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Research papers

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.

**Key words**: Asia, biodiversity, biogeography, *Cladrastis*, Leguminosae
1. Introduction

*Cladrastis* Raf. is a woody genus of four species, with a disjunct distribution in Eastern 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. Recent molecular study shows that *Cladrastis* is sister to the clade consisting of *Styphnolobium* Schott and *Pickeringia* Nutt.; together with *Platyosprion* Maxim., and the four genera constitute the “*Cladrastis* clade”, an early diverged lineage of Papilionoideae DC. in the Leguminosae.

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). 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 (Herendeen, 1992; Meyer and Manchester, 1997; Duan et al., 2020a) (Table 1). It remains unclear whether the lack of Paleogene _Cladrastis_ fossil records in Asia is due to Neogene establishment of the genus in Asia or taphonomic biases and 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 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, Southwestern 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-grey 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 $30 \pm 2/32 \pm 1$ 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 $30 \pm 2/32 \pm 1$ 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., *Cedrelosperrnum* Sapota, and *Deviceras* 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 *Cedrelosperrnum*, an extinct genus with extensive fossil records in the Cenozoic of Europe and North America (Jia et al., 2018). However, no *Cedrelosperrnum* 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 $30 \pm 2/32 \pm 1$ 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.

2.2. Morphological observations

A fossil infructescence and four fossil fruits representing *Cladraspis* 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
Genus: Cladrastis Raf., 1824
Species: Cladrastis hao-miniae 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 (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 2.3–3.6mm 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 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 fruit from the United States either is marked by “a wide keel or wing” at one side of the fruit (*C. oregonensis*) or has 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 fruit from Mexico did not preserve the fruit receptacle and apex, and is 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 as 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 either of 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 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 sites. 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 undistinguishable from the extant species which still inhibit in the region close to the fossil sites. 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).

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Declaration of Competing Interest

None

References


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

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

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 acuminated 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; sp, secondary peduncle; sl, sutural line; ap, apex. 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 sutures. MG0563.
6. Magnification of fruit showing acute apex. MG1405.
7. Magnification of fruit showing acuminated 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 III. Infructescence and detached fruits of extant *Cladrastis* Raf.
1–3, *C. wilsonii* Takeda; 4, 5, *C. delavayi* (Franch.) Prain. Scale bar = 5 mm.

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.

Table 1 Reported fossil records of *Cladrastis*.

| No. | Species       | Type | Age | Latitude | Longitude | Locality | Continent | Original Reference |
|-----|---------------|------|-----|----------|-----------|----------|-----------|------------|-------------------|

17
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### Table of Fossil Records

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<td>Leaf</td>
<td>Late Miocene</td>
<td>36.3</td>
<td>Itahana Flora Locality J, Gunma, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>18</td>
<td><em>C. japonica</em> (Tanai and Suzuki) Wolfe</td>
<td>Leaf</td>
<td>Late Miocene</td>
<td>36.3</td>
<td>Nam Chuitna River, Cook Inlet Region, Alaska</td>
<td>North America</td>
</tr>
<tr>
<td>19</td>
<td><em>C. inouei</em> (Huzioka) Ozaki</td>
<td>Leaf</td>
<td>Late Miocene</td>
<td>36.3</td>
<td>Kabutoiwa Flora, Gunma, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>20</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Late Miocene</td>
<td>36.3</td>
<td>Kabutoiwa Flora, Gunma, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>21</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Unknown</td>
<td>36.7</td>
<td>Daido, Gunma, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>22</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Unknown</td>
<td>36.4</td>
<td>Omi-mura, Nagano, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>23</td>
<td><em>C. cf. shikokiana</em> (Makino) Makino</td>
<td>Leaf</td>
<td>Unknown</td>
<td>34.9</td>
<td>Ootani, Oosani, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>24</td>
<td><em>C. cf. platycarpa</em> (Maxim.) Makino</td>
<td>Leaf</td>
<td>Unknown</td>
<td>34.9</td>
<td>Ootani, Oosani, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>25</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Unknown</td>
<td>36.0</td>
<td>Akina Flora, Gunma, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>26</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Unknown</td>
<td>36.4</td>
<td>Ohoka Kabauchi, Nagano, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>27</td>
<td><em>C. aniensis</em> Huzioka</td>
<td>Leaf</td>
<td>Unknown</td>
<td>35.0</td>
<td>Seto-Obata Locality, Aichi, Japan</td>
<td>Asia</td>
</tr>
<tr>
<td>28</td>
<td><em>C. prelutea</em> MacGinitie</td>
<td>Leaf</td>
<td>Unknown</td>
<td>42.0</td>
<td>Cook Inlet region, Alaska</td>
<td>North America</td>
</tr>
</tbody>
</table>

