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Fossil infructescence from southwestern China reveals Paleogene establishment of *Cladrastis* in Asia

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ABSTRACT

While a recent molecular phylogeographical study shows that, *Cladrastis*, a small woody genus in the bean family (Leguminosae), may have been established in Asia after the middle to late Eocene, fossils of the genus have not been previously documented in the Paleogene of Asia. Here we report an infructescence and four fossil fruits of *Cladrastis* from the Paleogene of southeastern Yunnan, China, which we described as a new species, *C. haominiae*, and this represents the first Paleogene record of *Cladrastis* in Asia. These fossils are characterized by a long stipe, an acuminate or acute proximal/distal end, wide sutures, and elliptical seed(s) nearly parallel or forming a small angle to the long axis of the fruit. Our finding supports the Paleogene establishment of *Cladrastis* in Asia and provides new significant evidence for the Paleogene origin of Yunnan biodiversity.

1. Introduction

Cladrastis Raf. (Leguminosae Juss.) is a woody genus of four species, with a disjunct distribution in East Asia and North America (Ma, 1982; Duley and Vincent, 2003; Duan et al., 2020a; Duan et al., 2020b). *Cladrastis delavayi* (Franch.) Prain and *C. wilsonii* Takeda have a roughly overlapping range in southern China, *C. shikokiana* (Makino) Makino is distributed in southern Japan, and *C. kentukea* (Dum.Cours.) Rudd is restricted to the southeastern United States (Duan et al., 2020a; Duan et al., 2020b) (Fig. 1). Plants of the genus are deciduous trees of 10–20 m in height and are cultivated as ornamentals, while their wood can be used to make dyes and household items such as bowls and paneling (Duley and Vincent, 2003). Recent molecular studies show that *Cladrastis* is sister to the clade consisting of *Styphnolobium* Schott and *Pickeringia* Nutt.; together with *Platyosprion* Maxim., and the three genera constitute the "*Cladrastis* clade", an early diverged lineage of Papilionoideae DC. in the Leguminosae (Duan et al., 2020a; Duan et al., 2020b).

Fossils of *Cladrastis* have been reported from the Paleogene and Neogene of North America (the early Eocene to late Miocene of the United State, the early Oligocene of Mexico in North America), and the Neogene of Asia (the Miocene of China and Japan in Asia) (Table 1). So far, the genus has not been documented from the Paleogene of Asia. However, a recent molecular phylogeographical study shows that *Cladrastis* may have been established in Asia during the middle to late Eocene (Duan et al., 2020a). It remains unclear whether the lack of Paleogene *Cladrastis* fossil records in Asia is due to Neogene establishment of the genus in Asia, taphonomic biases or insufficient fossil sampling. Here we present fossils of *Cladrastis* from the Paleogene of Yunnan, southwestern China, representing important data for examining this biogeographic question.

Yunnan, spanning three of the world's biodiversity hotspots (the Indo-Burma, the Mountains of Southwest China, and the Himalaya), is known for its rich botanical diversity (Li et al., 2015; Myers et al., 2000; Qian et al., 2020). In the past decades, abundant Neogene plant fossils have been uncovered from Yunnan and have been well-studied (Su et al., 2015; Su et al., 2016; Huang et al., 2017; Huang et al., 2019). These works consistently suggest that Yunnan plant diversity originated at least by the Neogene (Su et al., 2015; Su et al., 2016; Huang et al., 2017; Huang et al., 2019). However, the Paleogene appearance of the Yunnan flora remains unclear due to lack of fossils from this period and poor age constraint. Fortunately, recent paleobotanical

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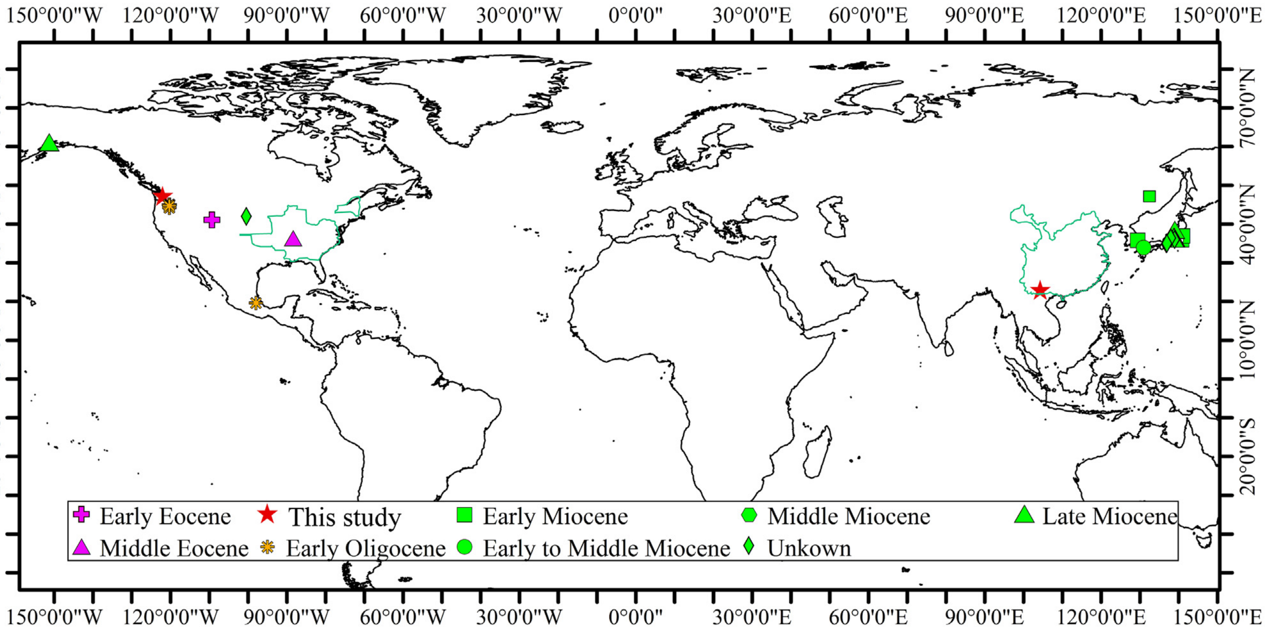

Fig. 1. Map showing the fossil occurrences and the extant distributional range of *Cladrastis*.

investigations, combined with absolute radiometric dating, report Paleogene floras from Yunnan that comprise abundant modern genera such as *Pinus* L., *Quercus* L., *Machilus* Rumph. ex Nees, *Acer* L., and *Populus* L. (Linnemann et al., 2017; Tian et al., 2020; Tian et al., 2021). These genera represent dominant elements of the extant Yunnan flora, thereby suggesting a Paleogene origin for Yunnan biodiversity (Linnemann et al., 2017; Tian et al., 2020). New discoveries of Paleogene plant fossils are thus crucial for improving our understanding for the evolution of Yunnan biodiversity.

In this study, we describe these newly recovered *Cladrastis* fossils from the Paleogene of southeastern Yunnan, China, and compare them with morphologically similar extant plant groups and fossil species assigned to *Cladrastis*. We then discuss the implications of these fossils for understanding the biogeographical history of *Cladrastis* and the evolution of Yunnan biodiversity.

