure 1 Historical and modern distribution of *Berchemia* and resembling taxa.

phaea and placed in Rhamnaceae. The tribe Rhamnaceae is mainly distributed in the Pantropics and temperate area of the Northern Hemisphere. Among them, six genera are distributed in China, i.e., *Berchemia*, *Berchemiella*, *Rhamnella*, *Rhamnus*, *Sageretia*, and *Scutia*.

Berchemia and its affinities, have abundant fossil records (Figure 1; Tables 1 and 2). The earliest fossil record of *Berchemia* and its affinities can be traced back to the latest late Cretaceous of Colombia, where there are fossil leaves assigned to *Berhamniphyllum* sp. (Correa et al., 2010). As for *Berchemia*, the earliest record was reported as an endocarp from the Middle Eocene Messel biota (Collinson et al., 2012). *Berchemia* and its affinities from the Cenozoic have been reported sporadically in North America, Europe, Asia and Africa (Becker, 1969; WGPC, 1978; Manchester, 2000; Bozukov et al., 2008; Collinson et al., 2009; Lazarević et al., 2013) (Figure 1; Tables 1 and 2). *Berhamniphyllum* sp.

comprises the earliest fossil record of the tribe Rhamnaceae, and might represent the common ancestor of *Berchemia* and *Rhamnidium*. In modern plants, these two genera show some resemblance in morphology to each other, and are clustered in one clade based on molecular phylogenetics (Hauenschild et al., 2018). *Berchemia* species are mostly distributed in East and Southeast Asia, while only a few species are found in North America and South Africa. The formation of the modern distribution pattern of *Berchemia* is similar to that of Malpighiaceae (Davis et al., 2002; Zhou et al., 2006). Both of them, adopting a so-called Malpighiaceae route of dispersal, originated from northern South America. Members of several clades repeatedly migrated northward to North America, and subsequently moved via the North Atlantic Land Bridge into Europe and Tropical Asia, or moved southward from Europe to Africa. Their distribution pattern today was formed in this way (Zhou et al., 2006), and gives rise to

Table 1 Fossil record of *Berchemia*

Species	Organ	Age	Locality	Reference
<i>Berchemia melleriae</i>	Endocarp	Middle Eocene	Messel, Germany	Collinson et al., 2012
<i>B. sp</i>	Leaf	Late Eocene	Wheeler County, Oregon, USA	Manchester, 2000
<i>B. althorhenana</i>	Leaf	Early Oligocene	Rauenberg, Germany	Kovar-Eder, 2016
<i>B. multinervis</i>	Leaf	Late Oligocene	Ebnat-Kappel, Switzerland	Büchler, 1990
<i>B. multinervis</i>	Leaf	Late Oligocene	Vulche Pole Molasse Formation, SE Bulgaria	Bozukov et al., 2008
<i>B. multinervis</i>	Leaf	Late Oligocene	Petrosani Basin, Romania	Givulescu, 1996
<i>B. huanoides</i>	Leaf	Late Oligocene	Beaverhead County, Montana, USA	Becker, 1969
<i>B. multinervis</i>	Leaf	Miocene	Western Rhodopes, Bulgaria	Bozukov, 2000
<i>B. priscaformis</i>	Leaf	Miocene	South Caroline, USA	Berry, 1916b
<i>B. sp</i>	Leaf	Miocene	Clarkia, Idaho, USA	Smiley et al., 1975
<i>B. pseudodiscolor</i>	Seed	Early Miocene	Rusinga Island, Kenya	Collinson et al., 2009
<i>B. acutangula</i>	Leaf	Early Miocene	Goldern, Bavaria	Spitzelberger, 1989
<i>B. miofloribunda</i>	Leaf	Early Miocene	Honshu, Japan	Yabe, 2008
<i>B. multinervis</i>	Leaf	Early Miocene	Valjevo-Mionica Basin, Serbia	Lazarević et al., 2013
<i>B. multinervis</i>	Leaf	Early Miocene	Most Basin, Czech	Sakala, 2000; Teodoridis, 2007
<i>B. multinervis</i>	Leaf	Early-middle Miocene	Canton Lucerne, Switzerland	Köecke and Uhl, 2015
<i>B. pseudodiscolor</i>	exocarp	Middle Miocene	Fort Ternan, Kenya	Retallack, 1992
<i>B. miofloribunda</i>	Leaf	Middle Miocene	Noto Peninsula, Japan	Ishida, 1970
<i>B. nepalensis</i>	Leaf	Middle Miocene	Koilabas, Nepal	Prasad and Dwivedi, 2007
<i>B. multinervis</i>	Leaf	Late Miocene	Lerch, Bavaria	Jung, 1968
<i>B. multinervis</i>	Leaf	Late Miocene	Oehingen, Switzerland	Hantke, 1954; Heer, 1855–1859
<i>B. miofloribunda</i>	Leaf	Late Miocene	Honshu, Japan	Ozaki, 1980
<i>B. miofloribunda</i>	Leaf	Late Miocene	Honshu, Japan	Ozaki, 1991
<i>B. calymmatophyllua</i>	Leaf	Late Miocene	Lincang, Yunnan Province, China	Guo, 2011
<i>B. miofloribunda</i>	Leaf	Pliocene	Tuantian, Yunnan Province, China	Wu, 2009
<i>B. cf. yunnanensis</i>	Leaf	Pliocene	Tuantian, Yunnan Province, China	Wu, 2009
<i>B. multinervis</i>	Leaf	Pliocene	Fossano, Italy	Macaluso et al., 2018
<i>B. floribunda</i>	Leaf	LateTertiary	Jharkhand, India	Singh and Prasad, 2007

Table 2 Fossil records of *Berchemia* affinities

Species	Age	Locality	Reference
<i>Berhamniphyllum</i> sp.	Late Cretaceous	Paz de Río, Boyacá, Columbia	Correa et al., 2010
<i>Berhamniphyllum claibornense</i>	Early Eocene	Puryear County and Henry County, Tennessee; Graves County, Kentucky	Berry, 1916a; Jones and Dilcher, 1980
<i>Berhamniphyllum claibornense</i>	Middle Eocene	Powers Pit, Western Tennessee	Dilcher and Lott, 2005
<i>Berhamniphyllum</i> sp.	Middle Eocene	Powers Pit, Western Tennessee	Dilcher and Lott, 2005
<i>Berhamniphyllum</i> sp.	Late Eocene	The Willamette flora, Oregon	Myers et al., 2002
<i>Berhamniphyllum junrongiae</i>	Late Eocene	Markam, Tibet, China	This study
<i>Karwinskia axamilpense</i>	Oligocene	Puebla, Mexico	de León et al., 1998
<i>Berhamniphyllum miofloribundum</i>	Miocene	Shanwang, Shandong Province, China; Wenshan and Xiaolongtan, Yunnan Province, China	WGCPC, 1978; Zhou, 1985; Huang, 2017; this study

important and interesting phytogeographic questions. Studying the fossil history, phylogenetic relationship, and developing processes of geographic distribution will provide a better understanding of how the modern distribution pattern of the tribe Rhamneae or even Rhamnaceae occurred. Furthermore, these studies can provide important evidence for the origin and development of Pantropic disjunct distribution.

