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A new fossil record of *Palaeosinomenium* (Menispermaceae) from the Upper Eocene in the southeastern margin of the Tibetan Plateau and its biogeographic and paleoenvironmental implications

Mengxiao Wu [a], Jian Huang [a,b], Steven R. Manchester [c], He Tang [d], Yi Gao [a,e], Tengxiang Wang [f], Zhekun Zhou [a], Tao Su [a,b,*]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China
[b] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Naypyitaw 05282, Myanmar
[c] Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA
[d] State Key Laboratory of Isotope Geochemistry, Guangzhou Institute of Geochemistry, Chinese Academy of Sciences, Guangzhou 510640, China
[e] University of Chinese Academy of Sciences, Beijing 100049, China
[f] Department of Geosciences and Earth and Environmental Systems Institute, Pennsylvania State University, University Park, PA 16802, USA

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ABSTRACT

Palaeosinomenium Chandler (Menispermaceae) was established to accommodate the fossil endocarps that share similar morphological characteristics with the tribe Menispermeae in Menispermaceae. Previous fossil records suggested that *Palaeosinomenium* was distributed in North America, Europe, and East Asia before the Middle Eocene. A new fossil species, *Palaeosinomenium hengduanensis* Meng-Xiao Wu et Zhe-Kun Zhou sp. nov., was established based on an endocarp impression fossil from the Upper Eocene (35 ± 1 Ma) Shuanghe Formation, Jianchuan Basin, southwestern China. The new species is characterized by a horseshoe-shaped endocarp, an excavated central area, surrounded by a slightly asymmetrical C-shaped lateral ridge, and an elliptic aperture located near the longer endocarp limb. The fossil site is located in the modern distribution area of the living species *Sinomenium acutum* (Thunb.) Rehd. et Wils, a potential nearest living relative of the new species. The finding of *P. hengduanensis* supports that the divergence within the tribe Menispermeae might have occurred by the Late Eocene and the species similar to modern *S. acutum* appeared in the southeastern margin of the Tibetan Plateau as early as in the Late Eocene.

1. Introduction

Menispermaceae Juss. (moonseed family) consists mainly of vines, rare shrubs or trees with unisexual flowers, and drupaceous fruits (Luo et al., 2008; Jacques, 2009a, 2009b). The fruits usually have a leathery or membranous exocarp, a fleshy or fibrous mesocarp, and a woody endocarp (Hoot et al., 2009). The endocarp shape (straight, boat-shaped, horseshoe-shaped, and hairpin-shaped) and ornamentations provide additional taxonomic characteristics for distinguishing between and within genera (Jacques, 2009a, 2009b). Menispermaceae includes 72 genera and around 520 species which are mainly distributed in tropical and subtropical regions; a few are present in temperate regions (Ortiz et al., 2007, 2016; Luo et al., 2008).

Menispermaceae has abundant fossil records that can be recognized via endocarps, leaves, woods, and pollen grains (Jacques, 2009a; Herrera et al., 2011; Jud et al., 2018; Han et al., 2020). Fossils have been reported as Menispermaceae (i.e., *Menispermites* Lesq., *Cocculus* DC., and *Anamirta* Colebr.), extending as early as the Cretaceous (Knobloch and Mai, 1984, 1986; Bonde, 1997; Golovneva et al., 2015). However, these identification results may need to be backed up by additional evidence as they are based on vegetative material without fruit remains (Wefferling et al., 2013; Jud et al., 2018). Menispermaceae fossils from the Paleogene have been widely reported in North America, South America, Europe, and Asia (Manchester, 1994, 2005; Jacques and De Franceschi, 2005; Doria et al., 2008; Herrera et al., 2011; Golovneva et al., 2015; Han et al., 2018, 2020; Del Rio et al., 2021). Besides living genera, organ genera established by leaves or endocarps have been reported, i.e., *Menispermites*, *Wardensheppeya* Chandler and *Sinomenites* V. P. Nikit (Lesquereux, 1874; Chandler, 1961b; Nikitin, 2006; Jacques, 2009a; Jud et al., 2018).

A recent phylogenetic study recognized nine clades of Menispermaceae which are grouped within the subfamilies Chasmantheroideae Luerss. (two clades) and Menispermoideae Arn.

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* Corresponding author.
E-mail address: sutao@xtbg.org.cn (T. Su).

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(seven clades) (Ortiz et al., 2016). The tribe Menispermeae DC. which includes *Menispermum* L. and *Sinomenium* Diels. is the sister to all other tribes of Menispermoideae (Ortiz et al., 2007, 2016; Wang et al., 2012; Wefferling et al., 2013). *Menispermum*, containing the two extant species *M. dauricum* DC. and *M. canadense* L., is distributed in East Asia and eastern North America respectively, whereas *Sinomenium* contains one species, namely *Sinomenium acutum* (Thunb.) Rehd. et Wils, and is endemic to East Asia (Jacques, 2009a; Wang et al., 2012). The morphogenus *Palaeosinomenium* Chandler, accommodates fossil endocarps similar to *Menispermum* and/or *Sinomenium*, but with a more oblique endocarp and an elongate aperture (Chandler, 1961b; Collinson et al., 2012). Up to now, six species and three unidentified species in this genus have been reported from North America, Europe, and East Asia (Chandler, 1961b, 1963; Dorofeev, 1974; Manchester, 1994; Manchester et al., 2005; Collinson et al., 2012). More fossil evidence is required to detect the morphological evolution between this morphogenus and the living genera.