2. Materials and methods

2.1. Fossil locality and age

Fossil fruits were collected from an outcrop in the northwestern part of the Maguan Basin, Southeastern Yunnan, China (23°1′N, 104°23′E, 1320 m a.s.l.) (Fig. 2). The fossiliferous sediments are characterized by cyclic deposits of light-yellow or light-gray pelitic laminated mudstone and siltstone, and belong to the Huazhige Formation (HF) (Zhang, 1976; Bureau of Geology and Mineral Resources, 1990) (Fig. 3). The HF is also well developed in the Wenshan Basin, approximately 50 km to the northwest of the Maguan Basin (Bureau of Geology and Mineral Resources, 1990; Lebreton-Anberrée et al., 2016; Tian et al., 2020). The HF in Wenshan forms the upper part of the succession, while that in Maguan forms the lower part (Zhang, 1976; Bureau of Geology and Mineral Resources, 1990; Zhang et al., 2018).

The age of the HF has been previously assigned to the Miocene based on stratigraphic comparisons and paleomagnetic study (Lebreton-Anberrée et al., 2015; Zhang et al., 2018). However, recent emerging evidence from mammal fossils and isotope dating (Qi, 1992; Averianov et al., 2016; Tian et al., 2021) shows that the HF is older. Determining the age of the HF is beyond the scope of this study, but the relative age of Maguan paleoflora can be constrained tentatively here. First, *Gigantamynodon* Gromova (Amynodontidae Scott et Osborn), a kind of mammal which lived in the Eocene and disappeared after the early Oligocene, was recovered from the HF in Maguan (Qi, 1992; Averianov et al., 2016), immediately beneath the sediments that yield fossils of this study (Maguan paleoflora). This suggests that the age of the Maguan paleoflora should be younger than the early Eocene. Second, the Wenshan paleoflora from the Wenshan Basin (the upper part of the HF) has been dated to 30 ± 2/32 ± 1 Ma based on high-resolution U–Pb dating (Tian et al., 2021). This indicates that the age of Maguan flora in the lower part of HF should be older than 30 ± 2/32 ± 1 Ma, although this could be compromised by potentially poor stratigraphic comparisons. From a floristic perspective, in-depth studies have been carried out for the geographically close Wenshan and Maguan paleofloras, and both represent subtropical evergreen forests and share similar elements (Huang, 2017; Jia, 2018). The major difference between the two paleofloras is that Maguan paleoflora contains numerous extinct taxa such as extinct lineage of *Carpinus* L., *Cedrelospermum* Sapota, and *Deviacer* Manchester (Jia et al., 2015; Jia, 2018; Xue et al., 2020), but these taxa are not present in the Wenshan paleoflora (Huang, 2017). In particular, the Maguan flora has yielded more than 400 winged fossil fruits of *Cedrelospermum*, an extinct genus with extensive fossil records in the Cenozoic of Europe and North America (Jia et al., 2018). However, no *Cedrelospermum* fossils have been found from the nearby and diverse Wenshan paleoflora (Huang, 2017; Jia, 2018). This suggests that the Maguan paleoflora is older than the Wenshan paleoflora and the two paleofloras seem to represent substantially different stages in the evolution of the Yunnan flora. Therefore, current evidence suggests that the age of Maguan paleoflora should be younger than the early Eocene but older than 30 ± 2 /32 ± 1 Ma (the early Oligocene).

Furthermore, the geology of southeastern Yunnan is overall stable in the Cenozoic (Jacques et al., 2014; Li et al., 2017). Together with that the Maguan and Wenshan paleofloras are geographically close and floristically similar, the disappearance of these extinct taxa from the Wenshan paleoflora was possibly related to the abrupt cooling taken place at the Eocene–Oligocene boundary (Westerhold et al., 2020). It shows that the age of the Maguan paleoflora possibly precedes the Eocene–Oligocene boundary, and are most likely the late Eocene.

Table 1
Reported fossil records of *Cladrastis*.

No.	Species	Type	Age	Latitude	Longitude	Locality	Continent	References
1	*C.* sp. (?)	–	Early Eocene	41.1	−109.3	USNM 41427, Wyoming, United States	North America	Wilf (2000)
2	cf. *C.* sp.	Fruit and leaf	Middle Eocene	36.4	−88.3	Puryear, Henry County, Tennessee, United States	North America	Herendeen (1992)
3	*C. pugetensis* Wolfe	Leaf	Late Eocene	47.3	−122.0	Puget Group, Washington, United States	North America	Burnham (1994)
4	*C. haominiae* L.B. Jia et Z.K. Zhou	Fruit	Late Eocene	23.0	104.4	Maguan, Yunnan, China	Asia	This study
5	*C. delgadoi* Calvillo-Canadell et Cevallos-Ferriz	Fruit	Early Oligocene	19.6	−97.9	Ahuehuetes, Tepexi de Rodríguez Town, Puebla, Mexico	North America	Calvillo-Canadell and Cevallos-Ferriz (2005)
6	*C. oregonensis* Brown	Fruit	Early Oligocene	44.2	−120.3	Bridge Creek, 9 miles northwest of Mitchell, Oregon, United States	North America	Brown (1937)
7	*C. oregonensis* Brown	Fruit	Early Oligocene	44.1	−120.3	Bridge Creek flora (Localities-Painted Hills, Fossil, Iron Mountain, Crooked River, Lost Creek), Oregon, United States	North America	Meyer and Manchester (1997)
8	*C.* sp.	Leaf	Early Oligocene	45.0	−120.2	Bridge Creek flora (Locality-Fossil), Oregon, United States	North America	Meyer and Manchester (1997)
9	cf. *C.* sp.	Leaf	Early Oligocene	44.9	−120.4	Bridge Creek flora (Locality-Fossil), Oregon, United States	North America	Meyer and Manchester (1997)
10	*C. oregonensis* Brown	Leaf	Early Oligocene	44.6	−120.3	Bridge Crooked River flora (Painted Hills, Fossil, Iron Mountain, Crooked River, Lost Creek), Oregon, United States	North America	Meyer and Manchester (1997)
11	*C.* sp.	Leaf	Early Miocene	37.0	141.0	Kunugidaira, Joban, Japan	Asia	Yabe (2008)
12	*C. aniensis* Huzioka	Leaf	Early Miocene	35.9	129.5	Korea	Asia	Paik et al. (2012)
13	*C. chaneyi* Tanai et N. Suzuki	Leaf	Early Miocene	36.0	140.8	Shichiku, Joban, Japan	Asia	Yabe (2008)
14	*C. chaneyi* Tanai et N. Suzuki	Leaf	Early to Middle Miocene	34.0	131.0	Nakayama, Yamaguchi, Japan	Asia	Yabe (2008)
15	*C.* sp.	Leaf	Middle to Late Miocene	36.1	139.2	Yagii Flora, Hirakata, Japan	Asia	Ozaki (1991)
16	*C. aniensis* Huzioka	Leaf	Late Miocene	36.3	138.5	Itahana Flora, Gunma, Japan	Asia	Ozaki (1991)
17	*C. inouei* (Huzioka) Ozaki	Leaf	Late Miocene	36.3	139.0	Itahana Flora Locality J, Gunma, Japan	Asia	Ozaki (1991)
18	*C. japonica* (Tanai and Suzuki) Wolfe	Leaf	Late Miocene	61.1	−151.3	Nam Chuitna River, Cook Inlet Region, Alaska	North America	Wolfe (1966)
19	*C. inouei* (Huzioka) Ozaki	Leaf	Late Miocene	36.3	138.8	Kabutoiwa Flora, Gunma, Japan	Asia	Ozaki (1991)
20	*C. aniensis* Huzioka	Leaf	Late Miocene	36.3	138.8	Kabutoiwa Flora, Gunma, Japan	Asia	Ozaki (1991)
21	*C. aniensis* Huzioka	Leaf	Unkown	36.7	138.8	Daido, Gunma, Japan	Asia	Ozaki (1991)
22	*C. aniensis* Huzioka	Leaf	Unkown	36.4	138.1	Omi-mura, Nagano, Japan	Asia	Ozaki (1991)
23	*C.* cf. *shikokiana* (Makino) Makino	Leaf	Unkown	34.9	136.9	Ootani, Oosani, Japan	Asia	Ozaki (1991)
24	*C.* cf. *platycarpa* (Maxim.) Makino	Leaf	Unkown	34.9	136.9	Ootani, Oosani, Japan	Asia	Ozaki (1991)
25	*C. aniensis Huzioka*	Leaf	Unkown	36.0	139.0	Akima Flora, Gunma, Japan	Asia	Ozaki (1991)
26	*C. aniensis* Huzioka	Leaf	Unkown	36.4	138.0	Ohoka Kabauchi, Nagano, Japan	Asia	Ozaki (1991)
27	*C. aniensis* Huzioka	Leaf	Unkown	35.0	137.0	Seto-Obata Locality, Aichi, Japan	Asia	Ozaki (1991)
28	*C. prelutea* MacGinitie	Leaf	Unkown	42.0	−100.4	Cook Inlet region, Alaska	North America	MacGinitie (1962)