The Markam Basin (also known as the Mangkang Basin) is located on the southeastern margin of the QTP, and is tectonically within the Qiangtang Terrane. The collision between the Indian subcontinent and Eurasia caused strong extrusion and deformation within the plateau and nearby regions, and also had a significant impact on the development of the Markam Basin. The basin falls within the Hengduan Mountain region, which is well known as a biodiversity hotspot (Myers et al., 2000). Studying how plant diversity has evolved through time in this region is not only important to understanding the changing processes of its biota, but is also critical to understanding the paleoaltitude and paleotopography of the southeastern margin of the QTP and even the uplift history of the entire QTP (Su et al., 2019b). Recently, we discovered fossil leaves of *Berhamniphyllum* in the Upper Eocene strata in the Markam Basin. These fossil leaves represent the earliest fossil record for this genus. Our discovery can provide new insights into the connection and communication among QTP flora and floras from other regions of the Northern Hemisphere during the Paleogene.

In this paper, we describe a new species, *Berhamniphyllum junrongiae* Z. K. Zhou, T. X. Wang et J. Huang sp. nov., and emend the previous fossil records of *Berchemia* from the Miocene of Yunnan and Shandong provinces, China. The phylogenetic relationship among *Rhamnidium*, *Berchemia*, and *Berhamniphyllum* is also discussed. Taking this discovery as an example, we discuss the lineage among the QTP flora and floras from other regions. In addition, the pattern of their distribution history is also discussed.

2. Materials and methods

2.1 Fossil locality and geological setting

The fossil materials in this study were found from the Lawula Formation near Kajun village, Markam, Tibet, China; the Huazhige Formation, Wenshan, Yunnan Province, China; and the Xiaolongtan Formation, Kaiyuan, Yunnan Province, China (Figure 2).

Fossil materials labeled MK3-1491 and MK3-2155 were collected from brownish-yellow mudstones in the Lawula Formation near Kajun village, Markam, Tibet, China. This fossiliferous layer was marked as MK3 in a previous study (Su et al., 2019b). The Lawula Formation mainly comprises grayish-white and grayish-yellow sandstone, siltstone, and mudstone and is regarded as fluvial and lacustrine facies deposits, interbedded with volcanic rocks. Numerous plant fossils were collected from siltstone and mudstone. Detailed information on the stratigraphy of this fossil-bearing stratum has been extensively described in Su et al. (2014, 2018, 2019b). The fossiliferous layer MK3 is interbedded between two layers of volcanic rocks, and the ages of the lower and upper layers are ca. 35.5 and 34.6 Ma, respectively, using $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating (Su et al., 2019b). Therefore, the age of MK3 is assigned to the latest late Eocene.

Fossil materials labeled DMS-1713 and DMS-3872 were collected from the Huazhige Formation, Dashidong village, Wenshan, Yunnan Province, China. The Huazhige Formation mainly comprises greenish-gray, grayish-white, or brownish-yellow lacustrine mudstone, calcareous mudstone, and siltstone (Li S F et al., 2015; Lebreton-Anberrée et al., 2016). Magnetostratigraphic analysis indicated that the fossiliferous layers were deposited between 16.5–15.2 Ma, middle Miocene in age (Lebreton-Anberrée et al., 2016).

Fossil material labeled PB12521 was collected from the Xiaolongtan Formation, Kaiyuan, Yunnan Province, China. The Xiaolongtan Formation mainly comprises gray marl and black lignite. Magnetostratigraphic analysis indicated the age of the Xiaolongtan Formation to be 12.7–10 Ma, late

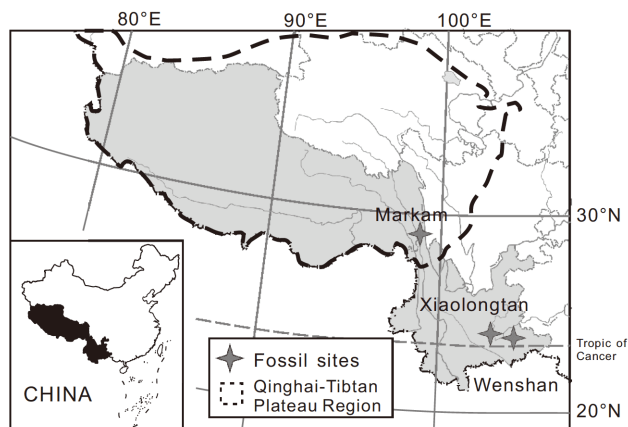


Figure 2 Fossil locality in Yunnan and Tibet, China.

Miocene (Li S H et al., 2015). This age is consistent with palynology (Wang, 1996) and paleontology results (Dong and Qi, 2013).

Other emended fossil materials were extracted from previous published literatures.

2.2 Methods

The fossil materials were labelled and photographed. Fossil records of *Berchemia* and its affinities were extracted from published literature. Fossil records compiled in this study were checked, and their credibility is assured.

Modern species for comparison were derived from the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN) and The Royal Botanic Garden, Kew (K). We also checked online databases including JSTOR Global Plants database and the Chinese Virtual Herbarium (CVH). Cleared leaf material of extant *Berchemia* species was collected from Xishuangbanna Tropical Botanical Garden (XTBG). Leaf architecture terminology follows Ellis et al. (2009). Classification system follows Angiosperm Phylogeny Group IV (APG IV).

3. Systematic paleontology

Order: Rosales Bercht. & J. Presl

Family: Rhamnaceae Juss

Genus: *Berhamniphyllum* Jones and Dilcher

(1) *Berhamniphyllum junrongiae* Z. K. Zhou, T.X. Wang et J. Huang sp. nov. (Figure 3a–3c and 3g)

Etymology: The specific epithet *junrongiae* is dedicated to a Chinese paleobotanist Prof. Junrong Tao for her significant contributions to the Cenozoic Paleobotany of China and pioneering work on Markam flora.

Holotype: MK3-1491 (Figure 3a–3b and 3g).

Paratype: MK3-2155 (Figure 3c).

Respiratory: Paleoecology Collections, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences.

Locality: Upper Eocene Lawula Formation, Kajun village, Markam, Tibet, China.

Diagnosis: Leaf form varied greatly. Leaf margin entire or sinuous. Secondaries eucamptodromous, spacing regular. Secondaries straight from the midvein to near margin then arching abruptly upward and entering into a margin vein (Figure 3b and g). Secondaries dense on the upper half portion of the blade. Tertiaries dense and parallel, percurrent, obtuse to the midvein.

