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Implications for Taxonomy, Biogeography, and Paleoclimate

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## FIRST FOSSIL FRUITS AND LEAVES OF *BURRETIODENDRON* S.L. (MALVACEAE S.L.) IN SOUTHEAST ASIA: IMPLICATIONS FOR TAXONOMY, BIOGEOGRAPHY, AND PALEOCLIMATE

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Editor: Michael T. Dunn

**Premise of research.** *Burretiodendron* Rehder is a genus of six species that are mainly found on limestone in Southeast Asian mountain forests with a monsoonal climate. Recent molecular evidence supports its placement in Malvaceae s.l. Presently, two species of *Burretiodendron* have been classified as vulnerable according to the International Union for the Conservation of Nature. Fossil *Burretiodendron* is also extremely rare in the record, and little is known about its evolutionary history.

**Methodology.** Fossil fruits and leaves were collected from upper Miocene sediments in Yunnan (SW China). Their macro and micro morphology were studied and compared with all extant species of *Burretiodendron* and with species of fossil and extant *Craigia* W.W. Sm. & W.E. Evans having somewhat similar fruits.

**Pivotal results.** We recognize fossil remains of *Burretiodendron* on the basis of fruits described as *Burretiodendron parvifructum* sp. nov. and associated leaves of *Burretiodendron miocenicum* sp. nov.

**Conclusions.** These Miocene fossils are the first confirmed occurrence of this genus in the Southeast Asian fossil record. This discovery supports the possibility that southeastern Yunnan was already experiencing frost-free winters and seasonal precipitation with wet summers and relatively dry winters. It also corroborates the hypothesis that this genus might have originated at the Sino-Vietnamese border, where the biodiversity center of the genus is today.

**Keywords:** *Burretiodendron*, Malvaceae, Miocene, East Asia, China, limestone flora.

### Introduction

*Burretiodendron* Rehder (Malvaceae s.l.) is a genus of only six species, all of which are rare trees found only in tropical East Asia (fig. 1). *Burretiodendron* primarily grows in montane rain forests or dry deciduous forests, most commonly between 300 and 550 m asl (Wang et al. 1986; Zhuge 1990), but occasionally specimens have been collected at much higher elevations. *Burretiodendron hsienmu* Chun & K.C. How and *Burretiodendron obconicum* Chun & K.C. How are endemic to limestone forests in China, while *Burretiodendron esquirolii* (H. Lévl.) Rehder, *Burretiodendron kyüifolium* Y.C. Hsu & R. Zhuge, and *Burretiodendron brilletii* Kosterm. are mainly—although not exclusively—distributed on limestone (Wang et al. 1986; Xu 1995). We surveyed herbarium data and Global Biodiversity Information Facility data (www.gbif.org) and found that the genus has a highly restricted distribution (fig. 1). Five species

grow only on the Sino-Vietnamese border, while one species, *Burretiodendron siamense* Kosterm., has a disjunct distribution in the North Malay Peninsula in Thailand and Myanmar (fig. 1). Tang et al. (2005a) stated that *Burretiodendron* is also present in Cambodia, although this is disputed (S. Hul, personal communication, 2014). The habitat of *Burretiodendron* is severely fragmented, and its populations continue to decline as a result of human exploitation of forests (Tang et al. 2005a). The vulnerability of *B. hsienmu* has long been recognized (Wang et al. 1986), and this species has been under protection since 1989 (Institute of Botany Academia Sinica 1989). Both *B. hsienmu* and *B. esquirolii* are presently classified as vulnerable on the International Union for Conservation of Nature Red List (IUCN 2012).

Originally, Rehder (1936) defined the genus with the type species *B. esquirolii*. Two additional species were described as *B. hsienmu* Chun & K.C. How and *B. obconicum* Chun & K.C. How (Chun and How 1956). Chang and Miao (1978) transferred both of Chun and How's species to a new genus *Excentrodendron* H.T. Chang & R.H. Miao, but the distinction between the two genera has never been fully accepted (Zhuge 1990; Tang 1998; Tang et al. 2005b; Gao et al. 2006).