Note. We compiled the *Cladrastis* fossil records as far as we could find from the literature and databases. Further reevaluation for the reliability of these records is necessary. Brown (1937) described *C. oregonensis* based on a specimen from the Oligocene of Bridge Creek, Oregon, United States, and indicated that “the placental suture line is marked by a wide keel or wing, but the other margin does not appear to be appreciably winged.” Because suture only presenting at one flank of the fruit is unusual in both *Cladrastis* and *Platyosprion* (previously included in *Cladrastis*), the fossil can be only taken as possible *Cladrastis*.

2.2. Morphological observations

A fossil infructescence and four fossil fruits representing *Cladrastis* were collected in total. These fossils are preserved as compressions in the fine laminated mudstone and siltstone shales. They were photographed using a digital camera (Nikon D750, Kanagawa, Japan). Fine-scale details of the fossils were further examined under a stereo microscope (Leica S8APO, Wetzlar, Germany), and images were taken. To compare the fossils with extant species, specimens of Leguminosae from the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), and the Herbarium of Institute of Botany, Chinese Academy of Sciences (PE) were studied. Fossil records of *Cladrastis* were compiled from published literature and the Cenozoic Angiosperm Database (Xing et al., 2016). Previously reported fossil fruits were compared with our new fossils by checking descriptions and images in the published literature.

3. Systematic descriptions

Order: Fabales Bromhead, 1838
Family: Leguminosae Juss., 1789
Tribe: Cladrastideae L. Duan et J. Wen, 2020

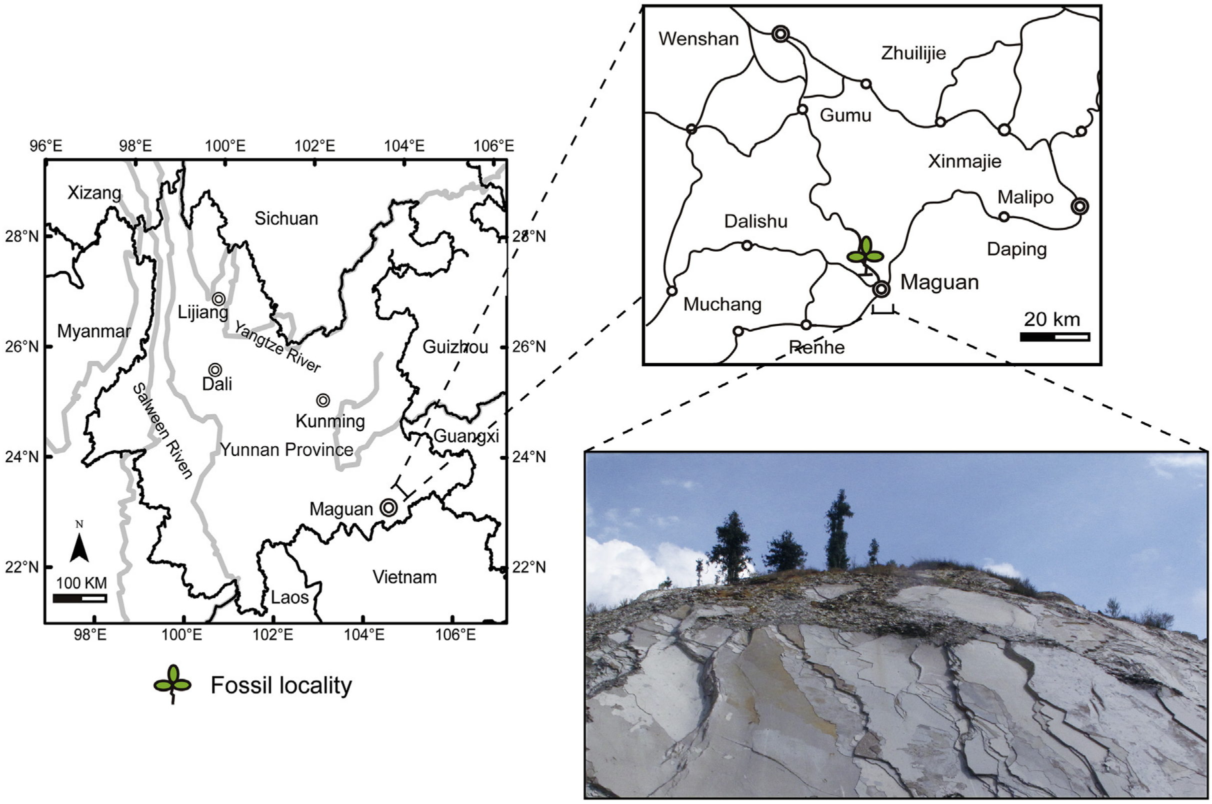

Fig. 2. The fossil locality in the Maguan Basin, southeastern Yunnan, South China.

Genus: **Cladrastis** Raf., 1824

Species: *Cladrastis haominiae* L.B. Jia et Z.K. Zhou sp. nov. (Plate I)

Holotype: MG1106 (Plate I, 1)

Paratypes: MG0558 (Plate I, 3), MG1405 (Plate I, 5), MG2006 (Plate I, 2), MG0563 (Plate I, 4)

Stratigraphic horizon: The Huazhige Formation

Age: Younger than the early Eocene and older than the early Oligocene (30 ± 2/32 ± 1 Ma), mostly likely the late Eocene.

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

Type locality: Maguan County, Yunnan, China.

Etymology: The specific epithet "*haominiae*" is named after the Chinese paleobotanist, Professor Hao-Ming Li, who made important contributions to paleobotanical research in China.