Description: Leaves oblong to narrowly ovate with a length of 2.8–9.3 cm, a width of 1.4–2.9 cm and length to width ratio of 2.0:1–3.2:1. Margin entire, sometimes sinuous; apex angle obtuse, apex shape straight or convex; base angle obtuse, base shape convex; apex and base symmetrical. Petiole missing. Venation pinnate; midvein straight; secondaries eucamptodromous, 10–14 pairs, 4–8 pairs on the upper half part of the blade, accounting for 40–57% of all secondaries, spacing regular, secondary angle smoothly increasing proximally ranging from 17°–46°, attachment excurrent; secondaries straight from the midvein to near margin then arching abruptly upward and entering into a margin vein (Figure 3b and g); intersecondaries rare or absent, parallel to major secondaries. Intercostal tertiary veins percurrent and straight opposite, sometimes dichotomous, obtuse to the midvein, vein angle consistent; quaternary veins not visible.

(2) *Berhamniphyllum miofloribundum* (Hu et Chaney) J. Huang, T. Su et Z. K. Zhou comb. nov. (Figure 3d–3f)

1940 *Berchemia miofloribunda* Hu et Chaney, p. 65, pl. 9: 5; pl. 40: 2–3

1978 *Berchemia miofloribunda* Hu et Chaney, p. 140, Fig. 1, 2; pl. 130: 3

Specimens examined: DMS-1713, DMS-3872 (Huazhige Formation, Wenshan, Yunnan Province, China); PB12521 (Xiaolongtan Formation, Kaiyuan, Yunnan Province, China)

Additional description: Previously assigned fossil leaves of *Berchemia miofloribunda* from Wenshan (Figure 3d–3e) and Xiaolongtan (Figure 3f) are emended and reassigned to *Berhamniphyllum miofloribundum*. Leaves elliptic with a length of 1.6–2.5 cm, a width of 1.1–1.4 cm, length to width ratio of 1.5:1–2.1:1. Margin entire, apex angle obtuse, apex shape rounded or convex; base angle obtuse, base shape convex or straight; apex and base symmetrical. Petiole missing. Venation pinnate; midvein straight; secondaries eucamptodromous, 5–9 pairs, 1–3 pairs on the upper half part of the blade, accounting for 20–33% of all secondaries, spacing regular, secondary angle smoothly increasing proximally ranging from 15°–52°, attachment excurrent or decurrent; secondary veins straight from the midvein to near margin then arching abruptly upward and entering into a

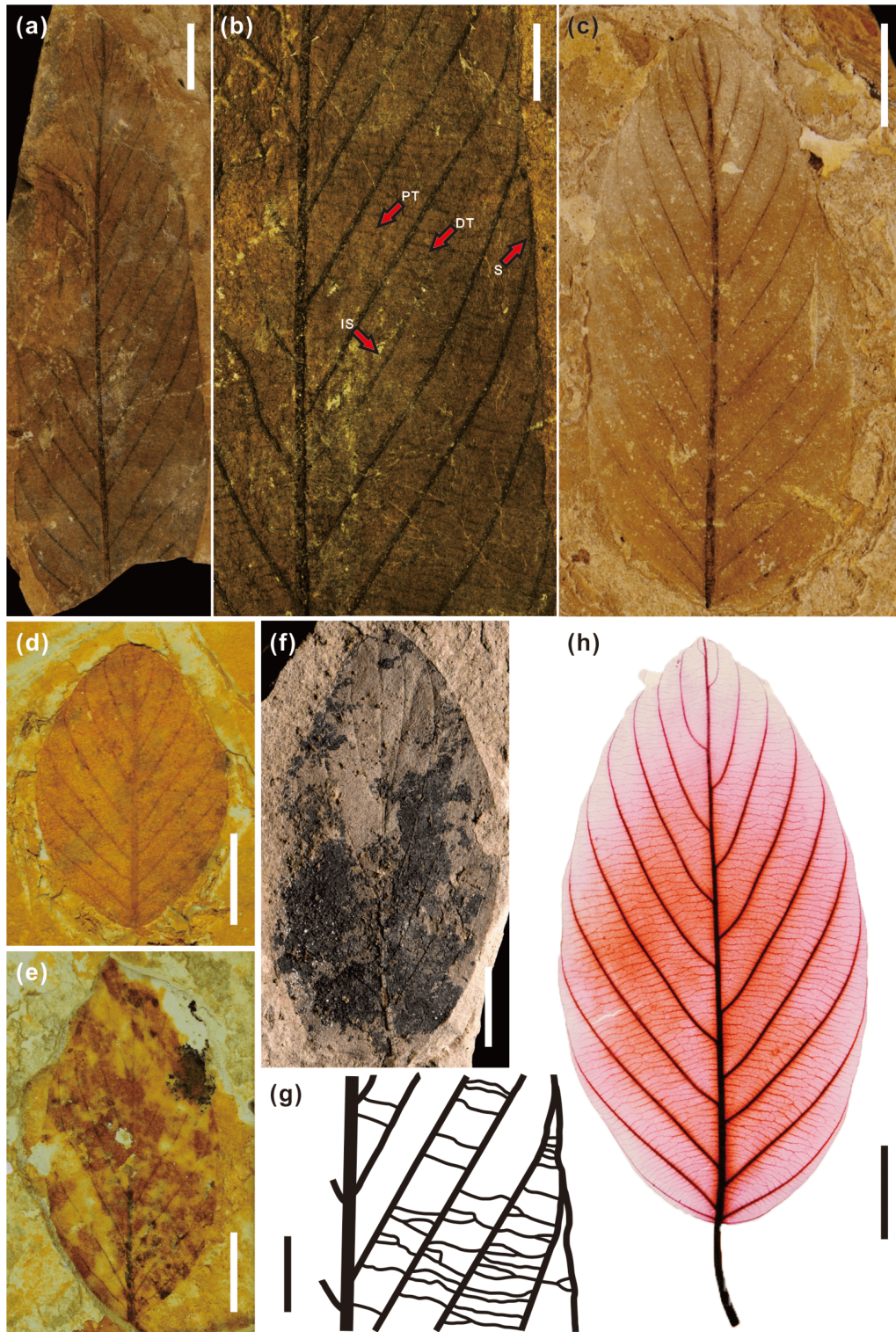


Figure 3 *Berhamniphyllum* fossils reported in this study and cleared leaf of extant species *Berchemia longipes*. (a)–(c) *Berhamniphyllum junrongiae* Z. K. Zhou, T. X. Wang et J. Huang sp. nov., (a) MK3-1491, scale bar=1 cm; (b) Details of MK3-1491, S, secondary veins; IS, inter secondary veins; PT, percurrent tertiary veins; DT, dichotomous tertiary veins, scale bar=0.5 cm; (c) MK3-2155, scale bar=0.5 cm. (d)–(f) *Berhamniphyllum miofloribundum* (Hu et Chaney) J. Huang, T. Su et Z. K. Zhou comb. nov., (d) DMS-1713, scale bar=0.5 cm; (e) DMS-3872, scale bar=0.5 cm; (f) PB12519, scale bar=0.5 cm. (g) Line drawing of MK3-1491, scale bar=0.5 cm; (h) Cleared leaf of *Berchemia longipes*, scale bar=1 cm.

margin vein; intersecondaries none. Intercostal tertiary veins percurrent and straight opposite, sometimes dichotomous,

obtuse to the midvein, vein angle consistent; quaternary veins not visible.