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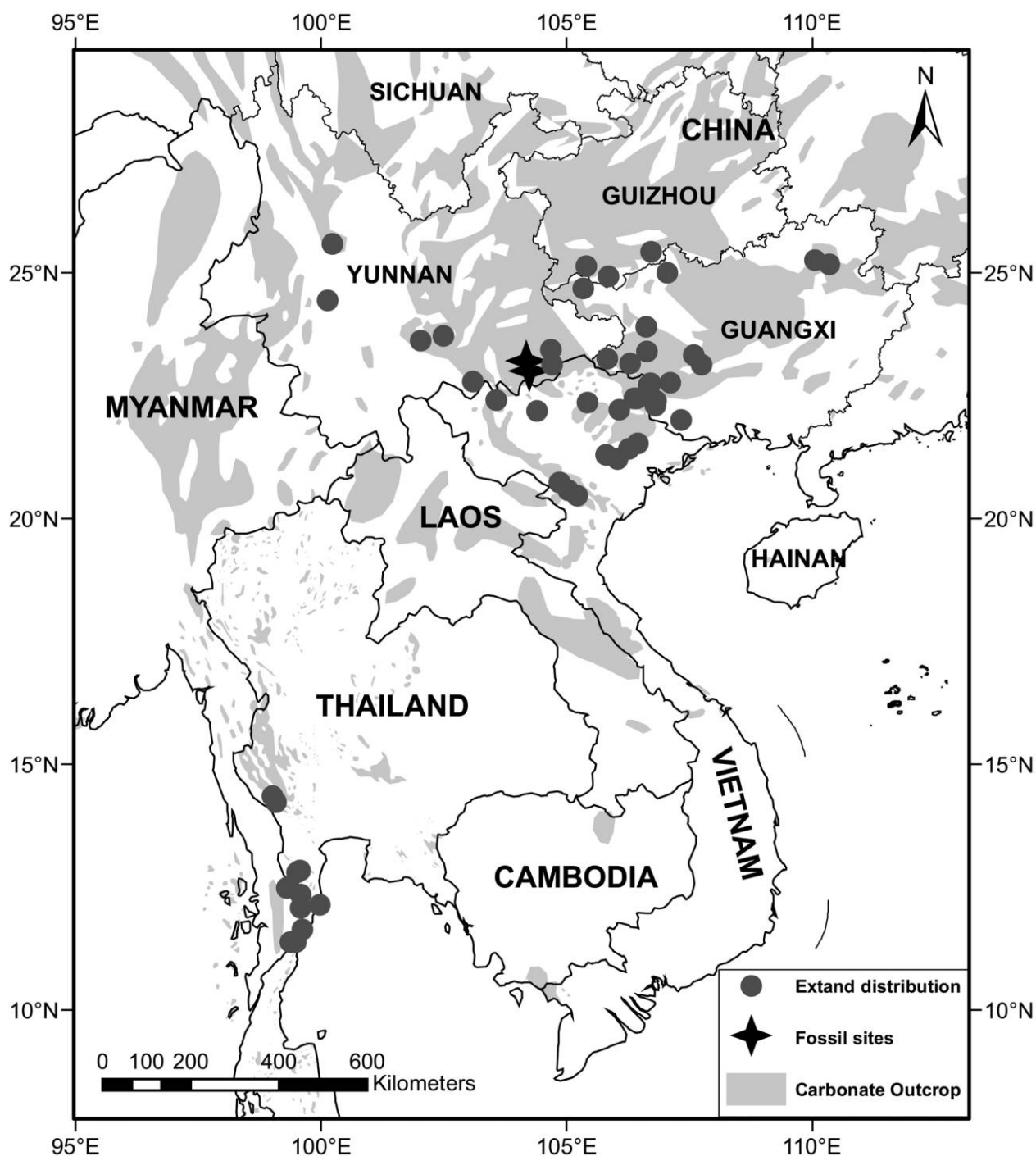


Fig. 1 Distribution map of present-day *Burretiodendron*. Circles represent extant occurrences, and stars represent the fossil sites. The northernmost site is Wenshan, whereas the southernmost site is Maguan.

Consequently, we consider all these species to represent *Burretiodendron* s.l. When Rehder (1936) first defined *Burretiodendron*, he assigned it to the family Tiliaceae L. *Burretiodendron* is now placed in the Malvaceae s.l. Jussieu because the Tiliaceae was nested within the expanded Malvaceae, following detailed morphological and molecular studies (Judd and Manchester 1997;

Alverson et al. 1999; Bayer et al. 1999; Bell et al. 2010). Recent plastid DNA analyses place *Burretiodendron* in the Dombeyoideae subfamily, closely related to *Sterculia* and the *Pterospermum-Schoutenia* clade (Won 2009).

At present, there are no known pollen, wood, or fruit fossils of the genus *Burretiodendron*, although two leaf impressions

were identified as belonging to the genus *Excentrodendron* from the Oligocene (Pavlyutkin 2011) and middle Miocene (Pavlyutkin 2007) of far eastern Russia. Despite its interesting phylogenetic position and extreme rarity, details of *Burretiodendron* fruit and foliage morphology and anatomy have not previously been studied in detail. Consequently, fossils of this genus may have been overlooked in the past. Indeed, *Burretiodendron* fruits somewhat resemble that of *Craigia* W.W. Sm. & W.E. Evans, so that the two genera are sometimes confused (Zhuge 1990). For example, *Burretiodendron combretoides* Chun and How (Chun and How 1956) and *Burretiodendron yunnanensis* Kosterm. (Kostermans 1961) are now both considered to be synonyms of *Craigia yunnanensis* W.W. Sm. & W.E. Evans (Smith and Evans 1921) on the basis of the observation of the locule area (Zhuge 1990). *Craigia* and *Burretiodendron* fruits consist of capsules of five two-winged loculicidal valves that alternatively can be described as septicidal schizocarps, separating into five two-winged mericarps at maturity. Modern *Craigia* fruits are mainly elliptic in outline, but some fossil specimens of fossil *Craigia* are obovate and oblong, such as some specimens of *Craigia brononii* (Unger) Kvaček, Bůžek & Manchester and *Craigia oregonensis* (Arnold) Kvaček, Bůžek & Manchester (Bůžek et al. 1989; Kvaček et al. 1991; Kvaček et al. 2005). However, *Craigia* and *Burretiodendron* can be easily distinguished by the shape of the locular area; it is oblong fusiform in *Craigia* (Bůžek et al. 1989; Kvaček et al. 1991) while it is obovate in *Burretiodendron*.

This study describes two new species of *Burretiodendron* on the basis of fossil fruits and fossil leaves, with a detailed study of the micro-morphology of both fossil and extant fruits and leaves. These fossils represent the first occurrence of *Burretiodendron* fruit in the fossil record and the first occurrence of fossil leaves in Southeast Asia, where its biodiversity center lies today. Then, the implications of this discovery on the taxonomy, paleoclimate, biogeography, and conservation of *Burretiodendron* are discussed.