Description: The infructescence is paniculate; the primary peduncle of the infructescence is stout, 5.2 mm long, giving arise to two secondary peduncles (Plate I, 1). The distinction between the secondary peduncle and the pedicel is unclear because of limited preservation (Plate I, 1). The fruit is linear to fusiform, 26–55 mm long and 4.2–8.6 mm wide. The fruit receptacle is an inverted V-shape (Plate I, 1, 2, 4; Plate II, 2, 4). The pedicel of the detached fruits is well-preserved and clear, 3.9–6.5 mm long (Plate I, 2–5). The stipe is 2.4–3.8 mm long (Plate I). The proximal and distal end of the fruit are variable in outline: when the proximal/distal ovule(s) matured to form seed(s) (Plate I, 4, 5; Plate II, 5, 6), the proximal/distal end tapered abruptly to the stipe/acute base, whereas when the proximal/distal ovule(s) was(were) abortive, the proximal/distal end tapered gradually to the stipe or acute base (Plate I, 3; Plate II, 1–4). The sutures of the fruits are wide

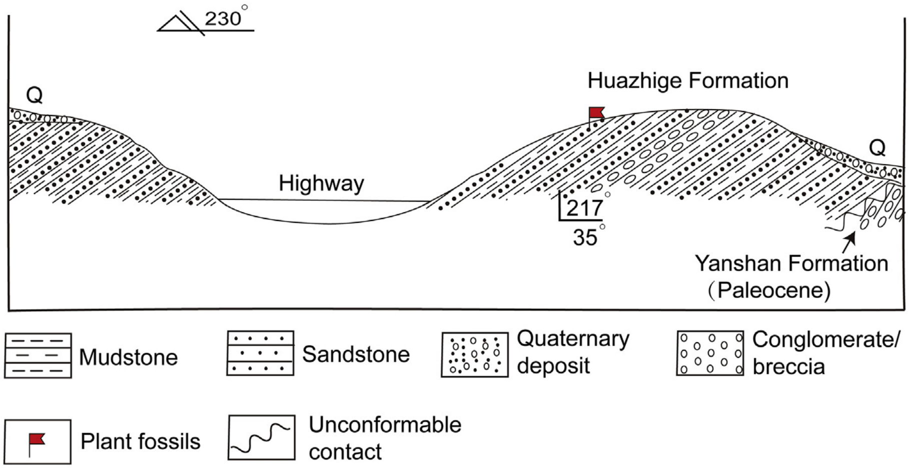

Fig. 3. Cross section of the fossil locality in the Maguan Basin, southeastern Yunnan, China.

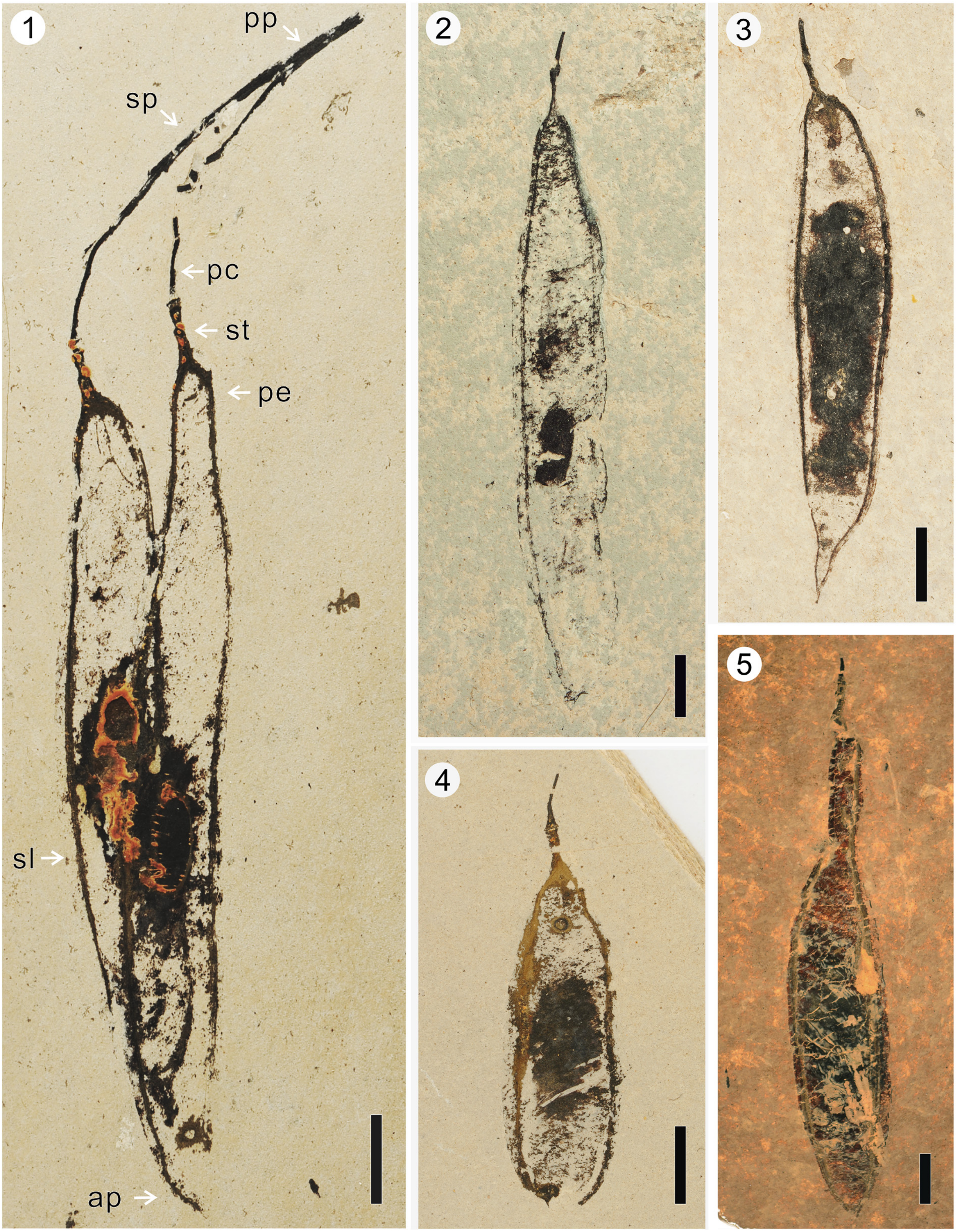

Plate I. Infructescence and detached fruits of *Cladrastis haominiae* L.B. Jia et Z.K. Zhou sp. nov. pp., primary peduncle; sp, secondary peduncle; pc, pedicel; st, stipe; pe, proximal end; sl, sutural line; ap, apex. Scale bars = 5 mm.

1. Infructescence of *C. haominiae* showing the primary peduncle with two fruits attached. MG1106.
2. Fruit showing long stipe, constricted proximal end, and seeds almost parallel to the long axis of the fruit. MG2006.
3. Fruit showing acuminate apex. MG0558.
4. Fruit showing inflated receptacle and acute apex. MG0563.
5. Fruit showing constricted proximal end. MG1405.