4. Discussion

4.1 Identification and comparison

The fossil materials from Markam have either an entire or slightly sinuous margin. The secondary veins are spaced regularly, forming eucamptodromous venation. They are straight from the midvein to near margin and then arch abruptly upward and enter into a margin vein. The tertiary veins are densely spaced and parallel, and are percurrent to secondary veins. This combination of leaf traits appears in *Cornus* of Cornaceae and some genera of the tribe Rhamneae, for example, *Berchemia* (Figure 3h), *Berchemiella* and their American relatives, *Rhamnidium* and *Karwinskia*. However, the leaf shape of *Cornus* is usually wide elliptic or wide ovate. Its secondary veins are more widely spaced. Its order of venation can reach a 6th degree. These characters are distinctly different from that of Rhamnaceae. Our fossils have different leaf traits from that of *Cornus* especially in secondary venation, and instead, share large amount of leaf traits with that of genera from the tribe Rhamneae, including *Berchemia*, *Berchemiella*, *Karwinskia* and *Rhamnidium*. In modern plants, *Berchemiella* and *Berchemia* have different habits and floral morphology. The former occurs as erect shrub or small tree, while the latter is mostly liana and rarely erect shrub. Besides, their leaf base morphology is also different: The former being oblique and the latter being symmetrical. This trait can be well observed in our fossils, which have a symmetrical leaf base and thus is conclusive for the differentiation of our fossil leaves from *Berchemiella*.

In terms of leaf shape and venation pattern, *Berchemia* resembles *Karwinskia* and *Rhamnidium* in modern plants (Figure 4). However, they are distinguishable by their phyllotaxis: *Berchemia* being alternate and the latter two being opposite (Figure 4). In addition, there are glands distributed on the leaves of *Karwinskia* and *Rhamnidium*, but not in *Berchemia* (Kubitzki, 2004). Phyllotaxis and glands are rarely preserved in fossil form and, therefore, the presence or absence of glands cannot be considered a main distinguishing character in fossil identification. *Karwinskia* has well developed quaternary venation, which is different from that of *Berchemia* and *Rhamnidium*. These two genera cannot be separated based solely on leaf architecture and, as a consequence, a fossil genus, *Berhamniphyllum*, was established to contain those leaf forms that both resemble *Berchemia* and *Rhamnidium* (Jones and Dilcher, 1980). This genus might represent an extinct clade that was phylogenetically and morphologically close to *Berchemia* and *Rhamnidium* (Jones and Dilcher, 1980). This taxonomic treatment has been accepted by subsequent researchers (Correa et al., 2010). We follow this treatment and assign our fossil leaves to *Berhamniphyllum*.

Our fossil leaves from Markam are also characterized by their dense secondaries on the upper half portion of the blade,

being 4–8 pairs and accounting for over 40% of all secondaries (Appendix Table S1, <http://earth.scichina.com>). Fossil leaves from Wenshan and Xiaolongtan have only 1–3 pairs of secondary veins on the upper half portion of the blade, accounting for 20–33% of all, which is distinct from the fossils obtained from Markam. Thus, we propose a new species for the fossil leaves obtained from Markam. The two specimens have different leaf shape, one being oblong (Figure 3c) and the other being narrowly ovate (Figure 3a), but their leaf architectures are the same. Both of them have dense secondary veins on the upper half portion of the blade. Modern *Berchemia* plants are mostly liana, whose leaf shape might vary along different parts of the liana. Therefore, this difference between the two specimens can be regarded as intraspecific variation.

Fossil leaves of Wenshan and Xiaolongtan are similar to *Berchemia miofloribunda* present in Miocene strata in Shanwang, Shandong Province, China, and thus were assigned to this fossil species in previous studies (Zhou, 1985; Huang, 2017). To follow the treatment proposed by Jones and Dilcher (1980), we reassign these fossil leaves into *Berhamniphyllum miofloribundum*.

4.2 Fossil history

In this paper, the fossil history discussed includes that of both *Berchemia* and *Berhamniphyllum*. As mentioned above, the leaf architecture of *Berchemia* is conspicuous and characterized by its eucamptodromous venation. Secondary veins are straight from the midvein to near margin and then arch abruptly upward and enter into a margin vein. The tertiary veins are densely spaced and parallel, and are percurrent to secondary veins (Figure 3h). Based on the presence of these leaf traits, these fossil leaves were easily assigned to *Berchemia* by most researchers. However, another genus *Rhamnidium* distributed in South America and Central America, has a leaf morphology that is almost the same as that of *Berchemia*, which also belongs to the tribe Rhamneae. Based solely on leaf morphology, it is impossible to distinguish these two genera. More interestingly, fossil leaves resembling *Rhamnidium* have been reported from the late Cretaceous strata in Colombia and Eocene strata in the USA (Jones and Dilcher, 1980; Correa et al., 2010) (Figure 1; Table 2). During Jones and Dilcher's reinvestigation of the Eocene Wilcox flora, they reexamined the leaf fossils previously assigned to *Rhamnus* and *Cornus*. They suggested that some of the fossils had similar leaf form as that of *Berchemia* and *Rhamnidium*, and proposed that confident assignment between these two genera cannot be made on the basis of leaf characters alone. Therefore, they established a new fossil genus, namely *Berhamniphyllum* Jones and Dilcher, to include those fossil leaves resembling *Berchemia* or *Rhamnidium*. Besides, this genus might represent an extinct

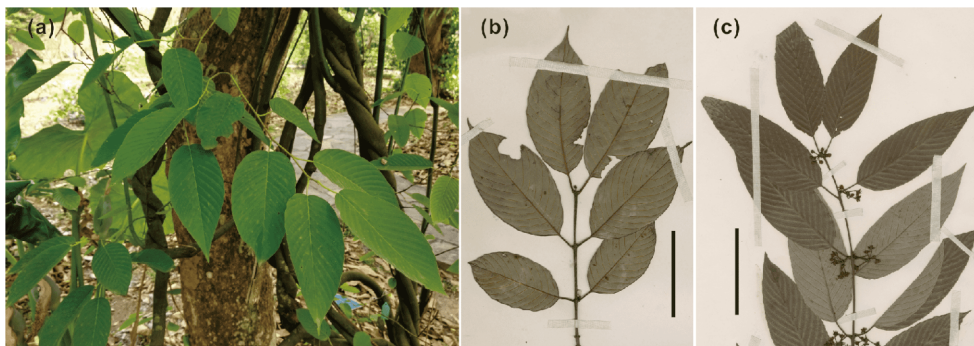


Figure 4 Specimens of *Berchemia*, *Karwinskia* and *Rhamnidium*. (a) *Berchemia longipes*, photographed from Xishuangbanna Tropical Botanical Garden, CAS, leaves alternate; (b) *Karwinskia calderonii*, scale bar=5 cm, extracted from JSTOR, leaves opposite; (c) *Rhamnidium caloneurum*, scale bar=5 cm, extracted from JSTOR, leaves opposite.

clade of the tribe Rhamneae, which was possibly the common ancestor of *Rhamnidium* and *Berchemia* (Jones and Dilcher, 1980). Subsequently, Correa et al. (2010) reported fossil leaves in late Cretaceous (68 Ma) strata in Colombia, and assigned them to *Berhamniphyllum* sp. (Table 2). Manchester (2000) reported fossil leaves of *Berchemia* from the late Eocene (39–38 Ma) strata in Wheeler, Oregon, USA, which is the earliest fossil record of *Berchemia* in North America. The latest fossil record of *Berchemia* occurred in the Miocene of Beaverhead Basin, SW Montana, USA (Manchester, 2000).