Here, we report a new species of *Palaeosinomenium* based on an endocarp collected from the Upper Eocene Shuanghe Formation in the Jianchuan Basin, Yunnan, China. The new species enriched the fossil records of *Palaeosinomenium* and was important to know the biogeographical history of the tribe Menispermeae. The fossil endocarp morphology was studied and compared with modern species of Menispermaceae and fossil species with similar characteristics. Furthermore, the biogeographical and paleoenvironmental implications of the new species are discussed.

2. Material and methods

2.1. Geological setting

One specimen was collected from Jinhua Town, Jianchuan County, Yunnan Province, southwestern China (26°35’ N, 99°52′ E, 2408 m a.s.l., Fig. 1). The locality is situated in the Jianchuan Basin, the southernmost part of the Qiangtang block (Gourbet et al., 2017). The Cenozoic sedimentary rocks in the basin consist of six formations; from bottom to top, they are Mengyejing, Baoxiangsi, Jiuziyan, Shuanghe, Jianchuan, and Sanying formations (Gourbet et al., 2017; Sorrel et al., 2017). The endocarp was discovered as an impression from sandstones within the Shuanghe Formation (Fig. 1).

The Shuanghe Formation consists of mudstones/marls and coal beds interbedded with sandstones (Fig. 1) (Gourbet et al., 2017; Sorrel et al., 2017; Wu et al., 2018). According to plant and animal fossils, this formation was previously considered to originate from the Miocene (WGCPC, 1978; BGMRYP Bureau of Geology and Mineral Resources of Yunnan Province, 1996). Recent U–Pb zircon and biotite ^{40}Ar/^{39}Ar measurement showed that the deposits of the Shuanghe Formation took place in a short time interval in the Late Eocene (~35.9 ± 0.9 Ma)

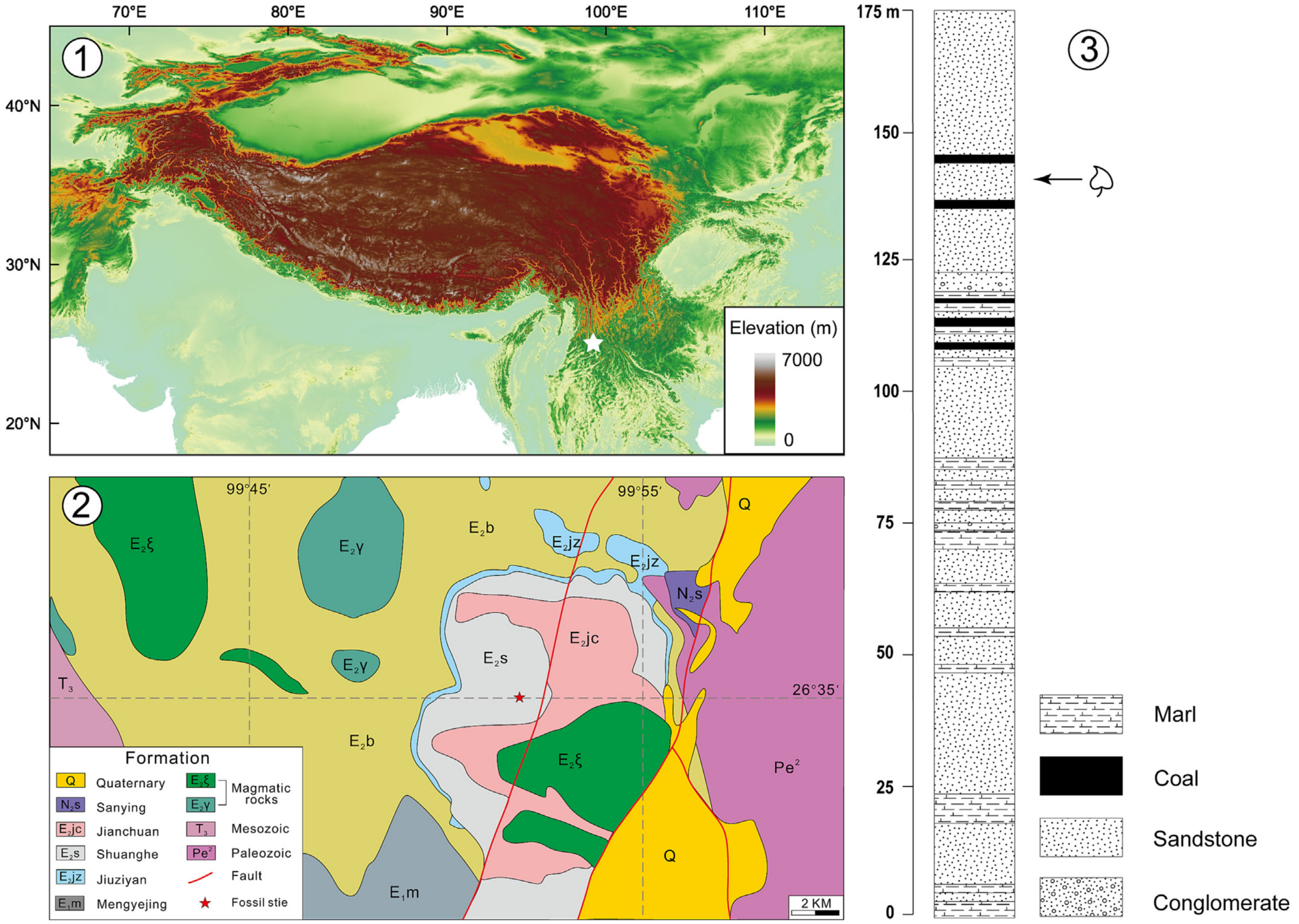

Fig. 1. Geographical context of the fossil site. 1. Map showing the fossil site (white star) in Jianchuan Basin, the southeastern margin of the Tibetan Plateau. 2. Geological map of the Jianchuan Basin, mainly based on Gourbet et al. (2017); the red star refers to the fossil site located in the Jianchuan Formation. 3. Generalized lithologic column of the Jianchuan Formation, modified from Wu et al. (2018).