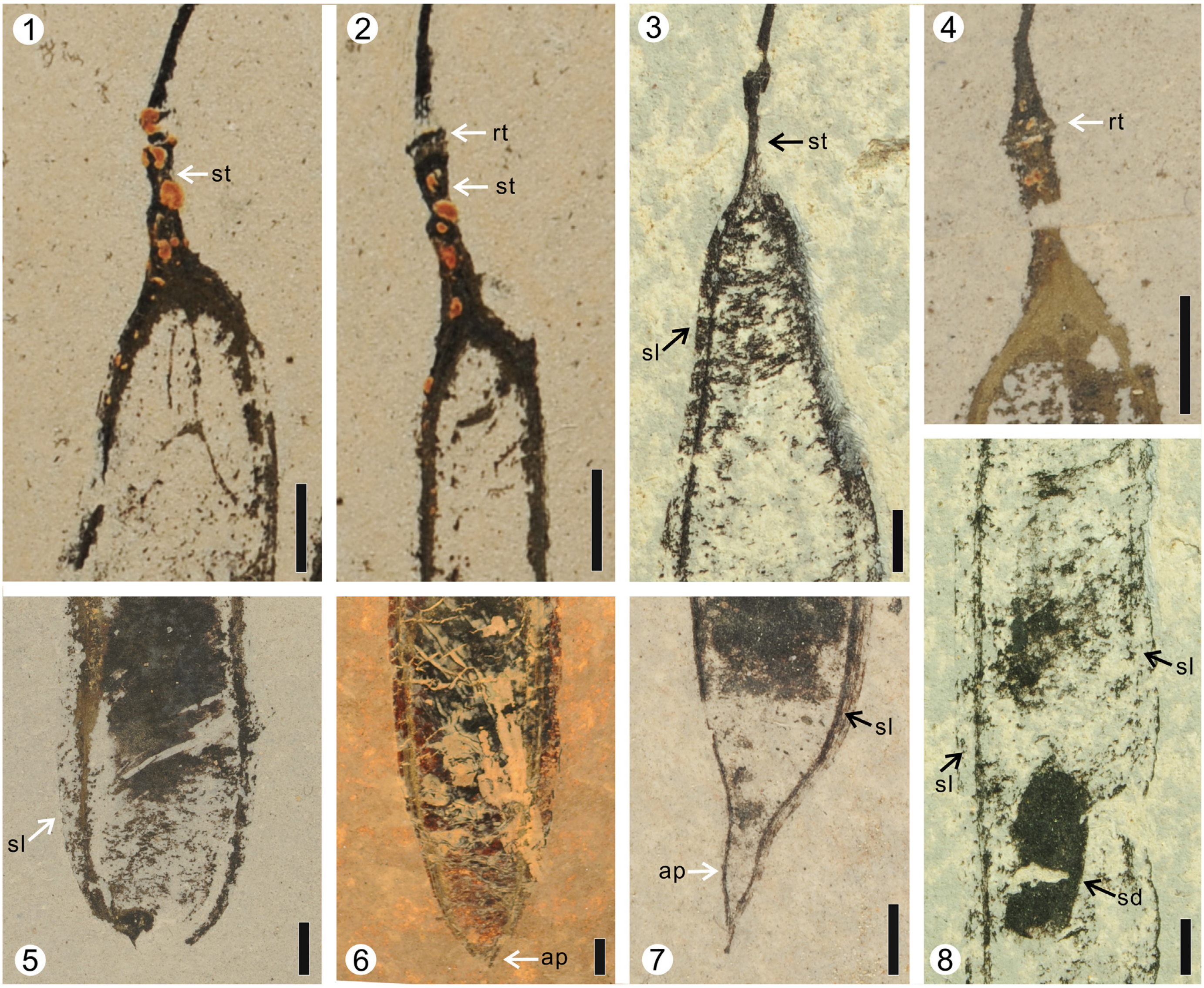

Plate II. Details of *Cladrastis haominiae* L.B. Jia et Z.K. Zhou sp. nov. fruits. st, stipe; rt., fruit receptacle; sl, sutural line; ap, apex; sd, seed. Scale bars = 2 mm.
1–2. Magnification of fruit showing elongated stipe, fruit receptacle, and constricted proximal end. MG1106.
3. Magnification of fruit showing elongated stipe and wide sutural lines. MG1106.
4–5. Magnification of fruit showing V-shaped fruit receptacle and wide suture. MG0563.
6. Magnification of fruit showing acute apex. MG1405.
7. Magnification of fruit showing acuminate apex. MG0558.
8. Magnification of fruit showing wide suture, and seed which forms a small angle to the long axis of the fruit. MG1106.

(Plate I; Plate II, 3,8). The fruits have one or more seed(s), which is(are) elliptical, 6.6–9.2 mm long and 2.3–3.6 mm wide (Plate I, 1, 2; Plate II, 8). The long axis of the seeds is almost parallel or forms an angle of less than 11.6° to the long axis of the fruits (Plate I, 1, 2).

4. Discussion

4.1. Morphological comparisons

The fossil fruits have long stipes, acuminate or acute proximal and distal ends, wide sutures, and elliptical seeds nearly parallel or forming a small angle to the long axes of the fruits. These characters are morphologically consistent with those of *Cladrastis* (Ma, 1982; Duley and Vincent, 2003) (Plate III). This is also supported by one specimen preserved as an infructescence, the branching type of which is identical with the panicle of *Cladrastis* (Plate III). Although the new fossils are more or less similar to the fruits of *Platyosprion* Maxim., *Styphnolobium* Schott and *Pickeringia* Nutt. in the *Cladrastis* clade, they can be readily distinguished from the three genera (Fig. 4). For example, the fruits of *Platyosprion* have wider valves and wings along both sides of the sutures, whereas the new fossil fruits have much narrower valves and no wings. The fruit valves of *Styphnolobium* and *Pickingia* are prominently constricted between seeds while that of *Cladrastis* are only slightly constricted. Therefore, the new fossils were assigned to *Cladrastis*.

Cladrastis consists of four extant species, i.e. *C. delavayi*, *C. kentukea*, *C. shikokiana*, and *C. wilsonii* (Duan et al., 2020a; Duan et al., 2020b). *Cladrastis kentukea* is restricted to the southeastern United States, while the remaining three species are distributed in East Asia (Duan et al., 2020a). The four species are primarily distinguished from each other by the number of leaflets, the shape and the size of terminal leaflet and calyx, and the state of inflorescence (erect or pendulous) (Ma, 1982; Duley and Vincent, 2003). Their fruit morphology overlaps, although the fruits of *C. kentukea* usually have longer valves and more

Plate III. Infructescence and detached fruits of extant *Cladrastis* Raf.
1–3, *C. wilsonii* Takeda; 4, 5, *C. delavayi* (Franch.) Prain. Scale bar = 5 mm.

prominent constrictions than those of *C. delavayi* and *C. wilsonii* (Table 2). Despite that the new fossils cannot be morphologically distinguished from these four extant species, they are most similar to *C. delavayi* and *C. wilsonii* which usually have no apparent constrictions between seeds (Table 2). *Cladrastis delavayi* and *C. wilsonii* also grow in the regions where our new fossils were uncovered, raising the possibility that the fossils may represent the ancestor of the two species.