The earliest reliable record for European *Berchemia* was reported as an endocarp from the middle Eocene of Messel, Germany, and its morphology and anatomy was extensively analyzed using Synchrotron Radiation X-Ray Tomographic Microscopy (SRXTM). Fossils of *Berchemia* in Europe have been reported from Eocene to Pliocene, and the fossil leaves have all been assigned to *Berchemia* (Givulescu, 1996; Bozukov, 2000; Teodoridis, 2007; Bozukov et al., 2008; Kovar-Eder, 2016; Macaluso et al., 2018) (Table 1). As we were unable to examine the fossil leaves of *Berchemia* from Europe, we could not emend their assignment. The fossil record shows that *Berchemia* went extinct in Europe after the Pliocene.

There are only two African records for *Berchemia*. One is fossil seeds from the Miocene Hiwegi Formation from Rusinga Island, Kenya, and the other is fossil exocarps from Miocene strata in Fort Terman, Kenya. Both of them were assigned to *Berchemia psedodiscolor* (Retallack, 1992; Collinson et al., 2009) (Table 1).

Modern *Berchemia* is mainly distributed in the subtropical forest of East Asia and the tropical forest of Southeast Asia. *Berchemia* and its affinities also have a rich fossil record in East Asia (Figure 1, Table 1). The fossil leaves reported in the late Eocene of Markam, Tibet, China in this study represent the earliest fossil record in Asia (Tables 1–2). *Berchemia* fossils have also been reported from the Miocene from several localities in Yunnan and Shandong Province,

China (Chaney and Hu, 1940; WGCPC, 1978; Tao and Chen, 1983; Zhou, 1985; Guo, 2011; Huang, 2017); those reported in Wenshan and Xiaolongtan of Yunnan Province and Shanwang of Shandong Province are reassigned to *Berhamniphyllum* in this study. In the Pliocene, leaves of *Berchemia* were still observed in Tuantian, Tengchong, Yunnan Province, China (Wu, 2009). In Japan, the *Berchemia* fossil record starts from the Miocene in Honshu (Ishida, 1970; Ozaki, 1980, 1991; Yabe, 2008) (Table 1).

4.3 Biogeography of *Berchemia* Complex

Before discussing this topic, it is necessary to review briefly the research history of the Rhamnaceae phylogeny. In the old classification, *Berchemia* and *Ziziphus* were placed under the tribe Zizipheae because their fruit type is drupe (Suessenguth, 1953). This treatment was followed by Flora of China (FOC). Subsequently, Richardson et al. (2000) proposed a new classification based on plastid phylogenetic analysis and showed that *Berchemia* should be removed from the tribe Zizipheae and placed in the tribe Rhamneae. The tribe Rhamneae is a monophyletic clade containing *Auerodendron*, *Berchemia*, *Berchemiella*, *Condalia*, *Dallachya*, *Karwinskia*, *Krugiodendron*, *Reynosa*, *Rhamnidium*, *Rhamnella*, *Rhamnus*, *Sageretia* and *Scutia* (Richardson et al., 2000). Among them, four genera, namely *Berchemia*, *Berchemiella*, *Karwinskia* and *Rhamnidium*, not only share similar leaf morphology, but are also phylogenetically close. For convenience, we regard them as the *Berchemia* Complex, and follow Correa et al. (2010) in considering *Berhamniphyllum* as the common ancestor of the *Berchemia* Complex.

Molecular evidence and the fossil record both indicate that Rhamnaceae originated in the early late Cretaceous in South America (Basinger and Dilcher, 1984; Hauenschild et al., 2018). The earliest fossil record for the *Berchemia* Complex occurred in the latest late Cretaceous in Colombia; therefore, the origin of the *Berchemia* Complex should be no later than

this time in the northern part of South America. During the Eocene, North and South America were linked by island arcs, through which exchange of fauna and flora existed between North and South America (MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent and MacPhee, 1999). It was possible that the *Berchemia* Complex migrated through this pathway to North America. This route of migration is supported by fossil evidence, and is consistent with the Malpighiaceae migrating route from South to North America.

In the Eocene, flora exchange between North America and Europe depended largely on the North Atlantic Land Bridge (Tiffney and Manchester, 2001), and this land bridge existed until the late Miocene (Denk et al., 2010). The Bering Land Bridge allowed flora exchange between North America and East Asia (Donoghue and Smith, 2004). Before the early Oligocene, Europe and Asia were separated by the Turgai Strait, and therefore a barrier existed which blocked the flora exchange between Europe and Asia (Tiffney and Manchester, 2001). Considering that reliable fossils of the *Berchemia* Complex have been discovered in the middle Eocene, we propose that the *Berchemia* Complex adopted two different dispersal routes toward Europe and Asia (Figure 5). Its dispersal to Europe was via the North Atlantic Land Bridge as early as the middle Eocene. Its dispersal to East Asia was possibly via the Bering Land Bridge; fossil records in China and Japan serve as evidence. This dispersal pattern is consistent with *Cedrelospermum* and *Lagokarpus*. The dispersal of *Cedrelospermum* is supported by evidence of morphological evolution (Jia et al., 2015, 2019; Tang et al., 2019).

Our new fossils indicate that the *Berchemia* Complex had already arrived at the south-eastern margin of the QTP in the late Eocene. At that time, the paleoaltitude of Markam was about 1000 m lower than present. The vegetation was evergreen and deciduous broadleaved mixed forest dominated by *Quercus* subg. *Cyclobalanopsis* and *Betula* (Su et al., 2019b; Xu et al., 2016). In the Paleogene, QTP had complex topography: A deep valley system no higher than 2300 m stretching west-east might have existed in the central QTP, and Markam was located in the eastern edge of this valley (Su et al. 2019a). Inside the valley, the environment was warm and humid as indicated by the fossil assemblage, including *Sabalites tibetensis* (Su et al., 2019a). Meanwhile, the climate system of China was mainly controlled by planetary wind system, and a wide spread west-east arid belt occurred in mid and low latitude China (Sun and Wang, 2005; Guo et al., 2008). The *Berchemia* Complex coming from North America might have first settled down in the south-eastern margin of the QTP. As the QTP continued to uplift, the arid belt collapsed by the Miocene, when the climate system of China experienced a transition such that the central-eastern and southeastern part became more humid, and the northwestern part became more arid (Sun and Wang, 2005; Guo et al., 2008). In the Miocene, the *Berchemia*