## Material and Methods

### *Geological Setting and Paleoenvironment*

Fossil fruits were collected from two localities in SE Yunnan, China, approximately 50 km apart (Wenshan and Maguan; fig. 1). The sediments of both basins belong to the Xiaolongtan Formation (Zhang 1997), which is dated as late Miocene by regional stratigraphic correlation (Yunnan Bureau of Geology and Mineral Resources 1990) and by biostratigraphy using palynology (Wang 1996) and vertebrate fossils (Dong 2001). The sediments in Wenshan and Maguan sit unconformably on Paleogene breccia and are composed of cyclic deposits of sandstone, siltstone, and mudstone. In Wenshan, the sediments are mainly creamy white to yellow, grading to dark gray in the lower portion. Maguan, however, has only dark gray sediments. In both localities, the fine, laminated sediments suggest a low-energy environment. Depositional environments are interpreted as forming from deep lakes surrounded by limestone mountains (Su et al. 2013; Zhang et al. 2015a). The bottom of the lake in Maguan was periodically anoxic, as indicated by the presence of pyrite on one of the fruit fossils, allowing the preservation of micromorphological details.

Both the Wenshan and Maguan sites yielded a very diverse flora, most of which has not yet been described. Among the described fossils are *Ailanthus confucii* Unger (Su et al. 2013), *Baobinia wenshanensis* H.H. Meng & Z.K. Zhou (Meng et al. 2014), *Sequoia maguanensis* J.W. Zhang & Z.K. Zhou (Zhang et al. 2015a), and *Pinus massoniana* var. *massoniana* Lamb. (Zhang et al. 2015b). A palynological study has been undertaken on a section belonging to the same formation and depositional setting but a few kilometers away from the site, and it revealed that the Wenshan basin experienced a warm, wet, and temperate to subtropical climate during the late Miocene (Li et al. 2015).

### *Morphological Study*

In total, nine fossil fruits and four fossil leaves of *Burretiodendron* were recognized from our collection of approximately 5000 fossil specimens from Maguan and Wenshan. Fossil and extant specimens were observed under a stereo microscope coupled with a digital camera (SAPO, Leica, Germany). The leaf is described following the terminology of Ellis et al. (2009). Measurements were made using Image J software (<http://rsb.info.nih.gov/ij/>). The fossils were compared with extant specimens of *B. bsiennu* cultivated in Xishuangbanna Tropical Botanical Garden and with specimens of this and other species in the herbaria of the Kunming Institute of Botany, CAS (KUN), and the Xishuangbanna Tropical Botanical Garden, CAS (HITBC). Virtual herbaria were also extensively used, in particular those from the Muséum National d'Histoire Naturelle in Paris (<http://science.mnhn.fr/institution/mnhn/search/form>), the Royal Botanical Gardens Kew (<http://www.kew.org/>), the New York Botanical Garden (<http://www.nybg.org/science/>), the Royal Botanic Garden Edinburgh ([www.rbge.org.uk](http://www.rbge.org.uk)), and the Chinese Virtual Herbarium ([http://www.cvh.org.cn/index\\_en.php](http://www.cvh.org.cn/index_en.php)). Because *Burretiodendron* fruits have sometimes been misidentified as *Craigia* (Zhuge 1990), we also studied modern fruits of *Craigia yunnanensis* in the Herbarium in Kunming Institute of Botany, CAS (KUN), and the Herbarium of Xishuangbanna Tropical Botanical Garden, CAS (HITBC). Fossils of *Craigia* (*Craigia brononii*, *Craigia oregonensis*, *Craigia hainanensis*) J.H. Jin & T.M. Kodrul from published literature were also compared with the fossil specimens of *Burretiodendron*.

*Fruit preparation.* In order to observe the micromorphology of the fossil fruit, we removed a small fragment from specimen MG 0021. We chose this specimen because it is partially covered with small crystals of pyrite, suggesting that it may have preserved the fruit micromorphological details. The fragment was prepared according to the method described by Kerp (1990); it was immersed in a solution of 10% HCl to remove carbonate material and then in a solution of 40% HF to remove silicate compounds. The fossil and extant fruits were observed under an SEM (ZEISS/EVO LS10).

*Leaf preparation.* Clearings of extant leaves were prepared according to the method described by Li (1987). In order to compare fossil and extant leaf cuticles, we selected specimen DMS 3816 because it is the only fossil leaf with preserved cuticles. Fossil leaf cuticles were prepared by immersing a small piece in a solution of 10% HCl and 40% HF, while modern leaf cuticles were soaked in a solution of 30% CrO<sub>3</sub> for 36 h, according to standard protocols (Kerp 1990). Fossil and extant

cuticles were mounted on microscope slides and observed by an epifluorescence microscope coupled with an AxioCam (Zeiss, Germany).

#### Statistical Analysis

A principal component analysis (PCA) was carried out using the vegan package in R not only to find the nearest leaving relative of the fossils but also to clarify the modern taxonomy of *Burretiodendron* and, notably, the division between *Burretiodendron* and *Excentrodendron*. The PCA was performed using nine measurements of the mericarp and endocarp and 10 measurements of the leaf lamina, venation and petiole. Data were marked as missing when the fossil was incomplete and a measurement could not be made.