Previously reported fruit fossils of *Cladrastis* include *C. oregonensis* Brown and *C.* sp. from the Oligocene of the United States, cf. *C.* sp. from the Eocene of the United States, and *C. delgadoi* Calvillo-Canadell et Cevallos-Ferriz from the Oligocene of Mexico (Herendeen, 1992; Meyer and Manchester, 1997; Calvillo-Canadell and Cevallos-Ferriz, 2005) (Table 2). However, these fossil species can be obviously distinguished from the new fossil fruits. The Oligocene fruits from the

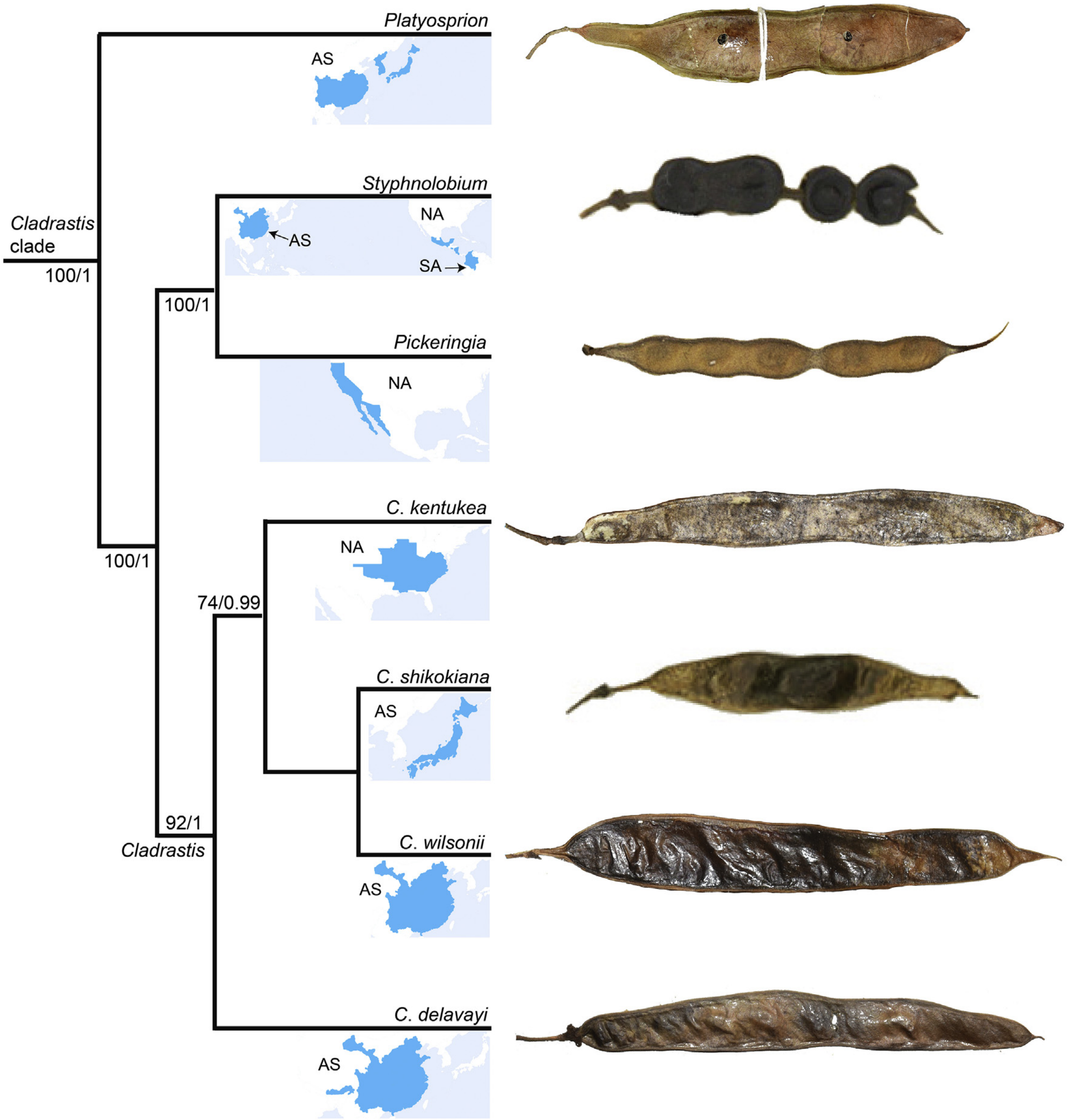

Fig. 4. Phylogeny of *Cladrastis* Clade (adapted from Duan et al. (2020a)) and fruit morphology of each taxon. AS, Asia; NA, North America; SA, South America. The numbers before and after the slashes indicate Bayesian posterior probabilities and maximum likelihood bootstrap values respectively.

United States either are marked by "a wide keel or wing" at one side of the fruit (*C. oregonensis*) or have a prominent constriction in the middle of the fruit body (*C.* sp.) (Brown, 1937; Meyer and Manchester, 1997), whereas the new fossils possess two wide sutures at both margins of the fruit and have no prominent constriction. The Eocene fruits from the United States have wide fruit valves (13–15 mm in width) and wings (Herendeen, 1992), but the new fossils have much narrower fruit valves (2.3–3.6 mm in width) and no wings. The Oligocene fruits from Mexico do not preserve the fruit receptacle and apex, and are 7 mm wide (Calvillo-Canadell and Cevallos-Ferriz, 2005), unlike the new fossils, which are 2.3–3.6 mm wide.

Based on the discussion above, the new fossils should be assigned to a new species of *Cladrastis*, here named as *C. haominiae*. Although the new fossils are indistinguishable from the fruits of extant *Cladrastis* species, we hesitate to assign them to the four species due to the lack of characters of leaves and flowers.

4.2. Implications for an early establishment of Cladrastis in Asia

Although a recent molecular phylogenetic study suggests that *Cladrastis* may have been established in Asia since the middle to late Eocene (Duan et al., 2020a), fossils of the genus have never been documented previously from the Paleogene of Asia. *Cladrastis haominiae* from the Paleogene of Maguan Basin, Yunnan, is the earliest fossil record and also the first Paleogene fossil record of the genus in Asia. It shows that *Cladrastis* inhabited Asia no later than the early Oligocene (most likely the late Eocene), supporting an early establishment of *Cladrastis* in Asia.

Currently, *Cladrastis* exhibits a typical East Asian and North American disjunct distribution pattern. This famous pattern is assumed to have been by floristic exchanges across the two most important land bridges (i.e. the North Atlantic and the Bering land bridge) and long distance dispersal (Tiffney, 1985; Tiffney and Manchester, 2001; Donoghue

Table 2
Morphological comparisons of the fossils with extant species and reported fossil species based on fruits within *Cladrastis*.

Species	Status	Overall shape of fruits	Length/width of fruits (cm)	Length of pedicels (cm)	Proximal end of fruits	Distal end of fruits	Number of seeds	Constriction between seeds	Orientation of seeds	Reference
C. delavayi (Franch.) Prain	Extant species	Elliptic or long elliptic, flat	3–8/1–2	0.4–0.8	***Acute or acuminate***	***Acute or acuminate***	1–3 (−5)	**Not prominent**	***Forming a small angle or parallel to the long axis of the fruit***	Bao and Vincent (2010)
C. wilsonii Takeda	Extant species	Elliptic or long elliptic, flat	4.5–8/0.8–1	0.5–1.1	***Acute or acuminate***	***Acute or acuminate***	1–5	**Not prominent**	***Forming a small angle or parallel to the long axis of the fruit***	Bao and Vincent (2010), Duley and Vincent (2003)
C. shikokiana (Makino) Makino	Extant species	Elliptic or long elliptic, flat	***(2.8)***–6–7/**ca.** ***0.4***	**ca.** ***0.4***	***Acute or acuminate***	***Acute or acuminate***	***(1)***–4–6	**Not prominent**	***Forming a small angle or parallel to the long axis of the fruit***	Duley and Vincent (2003)
C. kentukea (Dum.Cours.) Rudd	Extant species	Elliptic or long elliptic, flat	7–8/***0.7–1***	1–2	***Acute or acuminate***	***Acute or acuminate***	1–8	**Slightly prominent**	***Forming a small angle or parallel to the long axis of the fruit***	Duley and Vincent (2003)
C. haominiae L.B. Jia et Z.K. Zhou	Fossil species	***Elliptic or long elliptic***	***2.6–5.5/0.4–0.9***	***0.4–0.7***	***Acute or acuminate***	***Acute or acuminate***	***1–2–(?)***	***Not prominent***	***Forming a small angle or parallel to the long axis of the fruit***	This study
C. delgadoi Calvillo-Canadell et Cevallos-Ferriz	Fossil species	Fusiform to linear	5–6/7	Not preserved	***Slightly constricted***	***Not preserved***	Unclear	**Slightly prominent**	***Unclear***	Calvillo-Canadell and Cevallos-Ferriz (2005)
cf. *C.* sp.	Fossil species	***Elliptic***	3.8+/1.3–1.5	Not preserved	***Acute***	***obtuse to acute***	1–2	**Slightly prominent**	***Parallel to the long axis of the fruit***	Herendeen (1992)
C. sp.	Fossil species	***Elliptic to moniliform***	7.5/0.7	Not preserved	***Acute***	***Acuminate***	3	***Prominent***	***Unclear***	Meyer and Manchester (1997)
C. oregonensis Brown	Fossil species	Linear	6.5/1.2	Not preserved	***Acute***	***Acute***	1	No constriction	***Parallel to the long axis of the fruit***	Brown (1937)