(Gourbet et al., 2017). The age of sandstones between the two coal layers where the endocarp was discovered (Figs. 1, 3) is 35 ± 1 Ma (Gourbet et al., 2017).

The plant fossils collected from the marls in the upper part of the coal layer indicated that the Shuanghe flora was dominated by Fagaceae and Lauraceae, and the paleovegetation was subtropical evergreen broad-leaved forest (WGCPC, 1978; Ge and Li, 1999; Sun et al., 2011). Palynological research suggested a vertical zonation vegetation, consisting of mixed tropical-subtropical, deciduous, coniferous, and broad-leaved forest (Wu et al., 2018).

2.2. Methods

One specimen was observed under a stereomicroscope (Leica S8AP0, Germany), and photographs were taken with a digital microscope (Zeiss Smartzoom 5, Germany). To observe the surface of the endocarp, the adhering black carbonaceous material was carefully brushed away with a fine brush and an anatomical needle. The specimen without carbon pieces was observed in the same way as the original one. The fossil morphology was described mainly following Manchester (1994) and Jacques (2009b). The fruits of modern *S. acutum* were heated in a water bath at 70 °C for 2 h, and subsequently the mesocarps were separated with anatomical needles. The endocarps were placed in a petri dish to naturally dry. The modern distribution map was based on the Global Biodiversity Information Facility (GBIF.org (27 July 2022) GBIF Occurrence Download (https://doi.org/10.15468/dl.965tet); GBIF.org (27 July 2022) GBIF Occurrence Download (https://doi.org/10.15468/dl.y5q8u0z)). Based on the geographic coordinates of the modern distribution, the environment parameters of modern *Sinomenium* were extracted from the WorldClim database (www.worldclim.org, 30″ in resolution). Six modern climate parameters in Jianchuan were obtained from the National Meteorological Information Center (http://data.cma.cn/en), namely mean annual temperature (MAT), cold moth mean temperature (CMMT), warm moth mean temperature (WMMT), mean annual precipitation (MAP), three wettest months precipitation (3WET), and three driest months precipitation (3WDT).

3. Results

Order: Ranunculales Juss. ex Bercht. & J. Presl
Family: Menispermaceae Juss.
Subfamily: Menispermoideae Arn.
Tribe: Menispermeae DC.
Genus: **Palaeosinomenium** Chandler
Species: *Palaeosinomenium hengduanensis* Meng-Xiao Wu et Zhe-Kun Zhou
Etymology: The specific name, *hengduanensis*, is derived from the Hengduan Mountain Range, where the fossil site is located.
Locality: Jinhua Town, Jianchuan County, Dali Autonomous Prefecture, Yunnan Province, China (26°35’ N, 99°52′ E, 2408 m a.s.l.).
Holotype: XTBGPC-JC-100
Repository: Palaeobotanical Collections of the Qinghai-Tibetan Plateau, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences.
Age: 35 ± 1 Ma (the Priabonian)
Stratigraphic horizon: Shuanghe Formation.

Diagnosis: Endocarp horseshoe-shaped in lateral view, asymmetrical with one limb a litter longer; length/width ratio < 1; broad-rounded dorsal margin and nearly straight ventral margin; one dorsal ridge and one lateral ridge connected by at least 20 transverse ridges; no perforation; an elliptical aperture near the longer endocarp limb.

Description: Endocarp laterally compressed in bisymmetrical plane; horseshoe-shaped in lateral view, length 4.8 mm, width 6.1 mm, length/width ratio 0.8; dorsal margin broad-rounded (Plate I, 4) and ventral margin nearly straight (Plate I, 4); one limb longer; central area excavated, length 2.5 mm, width 3.4 mm, surrounded by a slightly asymmetrical C-shaped lateral ridge (Plate I, 7); one dorsal ridge and one lateral ridge bearing at least 20 transverse ridges (Plate I, 7); no perforation; an elliptic aperture located near the longer endocarp limb (Plate I, 4).

4. Discussion

4.1. Systematic assignment

Menispermaceae is characterized by distinctive horseshoe, reniform, straight, or hairpin-shaped endocarps (Jud et al., 2018); thus, endocarp morphology is important for the identification of the family (Jacques, 2009b; Jacques and Zhou, 2010; Herrera et al., 2011; Yang and Chen, 2016; Han et al., 2018, 2020; Del Rio et al., 2021). The endocarp from Jianchuan is characterized by a unique bilaterally compressed condyle (*Menispermum* type), and a horseshoe-shaped locule that could be assigned to the subfamily Menispermoideae (Ortiz, 2012). The horseshoe-shaped endocarps in Menispermaceae can be divided into U-shaped and C-shaped ones (Han et al., 2020), the presence of a C-shaped endocarp (endocarps longitudinally) with an aperture near one limb appears today only in the tribe Menispermeae (*Menispermum* and *Sinomenium*) (Jacques, 2009b; Ortiz et al., 2016; Han et al., 2020).