#### Bioclimatic Parameters of Extant *Burretiodendron*

We calculated climatic variables under which *Burretiodendron* grows today using the bioclimatic envelope model in the package Dismo in R. This model calculates the climate parameters by projecting coordinates of the distribution of the genus onto climate layers extracted from the WorldClim database (<http://www.worldclim.org>; 30-s resolution).

### Systematics

#### Fruit

Family—*Malvaceae* Jussieu s.l.

Subfamily—*Dombeyoideae* Beilschmied

Genus—*Burretiodendron* Rehder 1936

Species—*Burretiodendron parvifructum* sp. nov.

*J. Lebreton Anberrée & Z.K. Zhou*

*Holotype.* DMS 213, designated here (fig. 2F, 2J–2L).

*Paratypes.* DMS 203 (fig. 2I, 2M); DMS 194 A and DMS 194 B (fig. 2G–2I); MG 0021 (fig. 3A–3C).

*Other specimens.* DMS 176; MG 350; MG 351; MG 352.

*Diagnosis.* Two-winged mericarp, elliptic to obovate, ca. 15 mm long and 10 mm wide, base rounded, apex rounded to retuse; wing venation craspedodromous anastomosing and dichotomising but not forming elongated areoles, single-seeded obovate endocarp centrally placed on the fruit, endocarp ca. 7 mm long and 5 mm wide, acute basally; apex of endocarp rounded in abaxial view but retuse in adaxial view.

*Description.* Two-winged mericarp, elliptic to obovate 14.3–18.8 mm × 8.4–10.6 mm; length:width (L:W) ratio 1.4:1–1.9:1; base rounded, apex rounded to retuse, medial vein straight, strong, running from the base to the locule area; wing venation originating from the endocarp area, craspedodromous, anastomosing and dichotomising; papillae (fig. 3A) and trichome bases (fig. 3B, 3C) visible on abaxial side of the wing; obovate endocarp centrally placed on the fruit, 5.7–8.5 mm long × 3.6–6.2 mm wide; L:W ratio 1.0:1–2.2:1; endocarp base acute, endocarp apex rounded on abaxial view but retuse

on adaxial view (fig. 2L); endocarp contains a single seed obovate in outline with smooth seed surface (fig. 2M).

*Etymology.* The epithet *parvifructum* refers to the small size of the fruit, which is about half the size of fruits in extant species of this genus.

*Repository.* Palaeoecology Laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.

*Localities.* Locality of the holotype and of the paratypes DMS 203; DMS 194 A and DMS 194B: Wenshan (23°20'N, 104°17'E); locality of the paratype MG 0021: Maguan (23°01'N, 104°23'E).

*Type stratum.* Xiaolongtan Formation, upper Miocene.

#### Leaf

Genus—*Burretiodendron* Rehder 1936

Species—*Burretiodendron miocenicum* sp. nov.

*J. Lebreton Anberrée & Z.K. Zhou*

*Holotype.* Designated here: DMS 2417 (fig. 4A, 4D, 4E).

*Paratype.* DMS 3816 (fig. 5A–5C).

*Other specimens.* DMS 2610, DMS 2399.

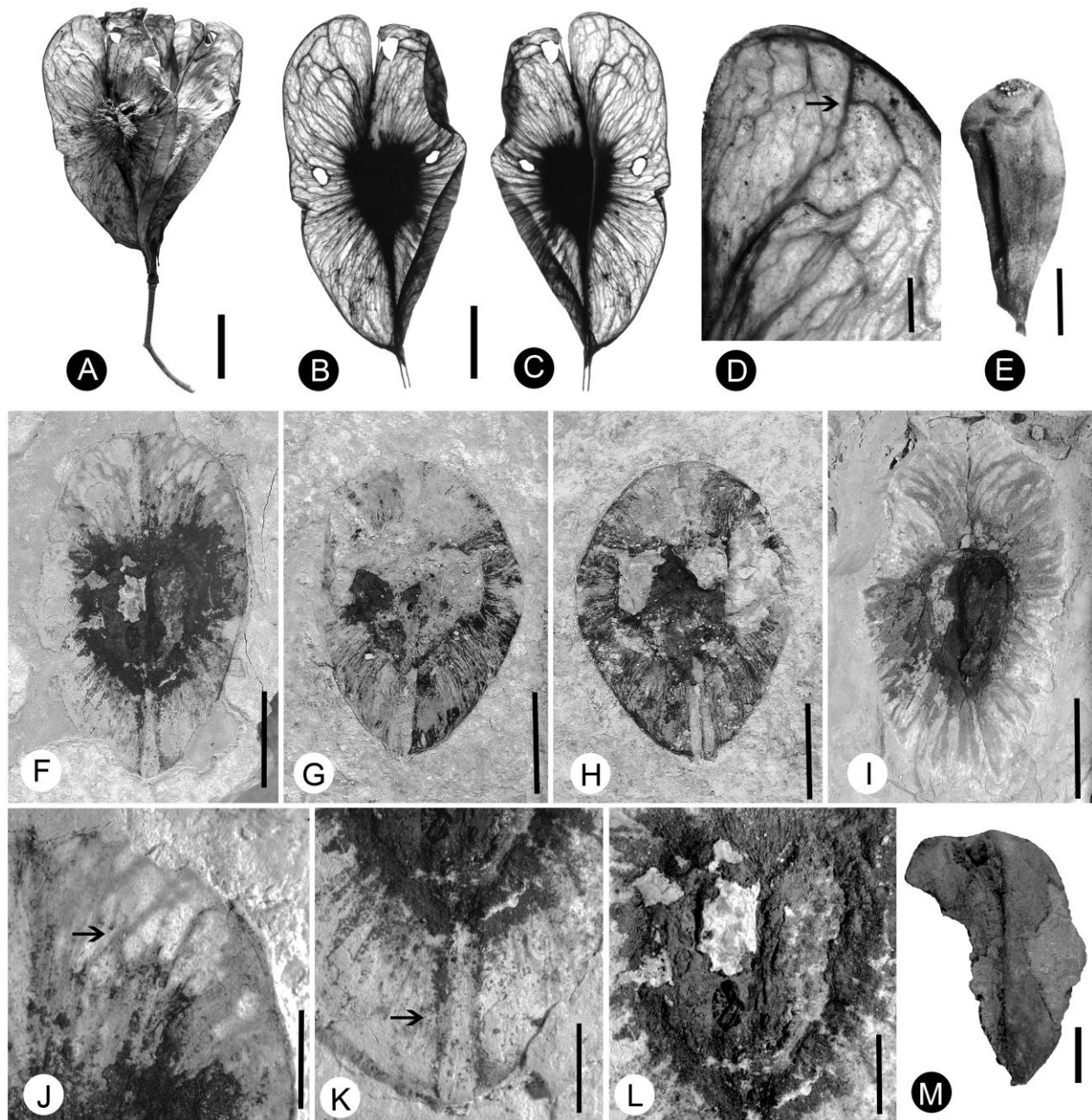
*Diagnosis.* Lamina elliptic to ovate ca. 40 mm long and 30 mm wide, margin entire, unlobed, apex acuminate, base rounded; primary venation basal actinodromous with three basal veins, agrophic veins present; first major secondary pair in the middle of the lamina, major and minor secondary venation brochidodromous, intersecondary veins absent, intercostal tertiary veins percurrent with opposite sinuous course, epimedial tertiary veins opposite percurrent, quaternary venation reticulate, areoles well developed and polygonal, free ramifying veinlets absent.