Note. The morphological states of the above taxa are mostly taken from the cited references, but for these that have not been documented in the references they have been observed by the authors from herbarium specimens or online images and are indicated in bold and italic font.

and Smith, 2004; Wen et al., 2016). As the fruits of *Cladrastis* have not been reported to be dispersed by ocean currents or eaten by birds, long distance dispersal seems unlikely. *Cladrastis* has neither fossil nor living representatives known from Europe, but *Cladrastis*-like fossils have been documented from the territories adjacent to the two ends of the Bering land bridge (the early Miocene of the Russian Far East and the late Miocene of Alaska, the United States) (Wolfe, 1966; Pavlyutkin et al., 2012). It is possible that *Cladrastis* might have once passed between North America and Asia by the Bering land bridge. However, this does not exclude the North Atlantic bridge as a plausible passage for *Cladrastis*, and future paloebotanical investigations may uncover fossils of the genus in Europe.

4.3. Implications for a Paleogene origin of Yunnan biodiversity

Our discovery of *C. haominiae* from the Maguan Basin, southeastern Yunnan, shows that the genus became established in southeastern Yunnan no later than the early Oligocene (most likely the late Eocene). Notably, the fruit morphology of *C. haominiae* is indistinguishable from that of *C. wilsonii* and *C. delavayi*, which still grow near the fossil site. Plants of this genus thus may have continuously survived in southeastern Yunnan since at least the early Oligocene. A similar phenomenon is also found in other taxa uncovered from the Maguan Basin such as *Carpinus* L., *Pterolobium* R. Br. ex Wight et Arn., *Sladenia* Airy Shaw, and *Ulmus* L (Jia et al., 2017; Zhang et al., 2018; Xue et al., 2020; Jia et al., 2021). They are all morphologically indistinguished from the extant species which still inhabit the region close to the fossil site. This scenario thus supports the assertion that the biodiversity of Yunnan can be traced back to the Paleogene (Linnemann et al., 2017). This is also consistent with the discovery of the early Oligocene Wenshan and Lvhe paleofloras in central Yunnan, where almost all of the recognized genera are extant and can be found in the region nearby today (Linnemann et al., 2017; Wang et al., 2019; Tian et al., 2020).

Declaration of Competing Interest

None.

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References

Averianov, A., Danilov, I., Jin, J., Wang, Y., 2016. A new amynodontid from the Eocene of South China and phylogeny of Amynodontidae (Perissodactyla: Rhinocerotoidea). J. Syst. Palaeontol. 15, 927–945.

Bao, B., Vincent, M.A., 2010. *Cladrastis*. In: Wu, Z.Y., Raven, P.H., Hong, D.Y. (Eds.), Flora of China, pp. 93–95.

Brown, R., 1937. Fossil legumes from Bridge Creek Oregon. J. Wash. Acad. Sci. 27, 414–418.

Bureau of Geology and Mineral Resources, 1990. Regional Geology of Yunnan Province. Geology Press, Beijing, China.

Burnham, R.J., 1994. Paleoecological and Floristic Heterogeneity in the Plant-Fossil Record-an Analysis Based on the Eocene of Washington. US Government Printing Office, Washington.

Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S., 2005. Diverse assemblage of Eocene and Oligocene Leguminosae from Mexico. Int. J. Plant Sci. 166, 671–692.

Donoghue, M.J., Smith, S.A., 2004. Patterns in the assembly of temperate forests around the Northern Hemisphere. Philos. Trans. R. Soc. B 359, 1633–1644.

Duan, L., Harris, A.J., Su, C., Ye, W., Deng, S.W., Fu, L., Wen, J., Chen, H.F., 2020a. A fossil-calibrated phylogeny reveals the biogeographic history of the *Cladrastis* clade, an amphi-Pacific early-branching group in papilionoid legumes. Mol. Phylogenet. Evol. 143, 106673.

Duan, L., Harris, A.J., Ye, W., Deng, S.W., Song, Z.Q., Chen, H.F., Wen, J., 2020b. Untangling the taxonomy of the *Cladrastis* clade (Leguminosae: Papilionoideae) by integrating phylogenetics and ecological evidence. Taxon 68, 1189–1203.

Duley, M., Vincent, M., 2003. A synopsis of the genus *Cladrastis* (Leguminosae). Rhodora 105, 205–239.

Herendeen, P.S., 1992. The fossil history of Leguminosae from the Eocene of southeastern North America. In: Herendeen, P.S., Dilcher, D.L. (Eds.), Advances in Legume Systematics: Part 4 the Fossil Records. Royal Botanic Gardens, Kew, London, UK, pp. 85–160.

Huang, J., 2017. The Middle Miocene Wenshan Flora, Yunnan, Southwestern China and its Palaeoenvironment Reconstruction. Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, p. 320.

Huang, Y.-J., Ji, X.-P., Su, T., Deng, C.-L., Ferguson, D.K., Yu, T.-S., Yang, X., Sun, H., Zhou, Z.-K., 2017. Habitat, climate and potential plant food resources for the late Miocene Shuitangba hominoid in Southwest China: Insights from carpological remains. Palaeogeogr. Palaeoclimatol. Palaeoecol. 470, 63–71.

Huang, Y.-J., Zhu, H., Momohara, A., Jia, L.-B., Zhou, Z.-K., 2019. Fruit fossils of Rosoideae (Rosaceae) from the late Pliocene of northwestern Yunnan, Southwest China. J. Syst. Evol. 57, 180–189.

Jacques, F.M.B., Su, T., Spicer, R.A., Xing, Y.W., Huang, Y.J., Zhou, Z.K., 2014. Late Miocene southwestern Chinese floristic diversity shaped by the southeastern uplift of the Tibetan Plateau. Palaeogeogr. Palaeoclimatol. Palaeoecol. 411, 208–215.

Jia, L.B., 2018. The Early Miocene Maguan Flora from Yunnan, Paleovegetation and Floristic Evolution. Kunming Institute of Botany, Kunming, p. 253.

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., Huang, Y.-J., Sun, H., Su, T., Huang, J., Zhou, Z.-K., 2017. First fossil of *Pterolobium* (Leguminosae) from the Middle Miocene Yunnan, South China. Rev. Palaeobot. Palynol. 242, 21–32.