The genus *Palaeosinomenium* was established to accommodate fossil endocarps similar to *Menispermum* and *Sinomenium* or both (Chandler, 1961b; Collinson et al., 2012). A morphometric study demonstrated that the endocarp shapes of *Menispermum* and *Sinomenium* are different from other horseshoe-shaped endocarps of the Menispermaceae (Jacques and Zhou, 2010). They usually have a more circular outline, the condyle area is not perforated in the central area, and an elliptic aperture is located near the longer endocarp limb (Yang and Chen, 2016; Han et al., 2020). The *Menispermum* endocarps (length 6.0–7.1 mm, width 5.0–6.7 mm) are a slightly larger than those of *Sinomenium* (length 4.9–5.7 mm, width 3.0–6.9 mm). The number of transverse ridges is less than 25 in *Sinomenium* and more than 25 in *Menispermum* (Jacques, 2009b; Yang and Chen, 2016). *Menispermum* possesses a smooth lateral crest which is also different from *Sinomenium* (Herrera et al., 2011). Moreover, the ventral margin of *Menispermum* has a greater concavity than that of *Sinomenium.* Mai (1997) suggested that the fossil genera *Palaeosinomenium* and *Wardensheppeya* (Chandler) Eyde ("*Wardenia*" of Chandler, 1961b, revised in Eyde, 1970) (Chandler, 1961b; Eyde, 1970) could be included in the modern genus *Sinomenium*. However, these morphological differences are not always available in fossils. For example, the fossil endocarps tend to be smaller than those of the modern relatives and the lateral crest smoothness is hard to judge from impression fossils. Thus, the morphogenus *Palaeosinomenium* is still useful when fossils are similar to both genera but with more oblique endocarp and elongate foramen (Collinson et al., 2012). The genus *Palaeosinomenium* was also confirmed by morphometric analysis (Jacques et al., 2011).

Wardensheppeya and *Sinomenites* are used to accommodate the fossil endocarps close to those of *Sinomenium*. The aperture of *Wardensheppeya* is not evident and the endocarp is more nearly symmetrical (Collinson et al., 2012), which is different from *Palaeosinomenium*. *Sinomenites* could be distinguished from *Palaeosinomenium* by a more curved ventral margin (Nikitin, 2006). The length of the Jianchuan endocarp (4.8 mm) is close to that of *Sinomenium* but its width (6.1 mm) is located in the overlap region of the two genera. At least 20 transverse ridges could be distinguished from the fossil, whereas the specific number cannot be determined. The ventral margin of *Menispermum* is V-shape, whereas that of *Sinomenium* is slightly concave (Liu and Jacques, 2010). The ventral margin of the Jianchuan endocarp is nearly straight, which distinguishes it from the other two genera. The more oblique endocarp and the elongate aperture of the Jianchuan endocarp also distinguish it from