*Description.* Gross morphology: petiole stout when present; lamina entire-margined, unlobed, elliptic to ovate, 4–4.5 cm × 2.2–3.3 cm; L:W ratio 1.2:1–2.1:1; apex acuminate, base rounded; primary venation basal palmate actinodromous with three basal primary veins; presence of agrophic veins; major secondary venation brochidodromous; first major secondary pair in the middle of the lamina; four pairs of alternate major secondary veins; spacing between major secondary gradually increases proximally; angle between the major secondary and the midvein smoothly decreases proximally; five to six pairs of minor brochidodromous secondary veins; intersecondary veins absent; intercostal tertiary veins percurrent, occasionally alternate, with opposite, convex to sinuous course, consistent in angles of origination; epimedial tertiary veins opposite, occasionally alternate; proximal course of the epimedial tertiary parallel to the intercostal tertiary; quaternary veins irregular reticulate; areoles well developed and polygonal when preserved; free ramifying veinlets absent.

*Epidermis.* Single trichome base on lower epidermis veins; six to seven radial base cells; epidermal vein cell rectangular and elongated; 17.7–42.2 μm (28.8 μm) × 9.4–14.6 μm (11.8 μm); L:W 1.2–3.80 (2.4); oblique and straight anticlinal cell walls (fig. 5B, 5C).

*Etymology.* The epithet *miocenicum* refers to the Miocene Epoch during which this species was growing.

*Repository.* Palaeoecology Laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.



**Fig. 2** Extant and fossil *Burretiodendron* fruit macromorphology. A–E, Extant *Burretiodendron kydiifolium* fruit. A, Whole schizocarp. B, Mericarp abaxial view. C, Mericarp adaxial view. D, Detail of C showing wing venation. E, Seed. F–M, Fossil *Burretiodendron parvifructum* sp. nov. F, Mericarp holotype DMS 213. G, H, Paratype DMS 194 part and counterpart. G, Adaxial view. H, Abaxial view. I, Paratype DMS 203. J–L, Detail of DMS 213. J, Wing venation. K, Strong medial vein. L, Endocarp. M, Seed from the paratype DMS 203. Scale bars = 10 mm (A–C), 2 mm (D, E, J–M), 5 mm (F–I).

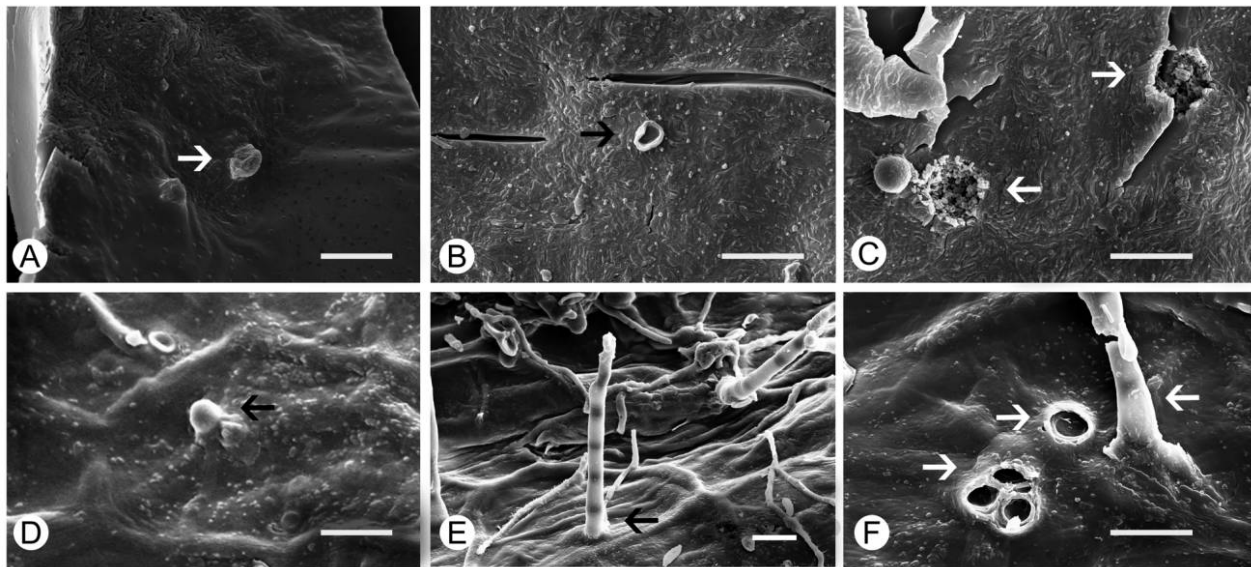
*Type locality.* Wenshan (23°20'N, 104°17'E).