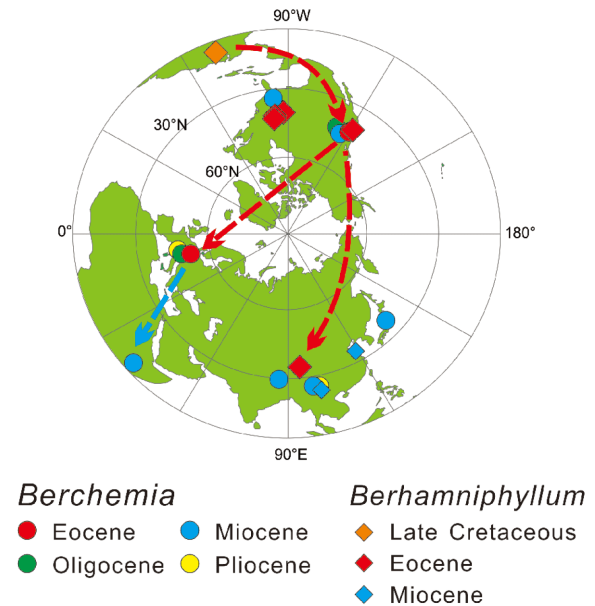


Figure 5 Hypothesized migration route modified from Jia et al. (2015).

Complex migrated out of the QTP and subsequently dispersed to Yunnan and Shandong provinces of China and Japan. As the *Berchemia* Complex gradually evolved, modern *Berchemia* came into being, and this continued to develop to form the present distribution pattern.

5. Conclusions

Based on morphological comparison, fossil leaves discovered in this study from the Upper Eocene of Markam, Tibet, China were assigned to *Berhamniphyllum*. Characterized by the dense secondary veins on the upper portion of the blade, which is distinct from other affinities, they are assigned to a new species, namely *Berhamniphyllum junrongiae* Z. K. Zhou, T. X. Wang et J. Huang sp. nov.. This new species represents the earliest fossil record for the *Berchemia* Complex in Asia. Based on speculation on the fossil record, the Asian *Berchemia* Complex dispersed from North America to East Asia via the Bering Land Bridge. As the QTP uplifted, the west-east stretching arid belt collapsed. The *Berchemia* Complex then scattered to other regions of Asia to form the present distribution pattern.

Acknowledgements We thank colleagues from Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS), and Kunming Institute of Botany, CAS for field work; Tibetan villagers from Kajun village for their kind help during field work; Dr. Gongle Shi for photographing fossil from Xiaolongtan flora; Prof. Lutz Kunzmann, Ms. Yuqing Wang and Prof. Steven Manchester for providing literature; Dr. Linbo Jia and Prof. Steven Manchester for discussion and comments; the Public Technology Service Center, XTBG, CAS for providing microscopes and experimental facilities; Teresa Spicer for improving the English manuscript. We are also grateful to two anonymous reviewers for their

constructive advices. This study was supported by the Strategic Priority Research Program of CAS (Grant Nos. XDA2007030102 & XDB26000000), the NSFC (the National Natural Science Foundation of China)-NERC (Natural Environment Research Council of the United Kingdom) joint research program (Grant Nos. 41661134049 & NE/P013805/1); The Second Tibetan Plateau Scientific Expedition and Research Program (STEP), CAS (Grant No. 2019QZKK0705), Youth Innovation Promotion Association, CAS (Grant No. 2017439) and Key Research Program of Frontier Sciences, CAS (Grant No. QYZDB-SSW-SMC016).