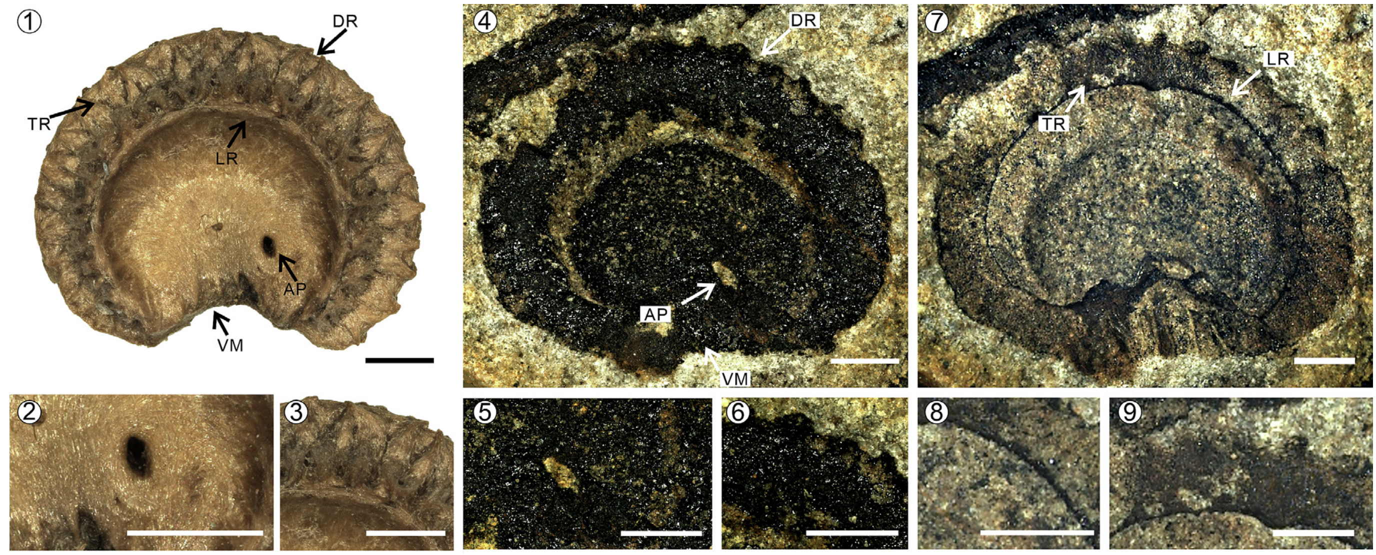

Plate I. Endocarps of *Sinomenium acutum* (1–3) and *Palaeosinomenium hengduanensis* (4–9). 2 and 3 are the enlargements of the aperture and transverse ridges respectively. 4–6 are the endocarp of *P. hengduanensis* with carbon pieces, 5 and 6 show the aperture and dorsal ridge respectively. 7–9 are the endocarp of *P. hengduanensis* which the carbon pieces were removed, 8 and 9 show the lateral ridge and transverse ridges respectively. DR = dorsal ridge; TR = transverse ridge; LR = lateral ridge; AP = aperture; VM = ventral margin. Scale bar = 1 mm.

the two genera. Thus, the Jianchuan endocarp was assigned to the morphogenus *Palaeosinomenium.*

The Jianchuan endocarp shows the characteristics of *Palaeosinomenium* but is different from previous fossil species in this genus (Table 1). From the Paleogene to the Middle Eocene, species belonging to *Palaeosinomenium* have occurred in Europe (Chandler, 1961a, 1961b, 1963; Collinson et al., 2012), eastern North America (Manchester, 1994) and East Asia (Manchester et al., 2005) (Fig. 2). *Palaeosinomenium venablesii* Chandler has the most abundant fossil records and shows high intra-species diversity (Table 1) (Manchester, 1994; Manchester et al., 2005). The aperture of *P. venablesii* from Paleogene England is close to the ventral margin, whereas there is a space of about 0.8 mm between the aperture and the ventral margin in the Jianchuan endocarp; besides, the Jianchuan endocarp is more asymmetrical. The *P. venablesii* endocarp from the Middle Eocene Oregon, western USA, shows a more rounded outline, differing from the semicircular outline of the Jianchuan endocarp. *Palaeosinomenium venablesii* from the Middle Eocene of Jilin, northeastern China, shows no significant differences in size and transverse ridges compared to the Jianchuan endocarp, but the lateral ridge of the *P. venablesii* endocarp from Jilin is smoother than that of the Jianchuan endocarp. *Palaeosinomenium ucrainicum* from Eocene Ukraine has the largest endocarp among any published species (Dorofeev, 1974). Three species of *Palaeosinomenium* are known from the Middle Eocene Messel Biota, Germany (Collinson et al., 2012). *Palaeosinomenium ornamentum* and *Palaeosinomenium* sp. are bigger than Jianchuan endocarp, and the *P. venablesii* endocarp from Messel Biota is more asymmetric than the Jianchuan endocarp (Collinson et al., 2012). These morphological distinctions support the recognition of the new species.

4.2. Biogeographic implications

Based on fossil records of *Palaeosinomenium*, the tribe Menispermeae was widely distributed in the Northern Hemisphere in

Table 1
Fossil records of *Palaeosinomenium*.

Taxon	Locality	Age	Length (mm)	Width (mm)	Transverse ridges	References
Palaeosinomenium hengduanensis Meng-Xiao Wu et Zhe-Kun Zhou	Jianchuan, Yunnan China	Late Eocene	4.8	6.1	20	Present study
P. ornamentum Collinson, Manchester and Wilde	Messel biota, Germany	Middle Eocene	4.5–6.0	5.7–6.6	15–20	Collinson et al., 2012
P. venablesii	Messel biota, Germany	Middle Eocene	3.0	3.5	18	Collinson et al., 2012
Palaeosinomenium sp.	Messel biota, Germany	Middle Eocene	5.3–6.3	7.8–6.3	25	Collinson et al., 2012
P. venablesii	Nut Bed flora, Clarno Formation, Oregon, western USA	Middle Eocene	2.1–3.7	2.2–4.3	18–21	Manchester, 1994
P. venablesii	Huadian, Jilin, northeastern China	Middle Eocene	3.0	3.5	20	Manchester et al., 2005
P. obliquatum Chandler	Lower Headon Beds, England	Early Eocene	3.0	4.0	Unknown	Chandler, 1961a
P. hantonense Chandler	Bournemouth Freshwater Beds, Southern England	Eocene	2.7	3.5	Unknown	Chandler, 1961b
Palaeosinomenium sp.	Bournemouth Freshwater Beds, Southern England	Eocene	3.6	Unknown	Unknown	Chandler, 1963
Palaeosinomenium sp.	Bournemouth Freshwater Beds, Southern England	Eocene	3.8	2.5	Unknown	Chandler, 1963
P. ucrainicum Dorofeev	Boltishka, Ukraine	Eocene	5.0–8.0	5.7–9.0	20–19	Dorofeev, 1974
P. venablesii Chandler	London Clay, Southern England	Paleocene	3.4–3.7	4.3–4.6	20–23	Chandler, 1961b
P. pulchrun Chandler	London Clay, Southern England	Paleocene	1.8–1.9	2.3–2.5	17–19	Chandler, 1961b