*Type stratum.* Xiaolongtan Formation, upper Miocene.

#### Statistical Results

*Fruit.* Nine traits were measured on extant *Burretiodendron* fruits as well as on *Craigia yunnanensis*. Results of the PCA

performed on these traits are displayed in figure 6. Note that *Burretiodendron brilletii* has coordinates of (0, 0), since the fruit of this extant species is still unknown because the holotype specimen stored in the Paris herbarium does not include fruits and no other collections were observed. PCA axis 1 accounts for 50.1% of the variation, while PCA axis 2 accounts for 30.4%. The most variable traits are the mericarp and endocarp lengths (F1 and F4)



**Fig. 3** Fossil and extant *Burretiodendron* fruit micromorphology. A–C, Fossil *Burretiodendron parvifructum* paratype, abaxial view MG 0021. A, Papilla. B, Trichome base with severed trichome. C, Two trichome bases. D–F, Extant *Burretiodendron kydiifolium* abaxial view. D, Papilla. E, Trichome. F, Severed trichome and trichome bases. Scale bars = 50  $\mu$ m.

and the distance between the base of the mericarp and the base of the endocarp (F8). The most important traits to distinguish *Burretiodendron parvifructum* are the endocarp L:W (F7) and the endocarp width (F5). The PCA confirms the designation of a new species because the fossils cluster together and the space they occupy by the fossil fruits does not overlap the space occupied by modern fruits.

**Leaf.** Ten traits were measured on extant *Burretiodendron* leaves to compare with the fossil *Burretiodendron* in a PCA analysis (fig. 7). PCA axis 1 explains 41.4% of the variation, while PCA axis 2 explains 23.3%. The most variable traits for PCA1 are the length of the petiole (L4) and the L:W of the petiole (L6), while the most variable traits for PCA2 are the lamina L:W (L3) and the number of primary veins (L8). The fossil leaves cluster together, and *B. brilletii* is positioned near this group, suggesting that it is the nearest living relative of the fossil species.

#### *Climatic Parameters of Extant Burretiodendron*

Today, *Burretiodendron* is found only in warm climates with a mean annual temperature of 21.7°C and where the temperature remains above freezing (minimum temperature of the coldest month is 10.3°C; table 1). Its habitat has a relatively high (1474 mm) mean annual precipitation that is concentrated during the warm period of the year (precipitation of the warm quartile is 701 mm), while winter is a period of relative drought (precipitation of the cold quartile is 95 mm; table 1).