Jia, L.B., Su, T., Huang, Y.J., Wu, F.X., Deng, T., Zhou, Z.K., 2018. First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai–Tibetan Plateau: implications for morphological evolution and biogeography. J. Syst. Evol. 57, 94–104.

Jia, L.B., Manchester, S.R., Huang, J., Su, T., Xue, L., Zhang, S.T., Huang, Y.J., Zhou, Z.K., 2021. First fossil record of an East Asian endemic genus *Sladenia* (Sladeniaceae) from its modern range: implications for floristic evolution and conservation biology. J. Syst. Evol. 59, 216–226.

Lebreton-Anberrée, J., Manchester, S.R., Huang, J., Li, S.-F., Wang, Y.-Q., Zhou, Z.-K., 2015. First fossil fruits and leaves of *Burretiodendron* s.l. (Malvaceae s.l.) in Southeast Asia: implications for taxonomy, biogeography, and paleoclimate. Int. J. Plant Sci. 176, 682–696.

Lebreton-Anberrée, J., Li, S.H., Li, S.-F., Spicer, R.A., Zhang, S.-T., Su, T., Deng, C.L., Zhou, Z.K., 2016. Lake geochemistry reveals marked environmental change in Southwest China during the Mid Miocene Climatic Optimum. Sci. Bull. 61, 897–910.

Li, R., Kraft, N.J., Yang, J., Wang, Y., 2015. A phylogenetically informed delineation of floristic regions within a biodiversity hotspot in Yunnan, China. Sci. Rep. 5, 9396.

Li, S., Advokaat, E.L., van Hinsbergen, D.J.J., Koymans, M., Deng, C., Zhu, R., 2017. Paleomagnetic constraints on the Mesozoic-Cenozoic paleolatitudinal and rotational history of Indochina and South China: review and updated kinematic reconstruction. Earth Sci. Rev. 171, 58–77.

Linnemann, U., Su, T., Kunzmann, L., Spicer, R.A., Ding, W.N., Spicer, T.E.V., Zieger, J., Hofmann, M., Moraweck, K., Gärtner, A., Gerdes, A., Marko, L., Zhang, S.T., Li, S.F., Tang, H., Huang, J., Mulch, A., Mosbrugger, V., Zhou, Z.K., 2017. New U-Pb dates show a Paleogene origin for the modern Asian biodiversity hot spots. Geology 41, 3–6.

Ma, C.Y., 1982. Classification of the genus *Cladrastis* Rafin. Bull. Bot. Res. Harbin 2, 105–116.

MacGinitie, H.D., 1962. The Kilgore Flora: A Late Miocene Flora from Northern Nebraska. University of California Press, Berkeley.

Meyer, H.W., Manchester, S.R., 1997. Oligocene Bridge Creek Flora of the John Day Formation, Oregon. University of California Press, California.

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., 1991. Late Miocene and Pliocene floras in central Honshu, Japan. Bull. Kanagawa Prefect. Museum 1–188.

Paik, I.S., Kim, H.J., Kim, K., Jeong, E.-K., Kang, H.C., Lee, H.I., Uemura, K., 2012. Leaf beds in the Early Miocene lacustrine deposits of the Geumgwangdong Formation, Korea: occurrence, plant-insect interaction records, taphonomy and palaeoenvironmental implications. Rev. Palaeobot. Palynol. 170, 1–14.

Pavlyutkin, B.I., Chekryzhov, I.Y., Petrenko, T.I., 2012. Geology and Flora of Lower Miocene in the South Primorye. Russian Academy of Sciences, Vladivostok.

Qi, T., 1992. A new species of *Gigantamynodon* (Amynodontidae) from Yunnan, China. Vertebr. PalAsiatica 30, 229–232.

Qian, L.-S., Chen, J.-H., Deng, T., Sun, H., 2020. Plant diversity of Yunnan: current situation and future. Plant Div. 41, 281–291.

Su, T., Wilf, P., Huang, Y., Zhang, S., Zhou, Z., 2015. Peaches preceded humans: fossil evidence from SW China. Sci. Rep. 5, 16794.

Su, T., Huang, Y.J., Meng, J., Zhang, S.T., Huang, J., Zhou, Z.K., 2016. A Miocene leaf fossil record of *Rosa* (*R. fortuita* n. sp.) from its modern diversity center in SW China. Palaeoworld 25, 104–115.

Tian, Y.-M., Huang, J., Su, T., Zhang, S.-T., 2020. Early Oligocene *Itea* (Iteaceae) leaves from East Asia and their biogeographic implications. Plant Div. https://doi.org/10.1016/j.arabjc.2021.103189.

Tian, Y., Spicer, R.A., Huang, J., Zhou, Z., Su, T., Widdowson, M., Jia, L., Li, S., Wu, W., Xue, L., Luo, P., Zhang, S., 2021. New early oligocene zircon U-Pb dates for the 'Miocene' Wenshan Basin, Yunnan, China: biodiversity and paleoenvironment. Earth Planet. Sci. Lett. 565, 116929.

Tiffney, B.H., 1985. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arnold Arbor. 66, 73–94.

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, T.-X., Huang, J., Ding, W.-N., Del Rio, C., Su, T., Zhou, Z.-K., 2019. Fossil involucres of *Ostrya* (Betulaceae) from the early Oligocene of Yunnan and their biogeographic implications. Palaeoworld 29, 752–760.

Wen, J., Nie, Z.-L., Ickert-Bond, S.M., 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. J. Syst. Evol. 54, 469–490.

Westerhold, T., Marwan, N., Drury, A.J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J.S.K., Bohaty, S.M., Vleeschouwer, D.D., Florindo, F., Frederichs, T., Hodell, D.A., Holbourn, A.E., Kroon, D., Lauretano, V., Littler, K., Lourens, L.J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R.H., Wilson, P.A., Zachos, J.C., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369, 1383–1387.

Wilf, P., 2000. Late Paleocene–early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. Geol. Soc. Am. Bull. 112, 292–307.

Wolfe, J.A., 1966. Tertiary plants from the Cook Inlet region, Alaska. U.S. Geol. Surv. Prof. Pap. 398, B1–B32.

Xing, Y., Gandolfo, M.A., Onstein, R.E., Cantrill, D.J., Jacobs, B.F., Jordan, G.J., Lee, D.E., Popova, S., Srivastava, R., Su, T., Vikulin, S.V., Yabe, A., Linder, H.P., 2016. Testing the biases in the rich Cenozoic angiosperm macrofossil record. Int. J. Plant Sci. 177, 371–388.

Xue, L., Jia, L., Nam, G.-s., Huang, Y., Zhang, S., Wang, Y., Zhou, Z., Chen, Y., 2020. Involucre fossils of *Carpinus*, a northern temperate element, from the Miocene of China and the evolution of its species diversity in East Asia. Plant Div. 42, 155–167.

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.

Zhang, C.-H., 1976. The Report to the Regional Geological Survey (1/200,000) of Wenshan/Maguan Scope (F-48-3, F-48-9). Geological Bureau of Yunnan Province, Yuxi.

Zhang, Q.Y., Huang, J., Jia, L.B., Su, T., Zhou, Z.K., Xing, Y.W., 2018. Miocene *Ulmus* fossil fruits from Southwest China and their evolutionary and biogeographic implications. Rev. Palaeobot. Palynol. 259, 198–206.