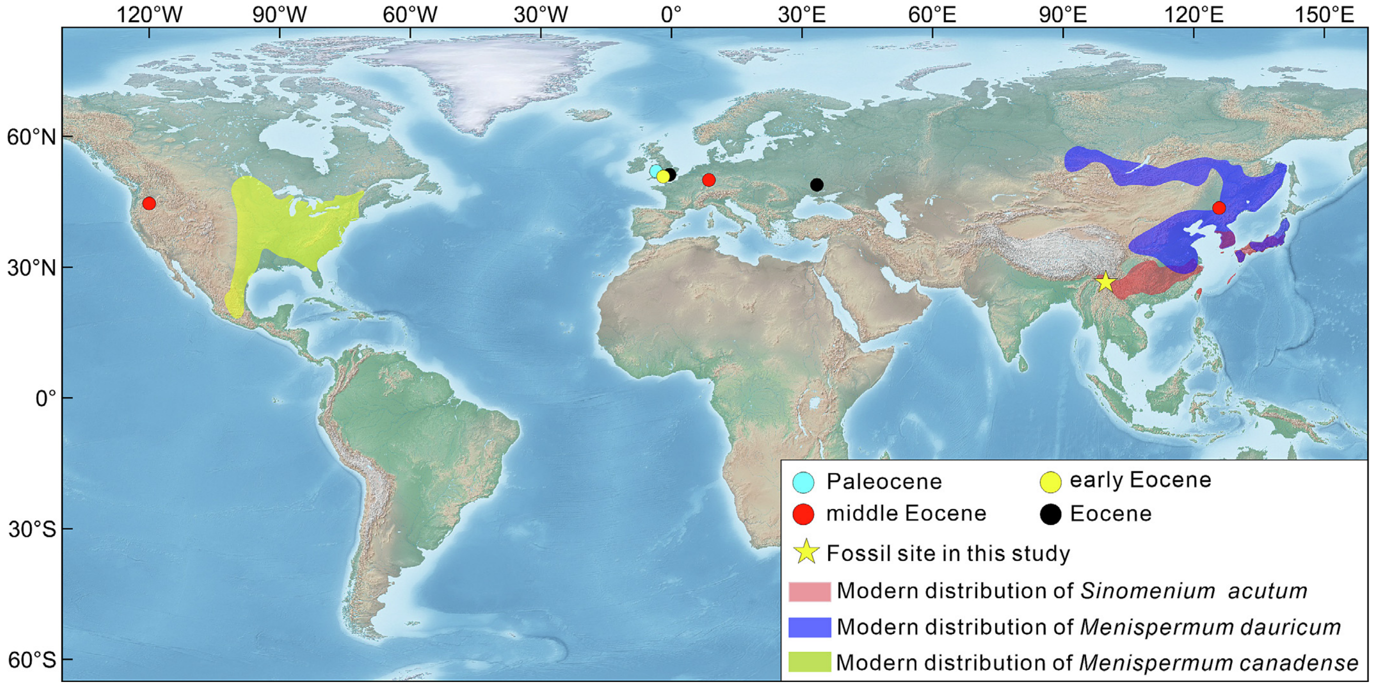

Fig. 2. Map showing the fossil occurrences of *Palaeosinomenium* and the modern distribution of the tribe Menispermeae.

the Eocene (Fig. 2). Europe has the most abundant fossil records of *Palaeosinomenium* from the Paleocene to the Middle Eocene (Chandler, 1961a, 1961b, 1963; Collinson et al., 2012). However, the extant distribution region of the tribe Menispermeae is narrower than that of the Eocene (Fig. 2). In the Middle Eocene, *P. venablesii* occurred in North America, Europe, and East Asia (Manchester, 1994; Manchester et al., 2005), but most fossil sites are not located in the distribution area of modern *Menispermum* or *Sinomenium* (Fig. 2). The presence of *Palaeosinomenium* in Europe, North America, and East Asia suggests a close link among Northern Hemisphere floras during the Paleogene. The occurrence of the extinct genera *Lagokarpos* McMurran & Manchester and *Cedrelospermum* Saporta as well as modern genera such as *Ailanthus* Defs., *Tsuga* (Endl.) Carrière also supports the close floristic affinity among these continents (Jia et al., 2019; Liu et al., 2019; Tang et al., 2019; Wu et al., 2020).

Based on phylogenic analyses, Wang et al. (2012) indicated that *Sinomenium* and *Menispermum* diverged in the early Neogene, but the fossil records indicate a much earlier divergence. The oldest fossil endocarps of *Sinomenium* from western Siberia, Russia, could be dated back to the Oligocene (Dorofeev, 1974). In the Neogene, *Sinomenium* was common in European floras (Van der Burgh, 1987; Cavallo and Martinetto, 2001; Jacques, 2009a; Manchester et al., 2009; Liu and Jacques, 2010), it occurred in North America until the Late Neogene (Liu and Jacques, 2010). The endocarps of *Sinomenium* occurring from the Early and Late Pliocene of Japan within its modern distribution area were assigned to *Sinomenium* aff. *acutum* and *S. acutum* respectively (Momohara et al., 1990; Momohara and Mizuno, 1999). The endocarp might belong to *Menispermum* appeared in the Early Eocene (Chandler, 1964), later on, Jacques et al. (2011) suggested that it might be included in *Sinomenium*, based on the features listed by the original author. Fossil endocarps of *Menispermum* were reported from Oregon, western USA, and have been dated backed to the Oligocene (Meyer and Mancherster, 1997). According to these fossil records, *Sinomenium* and *Menispermum* diverged before the Oligocene. *Palaeosinomenium hengduanensis* possesses the common characteristics of both *Sinomenium* and *Menispermum* while showing more morphological similarities with *Sinomenium*, such as endocarp length and the ventral margin shape. This supports the assumption that the divergence of the two genera might have started at least by the Late Eocene.