**Note.** We compiled the *Cladrastis* fossil records as far as we could find from the literature and database. Further reevaluation for the reliability of these records is necessary. Brown (1937) described *C. oreonensis* based on specimen from the Oligocene of Bridge Creek flora, 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.*
Table 2 Morphological comparisons of the fossils with extant species and reported fossil species based on fruits within *Cladrastis*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Status</th>
<th>Overall shape of fruits</th>
<th>Length/width of fruits (cm)</th>
<th>Length of pedicels (cm)</th>
<th>Proximal end of fruits</th>
<th>Distal end of fruits</th>
<th>Number of seeds</th>
<th>Constriction between seeds</th>
<th>Orientation of seeds</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. delavayi</em> (Franch.)</td>
<td>Extant species</td>
<td>Elliptic or long</td>
<td>3–8/1–2</td>
<td>0.4–0.8</td>
<td>Acute or acuminate</td>
<td>Acute or acuminate</td>
<td>1–5</td>
<td>Not prominent</td>
<td>Forming a small angle or parallel to the long axis of the fruit</td>
<td>Bao and Vincent (2010)</td>
</tr>
<tr>
<td><em>C. wilsonii</em> Takeda</td>
<td>Extant species</td>
<td>Elliptic or long</td>
<td>4.5–8/0.8–1</td>
<td>0.5–1.1</td>
<td>Acute or acuminate</td>
<td>Acute or acuminate</td>
<td>1–5</td>
<td>Not prominent</td>
<td>Forming a small angle or parallel to the long axis of the fruit</td>
<td>Bao and Vincent (2010), Duley and Vincent (2003)</td>
</tr>
<tr>
<td><em>C. shikokiana</em> (Makino)</td>
<td>Extant species</td>
<td>Elliptic or long</td>
<td>(2.8)–6–7/0.4</td>
<td>~0.4</td>
<td>Acute or acuminate</td>
<td>Acute or acuminate</td>
<td>(1)–4–6</td>
<td>Not prominent</td>
<td>Forming a small angle or parallel to the long axis of the fruit</td>
<td>Duley and Vincent (2003)</td>
</tr>
<tr>
<td><em>C. kentukea</em> (Dum.Cours.) Rudd</td>
<td>Extant species</td>
<td>Elliptic or long</td>
<td>7–8/3–7</td>
<td>1–2</td>
<td>Acute or acuminate</td>
<td>Acute or acuminate</td>
<td>1–8</td>
<td>Slightly prominent</td>
<td>Forming a small angle or parallel to the long axis of the fruit</td>
<td>Duley and Vincent (2003)</td>
</tr>
<tr>
<td><em>C. haominiae</em> L.B. Jia et Z.K. Zhou</td>
<td>Fossil species</td>
<td>Elliptic or long</td>
<td>2.6–5.5/0.4–0.9</td>
<td>0.4–0.7</td>
<td>Acute or acuminate</td>
<td>Acute or acuminate</td>
<td>1–2–(?‘)</td>
<td>Not prominent</td>
<td>Forming a small angle or parallel to the long axis of the fruit</td>
<td>This study</td>
</tr>
<tr>
<td><em>C. delgadoi</em></td>
<td>Fossil species</td>
<td>Fusiform to</td>
<td>Not preserved</td>
<td>Not preserved</td>
<td>Slightly</td>
<td>Not</td>
<td>Slightly</td>
<td>Slightly</td>
<td>Prominent</td>
<td>Calvillo-Canadell and Cevallos-Ferriz (2005)</td>
</tr>
<tr>
<td><em>C. delgadoi</em></td>
<td>Fossil species</td>
<td>Linear</td>
<td>5–6/7</td>
<td>Not preserved</td>
<td>Constricted</td>
<td>Preserved</td>
<td>Unclear</td>
<td>Prominent</td>
<td>Unclear</td>
<td>Calvillo-Canadell and Cevallos-Ferriz (2005)</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Fossil</th>
<th>species</th>
<th>Fossil</th>
<th>species</th>
<th>Fossil</th>
<th>species</th>
<th>Fossil</th>
<th>species</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. sp.</td>
<td><strong>Elliptic</strong></td>
<td>Not preserved</td>
<td><strong>Acute obtuse to</strong></td>
<td>acute</td>
<td>1–2</td>
<td>prominent</td>
<td>Parallel to the long axis of the fruit</td>
</tr>
<tr>
<td></td>
<td><strong>Elliptic to</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. sp.</td>
<td><strong>moniliform</strong></td>
<td>Not preserved</td>
<td><strong>Acute</strong></td>
<td><strong>Acuminate</strong></td>
<td>3</td>
<td><strong>Prominent</strong></td>
<td><strong>Unclear</strong></td>
</tr>
<tr>
<td>C. oregonensis Brown</td>
<td>Linear</td>
<td>Not preserved</td>
<td><strong>Acute</strong></td>
<td><strong>Acute</strong></td>
<td>1</td>
<td>No constriction</td>
<td>Parallel to the long axis of the fruit</td>
</tr>
</tbody>
</table>

Note. The morphological states of the above taxa are mostly taken from the cited references, but for those 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.

**Highlights**

- The earliest fossil record of *Cladrastis* in Asia was described.
- *Cladrastis* has been established in Asia at least by the Paleogene.
- *Cladrastis* might have once traversed the Bering land bridge.
- Our finding supports the Paleogene origin of the Yunnan biodiversity.