References

- Ai K K, Shi G L, Zhang K X, Ji J L, Song B W, Shen T Y, Guo S X. 2019. The uppermost Oligocene Kailas flora from southern Tibetan Plateau and its implications for the uplift history of the southern Lhasa terrane. *Palaeogeogr Palaeoclimatol Palaeoecol*, 515: 143–151
- Basinger J F, Dilcher D L. 1984. Ancient bisexual flowers. *Science*, 224: 511–513
- Becker H F. 1969. Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. *Palaeontogr Abt B*, 127: 1–142
- Berry E W. 1916a. The lower Eocene floras of southeastern North America. *US Geol Surv Prof Pap*, 91: 1–149
- Berry E W. 1916b. The physical conditions indicated by the flora of the Calvert formation. *US Geol Surv Prof Pap*, 98: 61–73
- Bozukov V. 2000. Miocene macroflora of the Satovcha Graben (Western Rhodopes). *Phytol Balcan*, 5: 15–30
- Bozukov V, Palamarev E, Petkova A. 2008. The fossil macroflora of the Vulche Pole Molasse formation (SE Bulgaria). *Phytol Balcan*, 14: 173–184
- Büchler W. 1990. Eine fossile Flora aus dem oberen Oligozän von Ebnat-Kappel. *Bot Helv*, 100: 133–166
- Chaney R W, Hu H H. 1940. A Miocene Flora from Shantung Province, China. Washington: Publication of Carnegie Institute. 1–507
- Chen Y, Schirarend C. 2007. Rhamnaceae. In: Wu Z Y, Raven P H, Hong D Y, eds. *Flora of China*. Beijing: Science Press. St. Louis: Missouri Botanical Garden Press. 12: 115–168
- Collinson M E, Andrews P, Bamford M K. 2009. Taphonomy of the early miocene flora, Hiwegi formation, Rusinga Island, Kenya. *J Human Evol*, 57: 149–162
- Collinson M E, Manchester S R, Wilde V. 2012. Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. *Abh Senckenb Ges Naturforsch*, 570: 1–251
- Correa E, Jaramillo C, Manchester S, Gutierrez M. 2010. A fruit and leaves of Rhamnaceae affinities from the late Cretaceous (Maastrichtian) of Colombia. *Am J Bot*, 97: 71–79
- Davis C C, Bell C D, Mathews S, Donoghue M J. 2002. Laurasian migration explains Gondwanan disjunctions: Evidence from Malpighiaceae. *Proc Natl Acad Sci USA*, 99: 6833–6837
- Denk T, Grimsson F, Zetter R. 2010. Episodic migration of oaks to Iceland: Evidence for a North Atlantic “land bridge” in the latest Miocene. *Am J Bot*, 97: 276–287
- Deng T, Wang X, Wu F, Wang Y, Li Q, Wang S, Hou S. 2019. Review: Implications of vertebrate fossils for paleo-elevations of the Tibetan Plateau. *Glob Planet Change*, 174: 58–69
- Dilcher D L, Lott T A. 2005. A middle Eocene fossil plant assemblage (Powers Clay Pit) from western Tennessee. *Bull Florida Museum Nat Hist*, 45: 1–43
- Ding L, Spicer R A, Yang J, Xu Q, Cai F, Li S, Lai Q, Wang H, Spicer T E V, Yue Y, Shukla A, Srivastava G, Khan M A, Bera S, Mehrotra R. 2017. Quantifying the rise of the Himalaya orogen and implications for the South Asian monsoon. *Geology*, 45: 215–218
- Dong W, Qi G. 2013. Hominoid-producing localities and biostratigraphy in Yunnan. In: Wang X M, Flynn L J, Fortelius M, eds. *Fossil Mammals of Asia—Neogene Biostratigraphy and Chronology*. New York: Columbia University Press. 293–313
- Donoghue M J, Smith S A. 2004. Patterns in the assembly of temperate forest around the Northern Hemisphere. *Phil Trans R Soc Lond B*, 359: 1633–1644
- Ellis B, Daly D C, Hickey L J, Johnson K R, Mitchell J D, Wilf P, Wing S L. 2009. *Manual of Leaf Architecture*. Ithaca: Cornell University Press
- Flora of North America Editorial Committee, eds. 1993+. *Flora of North America North of Mexico*. 19+ vols. New York: Oxford University Press
- Givulescu R. 1996. *Flora Oligocena Superioara din Bazinul Petrosani*. Casa Cartii de Stiinta, Cluj-Napoca, 1–177
- Guo S X. 2011. The late Miocene Bangmai flora from Lincang county of Yunnan, southwestern China (in Chinese with English Abstract). *Acta Palaeontol Sin*, 50: 353–408
- Guo Z T, Sun B, Zhang Z S, Peng S Z, Xiao G Q, Ge J Y, Hao Q Z, Qiao Y S, Liang M Y, Liu J F, Yin Q Z, Wei J J. 2008. A major reorganization of Asian climate by the early Miocene. *Clim Past*, 4: 153–174
- Hauenschild F, Favre A, Michalak I, Muellner-Riehl A N. 2018. The influence of the Gondwanan breakup on the biogeographic history of the ziziphoids (Rhamnaceae). *J Biogeogr*, 45: 2669–2677
- Hantke R. 1954. *Die fossile Flora der obermiozänen Oehninger-Fundstelle Schrotzburg (Schienberg, Süd-Baden)*. Doctoral Dissertation. Zürich: ETH Zürich
- Heer O. 1855–1859. *Flora Tertiaria Helveticae. Die Tertiäre flora der Schweiz*. Winterthur: J. Wurster and Compagnie
- Huang J. 2017. *The middle Miocene Wenshan flora, Yunnan, southwestern China and its palaeoenvironment reconstruction*. Doctoral Dissertation (in Chinese). Xishuangbanna: Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
- Ishida S. 1970. *The Noroshi Flora of Noto Peninsula, Central Japan*. Memoirs of the Faculty of Science Kyoto University, Series of Geology and Mineralogy, 37: 1–112
- Iturralde-Vinent M A, MacPhee R D E. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bull Am Mus Nat Hist*, 238: 1–95
- Jia L B, Manchester S R, Su T, Xing Y W, Chen W Y, Huang Y J, Zhou Z K. 2015. First occurrence of *Cedrelospermum* (Ulmaceae) in Asia and its biogeographic implications. *J Plant Res*, 128: 747–761
- Jia L B, Su T, Huang Y J, Wu F X, Deng T, Zhou Z K. 2019. First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai-Tibetan Plateau: Implications for morphological evolution and biogeography. *Jnl Sytemat Evol*, 57: 94–104
- Jiang H, Su T, Wong W O, Wu F, Huang J, Shi G. 2019. Oligocene *Koelreuteria* (Sapindaceae) from the Lunpola Basin in central Tibet and its implication for early diversification of the genus. *J Asian Earth Sci*, 175: 99–108
- Jones J H, Dilcher D L. 1980. Investigations of angiosperms from the Eocene of North America: *Rhamnus marginatus* (Rhamnaceae) reexamined. *Am J Bot*, 67: 959–967
- Jung W. 1968. *Pflanzenreste aus dem Jungtertiär Nieder-und Oberbayerns und deren lokalstratigraphische Bedeutung*. *Ber Naturwiss Ver Langshut*, 25: 43–71
- Köecke V, Uhl D. 2015. The leaf assemblage from the Early-Middle Miocene locality Sulzigtobel near Werthenstein (Canton Lucerne, Switzerland). *Phytol Balcan*, 21: 99–109
- Kovar-Eder J. 2016. Early Oligocene plant diversity along the Upper Rhine Graben: The fossil flora of Rauenberg, Germany. *Acta Palaeobot*, 56: 329–440
- Kubitzki K. 2004. *The Families and Genera of Vascular Plants*. Vol. 6. Flowering Plants—Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales. Berlin: Springer
- Lazarević Z, Milivojević J, Bogičević K, Nenadić D. 2013. Early Miocene flora from the Valjevo-Mionica Basin (Western Serbia). *N J Geol Pal A*, 267: 297–307
- Lebreton-Anberrée J, Li S, Li S F, Spicer R A, Zhang S T, Su T, Deng C, Zhou Z K. 2016. Lake geochemistry reveals marked environmental change in Southwest China during the Mid Miocene Climatic Optimum. *Chin Sci Bull*, 61: 897–910
- de León P V, Cevallos-Ferriz S R, Silva-Pineda A. 1998. Leaves of *Kar-*