In East Asia, the earliest endocarps of the Menispermaceae were discovered in the Paleogene Sanshui Basin, southern China (Han et al., 2020). The abundant fossil records of Menispermaceae in southern China indicated that East Asia might have been an important region for the radiation and dispersal of Menispermaceae during the Paleogene (Han et al., 2018, 2020). The Middle Eocene Jianglang flora from central Tibetan Plateau, China, also showed a high diversity of Menispermaceae, with three genera having been reported (Del Rio et al., 2021). Since the Neogene, East Asia has been serving as a refugium for *Sinomenium*, which led to the present "eastern Asian endemic" pattern of this genus (Manchester et al., 2009). In contrast, *Menispermum* experienced long-distance dispersal from North America to East Asia and formed a disjunct distribution (Xiang et al., 2000). *Palaeosinomenium hengduanensis* was discovered at the site located in the modern distribution area of *Sinomenium acutum* (Fig. 2). This implicated that the fossil species shares similar morphological characteristics with *Sinomenium*, which appeared in the southeastern margin of the Tibetan Plateau by the Eocene.

4.3. Paleoenvironment implications

The extant species of the tribe Menispermeae are lianas (Plate II) distributed in Asia and North America (Luo et al., 2008). They are usually common taxa in temperate or secondary communities (Plate II, 1). The Middle Eocene climate optimum (Westerhold et al., 2020) led to the expansion of thermophilic floras in the Northern Hemisphere, and a high portion (ca. 30%–40%) of taxa associated with liana habits (such as Menispermaceae, Icacinaceae, and Vitaceae) occurred in the central Tibetan Plateau, central Europe, and western USA (Manchester, 1994; Collinson et al., 2012; Del Rio et al., 2021). However, *Palaeosinomenium hengduanensis* is, so far, the only undisputed liana that occurred in the Late Eocene Shuanghe flora (WGCPC, 1978; Ge and Li, 1999).

Lianas are important components of the modern tropical vegetation (Schnitzer and Bongers, 2002; Wang et al., 2012). *Menispermum* occurs in temperate and subtropical climate in North America and eastern Asia, whereas *Sinomenium* is distributed in subtropical climates in eastern Asia (GBIF.org (27 July 2022) GBIF Occurrence Download (https://doi.org/10.15468/dl.965tet); GBIF.org (27 July 2022) GBIF Occurrence Download (https://doi.org/10.15468/dl.y5q8u0z)). The present climate