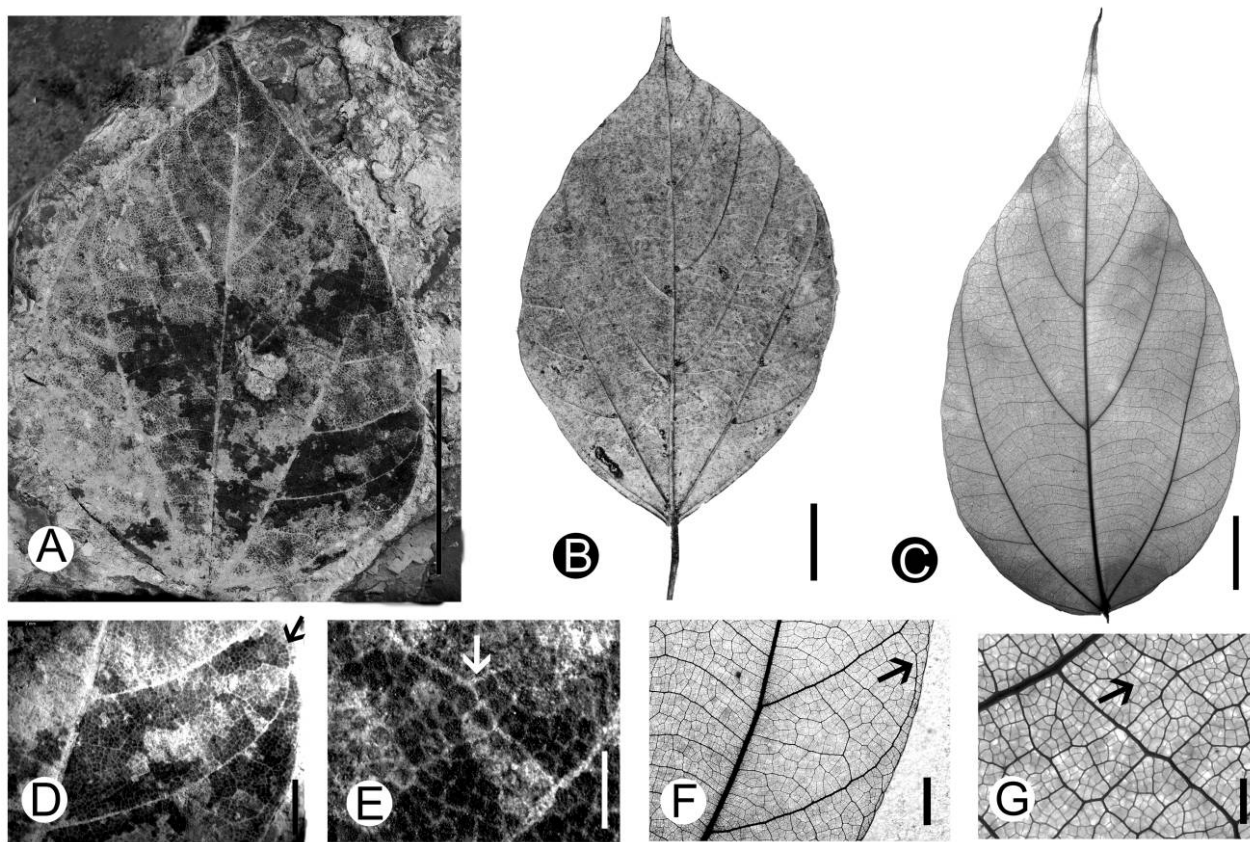
#### Discussion

In this study, the first fossil fruit species of *Burretiodendron* and a new leaf species of the same genus are defined and de-

scribed. Here we compare these new fossil species with extant species. We also compare the newly discovered fossil leaves to previously described *Burretiodendron* fossil leaves. We discuss the taxonomical, biogeographical, paleoenvironmental, and conservational implications of this find.

#### *Fossil Identification and Comparison with Modern Plants*

Manchester and O'Leary (2010) compiled an inventory of fin-winged fruits and observed that such fruits occur in more than 140 genera scattered across at least 45 families. Our fossil fruits are characterized by the presence of two wings, with an elliptic to obovate outline and a rounded to retuse apex. These features are found in fin-winged fruits of Brassicaceae, Lophopyxidaceae, Combretaceae, Begoniaceae, Polygonaceae, Rutaceae, and Malvaceae. Among these families, *Fortuynia* Schuttlev. ex Boiss. (Brassicaceae), *Lophopyxis* Hook (Lophopyxidaceae) and the genera *Combretum* Loefl., *Terminalia* L., and *Pteleopsis* Engl. (Combretaceae) differ by their subparallel and much denser wing venation. *Begonia* L. (Begoniaceae) fruits have a similar outline to *Burretiodendron* but differ in their larger locule region. *Podopterus* Bonpl. (Polygonaceae) varies from *Burretiodendron* by the position of the endocarp, which is situated in the upper two-thirds of the fruit, whereas it is centrally placed in *Burretiodendron*. Finally, *Ptelea* L. (Rutaceae) and *Craigia* (Malvaceae s.l.) both possess dichotomizing and anastomosing wing venation but differ from *Burretiodendron* by the presence of elongated areoles and dense venation. The outline of the fruit modern *Craigia* is mainly elliptic, but it can be obovate in fossil *Craigia* (Bůžek et al. 1989; Kvaček et al. 1991, 2005; Jin et al. 2009; Liu et al. 2012). The main characteristic to distinguish both genera is the shape of the locular area; it is oblong fusiform in modern and fossil *Craigia* (Bůžek et al.