- winskia axamilpense* sp. nov. (Rhamnaceae) from Oligocene sediments, near Tepexi de Rodriguez, Puebla, Mexico. *Can J Bot*, 76: 410–419
- Li S F, Mao L M, Spicer R A, Lebreton-Anberrée J, Su T, Sun M, Zhou Z K. 2015. Late Miocene vegetation dynamics under monsoonal climate in southwestern China. *Palaeogeogr Palaeoclimatol Palaeoecol*, 425: 14–40
- Li S H, Deng C L, Dong W, Sun L, Liu S Z, Qin H F, Yin J Y, Ji X P, Zhu R X. 2015. Magnetostratigraphy of the Xiaolongtan Formation bearing *Lufengpithhecus keiyuanensis* in Yunnan, southwestern China: Constraint on the initiation time of the southern segment of the Xianshuihe-Xiaojiang fault. *Tectonophysics*, 655: 213–226
- Liu J, Su T, Spicer R A, Tang H, Deng W Y D, Wu F X, Srivastava G, Spicer T, Van Do T, Deng T, Zhou Z K. 2019. Biotic interchange through lowlands of Tibetan Plateau suture zones during Paleogene. *Palaeogeogr Palaeoclimatol Palaeoecol*, 524: 33–40
- Macaluso L, Martinetto E, Vigna B, Bertini A, Cilia A, Teodoridis V, Kvaček Z. 2018. Palaeofloral and stratigraphic context of a new fossil forest from the Pliocene of NW Italy. *Rev Palaeobot Palynol*, 248: 15–33
- MacPhee R D E, Iturralde-Vinent M A. 1995. Origin of the Great Antillean land mammals, 1: New Tertiary fossils from Cuba and Puerto Rico. *Am Mus Novitates*, 3141: 1–31
- Manchester S R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. *Oregon Geol*, 62: 51–63
- Myers J A, Kester P R, Retallack G J. 2002. Paleobotanical record of Eocene-Oligocene climate and vegetational change near Eugene, Oregon. *Oregon Dep Geol Min Ind Spec Pap*, 36: 145–154
- Myers N, Mittermeier R A, Mittermeier C G, da Fonseca G A B, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–858
- Ozaki K. 1980. Late Miocene Tatsumitoge flora of Tottori Prefecture, Southwest Honshu, Japan (III). *Sci Rep Yokohama Natl Univ*, 27: 19–45
- Ozaki K. 1991. Late Miocene and Pliocene Floras in Central Honshu, Japan. *Bulletin of Kanagawa Prefectural Museum Natural Science Special Issue*. Yokohama: Kanagawa Prefectural Museum. 1–244
- Palgrave K C. 2015. *Palgrave's Trees of Southern Africa*. 3rd ed. Cape Town: Struik Publishers
- Prasad M, Dwivedi H D. 2007. Systematic study of the leaf impressions from the Churia Formation of Koilabas area, Nepal and their significance. *Palaeobotanist*, 56: 139–154
- Retallack G J. 1992. Middle Miocene fossil plants from Fort Ternan (Kenya) and evolution of African grasslands. *Paleobiology*, 18: 383–400
- Richardson J E, Fay M F, Cronk Q C B, Chase M W. 2000. A revision of the tribal classification of rhamnaceae. *Kew Bull*, 55: 311–340
- Sakala J. 2000. Flora and vegetation of the roof of the main lignite seam in the Bilina Mine (Most Basin, Lower Miocene). *Acta Mus Nat Pragae Ser B Hist Nat*, 56: 49–84
- Singh S K, Prasad M. 2007. Late Tertiary leaf flora of mahua dan valley, Jharkhand. *J Palaeontol Soc India*, 52: 175–194
- Smiley C J, Gray J, Huggins L M. 1975. Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho. *J Paleontol*, 49: 833–844
- Spicer R A. 2017. Tibet, the Himalaya, Asian monsoons and biodiversity—In what ways are they related? *Plant Divers*, 39: 233–244
- Spitzelberger V G. 1989. Die Miozänfundstelle Goldern bei Landshut (Niederbayern). *Geol Bavarica*, 94: 371–407
- Su T, Wilf P, Xu H, Zhou Z K. 2014. Miocene leaves of *Elaeagnus* (Elaeagnaceae) from the Qinghai-Tibet Plateau, its modern center of diversity and endemism. *Am J Bot*, 101: 1350–1361
- Su T, Li S F, Tang H, Huang Y J, Li S H, Deng C L, Zhou Z K. 2018. *Hemitrapa Miki* (Lythraceae) from the earliest Oligocene of south-eastern Qinghai-Tibetan Plateau and its phytogeographic implications. *Rev Palaeobot Palynol*, 257: 57–63
- Su T, Farnsworth A, Spicer R A, Huang J, Wu F X, Liu J, Li S F, Xing Y W, Huang Y J, Deng W Y D, Tang H, Xu C L, Zhao F, Srivastava G, Valdes P J, Deng T, Zhou Z K. 2019a. No high Tibetan Plateau until the Neogene. *Sci Adv*, 5: eaav2189
- Su T, Spicer R A, Li S H, Xu H, Huang J, Sherlock S, Huang Y J, Li S F, Wang L, Jia L B, Deng W Y D, Liu J, Deng C L, Zhang S T, Valdes P J, Zhou Z K. 2019b. Uplift, climate and biotic changes at the Eocene-Oligocene transition in south-eastern Tibet. *Natl Sci Rev*, 6: 495–504
- Suessenguth K. 1953. Rhamnaceae. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien*. 2nd ed. Berlin: Dunker et Humboldt
- Sun X J, Wang P X. 2005. How old is the Asian monsoon system?—Palaeobotanical records from China. *Palaeogeogr Palaeoclimatol Palaeoecol*, 222: 181–222
- Tang H, Liu J, Wu F X, Spicer T, Spicer R A, Deng W Y D, Xu C L, Zhao F, Huang J, Li S F, Su T, Zhou Z K. 2019. Extinct genus *Lagokarpos* reveals a biogeographic connection between Tibet and other regions in the Northern Hemisphere during the Paleogene. *J Syst Evol*, 18: jse.12505
- Tao J R, Chen M H. 1983. Cenozoic flora of southern Hengduan Mountain-Lincang, Yunnan. In: The CAS Scientific Expedition to the Tibetan Plateau, eds. *Hengduan Mountain Investigation Collection (I)* (in Chinese). Kunming: Yunnan People's Publishing House. 74–89
- Taylor T N, Taylor E L, Krings M. 2008. *Paleobotany: The Biology and Evolution of Fossil Plants*. 2nd ed. New York: Academic Press. 1230
- Teodoridis V. 2007. Revision of Potamogeton fossils from the Most Basin and their palaeoecological significance (Early Miocene, Czech Republic). *Bull Geosci*, 82: 409–418
- Tiffney B H, Manchester S R. 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern hemisphere tertiary. *Int J Plant Sci*, 162: S3–S17
- Wang W M. 1996. A palynological survey of Neogene strata in Xiaolongtan Basin, Yunnan Province of south China (in Chinese with English Abstract). *Bull Bot*, 38: 743–748
- Writing Group of Cenozoic Plants of China (WGPC). 1978. *Cenozoic plants from China, Fossil Plants of China* (in Chinese). Vol. 3. Beijing: Science Press
- Wu F X, Miao D S, Chang M M, Shi G L, Wang N. 2017. Fossil climbing perch and associated plant megafossils indicate a warm and wet central Tibet during the late Oligocene. *Sci Rep*, 7: 878
- Wu J Y. 2009. The Pliocene Tuantian flora of Tengchong, Yunnan Province and its paleoenvironmental analysis (in Chinese). Doctoral Dissertation. Lanzhou: Lanzhou University
- Wu Z Y, Zhou Z K, Sun H, Li D Z, Peng H. 2006. *The Areal-Types of Seed Plants and Their Origin and Differentiation* (in Chinese). Kunming: Yunnan Science and Technology Press. 566
- Xu C L, Su T, Huang J, Huang Y J, Li S F, Zhao Y S, Zhou Z K. 2019. Occurrence of *Christella* (Thelypteridaceae) in Southwest China and its indications of the paleoenvironment of the Qinghai-Tibetan Plateau and adjacent areas. *J Syst Evol*, 57: 169–179
- Xu H, Su T, Zhang S T, Deng M, Zhou Z K. 2016. The first fossil record of ring-cupped oak (*Quercus* L. subgenus *Cyclobalanopsis* (Oersted) Schneider) in Tibet and its paleoenvironmental implications. *Palaeogeogr Palaeoclimatol Palaeoecol*, 442: 61–71
- Xu H, Su T, Zhou Z K. 2019. Leaf and infructescence fossils of *Alnus* (Betulaceae) from the late Eocene of the southeastern Qinghai-Tibetan Plateau. *J Syst Evol*, 57: 105–113
- Yabe A. 2008. Early Miocene terrestrial climate inferred from plant megafossil assemblages of the Joban and Soma areas, Northeast Honshu, Japan. *Bull Geol Surv Jpn*, 59: 397–413
- Zhou Z K. 1985. *The Miocene Xiaolongtan fossil flora in Kaiyuan, Yunnan, China* (in Chinese). Master Dissertation. Nanjing: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
- Zhou Z K, Yang X F, Yang Q S. 2006. Land bridge and long-distance dispersal—Old views, new evidence. *Chin Sci Bull*, 51: 1030–1038