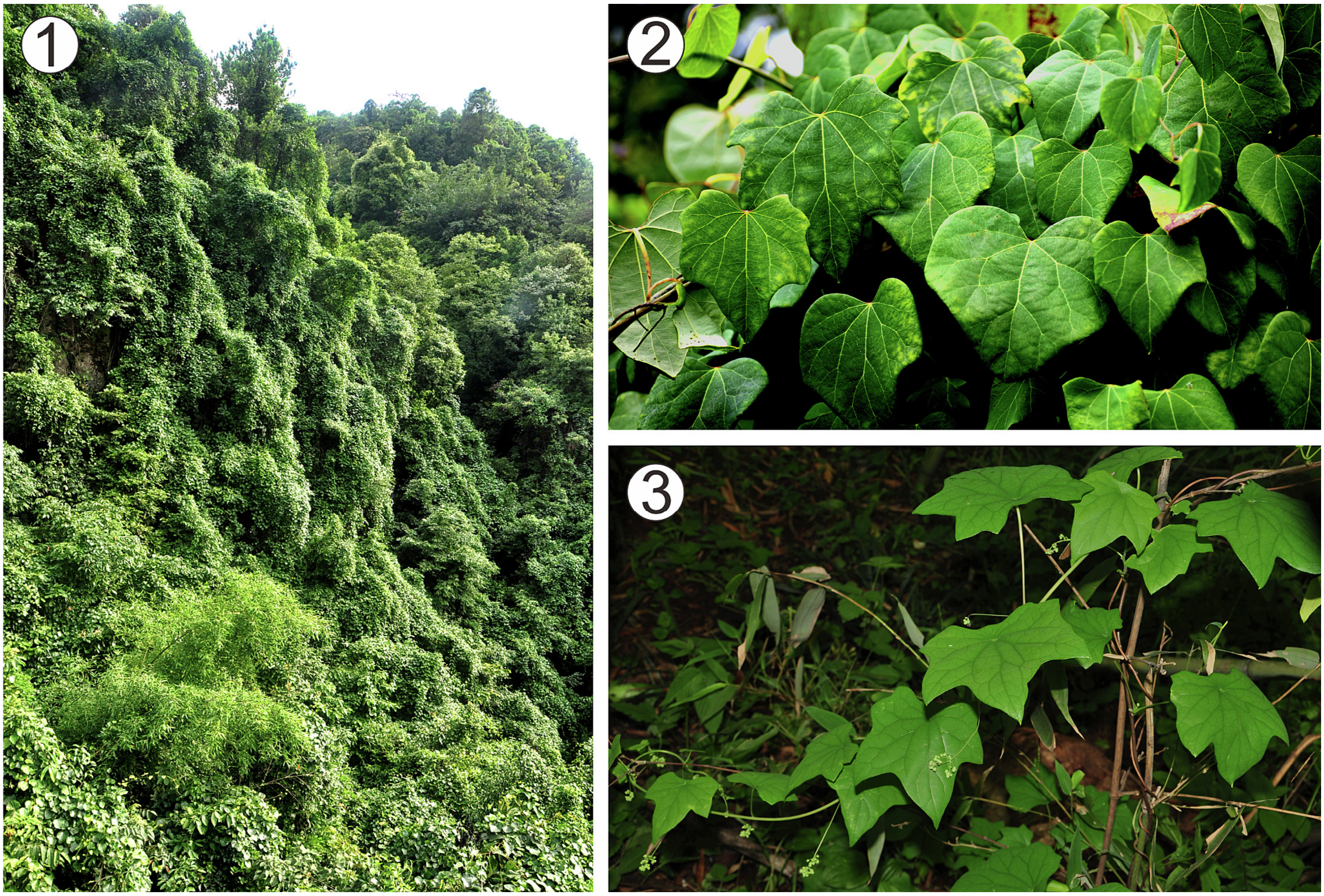

Plate II. Modern species of the tribe Menispermeae. 1. *Sinomenium acutum* as a dominant species on the edge of the subtropical forest, Zhejiang, China (middle in the photo). 2. *Sinomenium acutum*. 3. *Menispermum dauricum*.

condition in Jianchuan could meet the temperature and precipitation requirements of both *Sinomenium* and *Menispermum*, but only *Sinomenium* is distributed in the area near the fossil site today. Besides climate, topographic variables, stem anatomical features, tree species in the same community, and other factors could also influence the distribution of lianas (Carlquist, 1995; Li et al., 2022).

On a regional scale, a drastic climatic change from general aridity to monsoonal conditions in the southeastern flank of the Tibetan Plateau was recorded by the sedimentary rocks (Zheng et al., 2022). The monsoon-like climate in Jianchuan preceded the Eocene–Oligocene transition (Fang et al., 2021; Sakuma et al., 2021; Zheng et al., 2022). Sedimentological data from the Jianchuan Basin also indicates a significant climatic change associated with amplified precipitation during the Late Eocene and a swamp forest environment that was established before 35.5 Ma (Sorrel et al., 2017). Pollen-based climate reconstruction showed that the Jianchuan Basin had a warm, subtropical climate with a mean annual temperature of 16.8–21.7 °C, similar to that reconstructed by macrofossils (13.8–21.7 °C) (Table 2) (Sun et al., 2011; Wu et al., 2018). The Late Eocene climate condition in Jianchuan is in the climate range of the modern distribution area of *Sinomenium* and *Menispermum* (Table 2).

However, the modern climate values are lower than those of the Late Eocene in Jianchuan except for WMMT which is within the temperature range of the Late Eocene (Table 2). The higher temperature and precipitation in the late Eocene were consistent with the high percentage of evergreen species such as *Cinnamomum* Trew, *Phoebe* Ness, and *Quercus* L. in the Shuanghe flora (WGCPC, 1978; BGMRYP Bureau of Geology and Mineral Resources of Yunnan Province, 1996). Previous studies have suggested that the modern topography of the southeastern margin of the Tibetan Plateau had already been established by the Early Oligocene

Table 2
Modern and early Oligocene climate parameters of Jianchuan and the climate condition of the *Sinomenium* and *Menispermum* distribution ranges.

	Modern	Pollen CA	Macrofossil CA	*Sinomenium* distribution area	*Menispermum* distribution area
MAT (°C)	12.6	16.8–21.7	13.8–21.7	8.5–21.9	−7.0–22.0
WMMT (°C)	18.8	–	18.6–23.7	15.5–28.4	10.0–28.0
CMMT (°C)	6.5	–	7.7–18.9	−4.6–15.9	−27.3–17.3
MAP (mm)	749.2	–	987.2–1546.4	731.4–3464.2	226.3–2781.3
3WET (mm)	453.1	–	–	395.8–1500.5	46.8–1317.3
3DRY (mm)	18.8	–	–	12.9–382.5	10.0–1185.3
Reference	http://data.cma.cn/en	Wu et al., 2018	Sun et al., 2011	Present study	Present study

CA = coexistence approach; MAT = mean annual temperature, CMMT = cold moth mean temperature, WMMT = warm moth mean temperature, MAP = mean annual precipitation, 3WET = three wettest months' precipitation, 3WDT = three driest months' precipitation.

(Hoke, 2018; Wu et al., 2018; Su et al., 2019; Wu et al., 2022). Accompanying by the establishment of modernized climate and topography (Wu et al., 2022) in the Late Eocene, species belonging to the tribe Menispermeae may exist in this region until today.

5. Conclusion

The fossil endocarp from the Late Eocene of the Shuanghe Formation of Jianchuan Basin was assigned to a new species, *Palaeosinomenium hengduanensis* Meng-Xiao Wu et Zhe-Kun Zhou sp. nov. The new species supports the close floristic affinity among the North Hemisphere and divergence within the tribe Menispermeae might have occurred by the Upper Eocene. Modern and the Late Eocene climate in Jianchuan Basin are both suitable for the tribe Menispermeae. The species belonging to the tribe Menispermeae have existed in the southeastern margin of the Tibetan Plateau since the Late Eocene.

Data availability

The authors are unable or have chosen not to specify which data has been used.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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