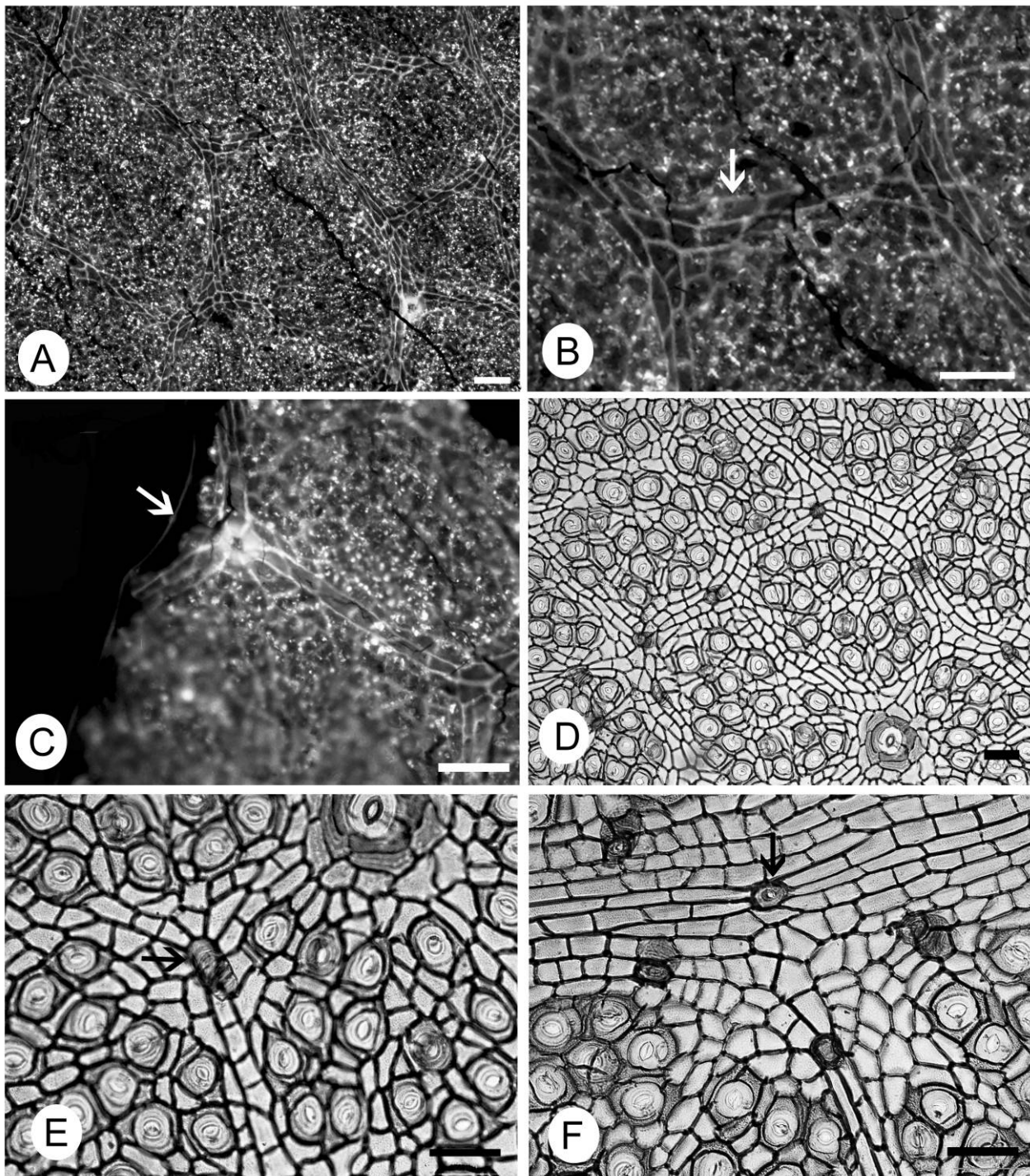
**Fig. 4** Fossil and extant *Burretiodendron* leaf macromorphology. A, Fossil *Burretiodendron miocenicum* sp. nov. lamina holotype DMS 2417. B, Extant *Burretiodendron hsiennmu* whole leaf. C, *Burretiodendron hsiennmu* clearing. D, Detail of DMS 2417: brochidodromous minor secondary vein. E, Detail of DMS 2417: irregular reticulate quaternary vein fabric and areoles without free ramifying veinlets. F, Detail of C: brochidodromous minor secondary venation. G, Detail of F: irregular reticulate quaternary vein fabric and areoles without blind free ramifying veinlets. Scale bars = 20 mm (A–C), 2 mm (D), 1 mm (E, G), 4 mm (F).

1989), whereas it is obovate in *Burretiodendron*. Finally, the vein density of the wings is smaller in *Craigia* than in *Burretiodendron* (Manchester and O’Leary 2010). Therefore, we can confidently assign *Burretiodendron parvifructum* to the genus *Burretiodendron* on the basis of the obovate fruit and locular area outline, the presence of two wings with anastomosing and dichotomising craspedodromous venation but where elongated areoles are absent, and a centrally placed obovate endocarp. However, the fossil is readily distinguished from extant species by its size, which is half as big while maintaining the same L:W ratio as the extant fruits (table 2). It is interesting to note that fossil *Craigia* fruits are also smaller than the modern *Craigia* fruits (table 2). The PCA did not yield conclusive results for the identification of a nearest living relative for the fruit. This may be due to the fact that the fruit of *Burretiodendron brilletii* is still unknown since the nearest living relative in the leaf analysis is *B. brilletii*, and it is possible that the fruits and the leaves share a common nearest leaving relative.

Once the fruit was identified, we searched for *Burretiodendron* leaves among the fossils collected in Wenshan and Maguan matching the description of extant *Burretiodendron*. Among a diverse flora comprising more than 50 taxa (J. Huang,

unpublished data), DMS 2392, DMS 2610, DMS 2399, DMS 2417, and DMS 3816 corresponded to the description of *Burretiodendron* by Zhuge (1990). However, when viewed under a light microscope, DMS 2392 showed free ramifying veinlets that are not visible in the extant *Burretiodendron* leaf clearing (fig. 4G); this feature excludes it from this genus. The PCA does not include information on the presence of free ramifying veinlets in the areole, and the result of the PCA shows that DMS 2392 clusters with the *Burretiodendron* samples. Therefore, low-order venation is not enough to identify *Burretiodendron* leaves, but the absence of free ramifying veinlets in areoles is decisive. Since there are other genera that have the same venation as *Burretiodendron*, leaf cuticle from the specimen DMS 3816 was studied under the microscope. Stomata are not observed on the abaxial side, but the cells of the veins and a trichome base on the veins were clearly distinguishable (fig. 5C). The cells of the veins are rectangular, linear, and elongated with straight cell walls. They are 17.7–43.3  $\mu\text{m}$  long and 9.4–14.6  $\mu\text{m}$  wide, with an L:W ratio between 1.2:1 and 3.8:1. Cells are most often four-sided but occasionally five- and six-sided (fig. 5A–5C). The trichome bases are found only on veins and are surrounded by six to seven cells pinching to-

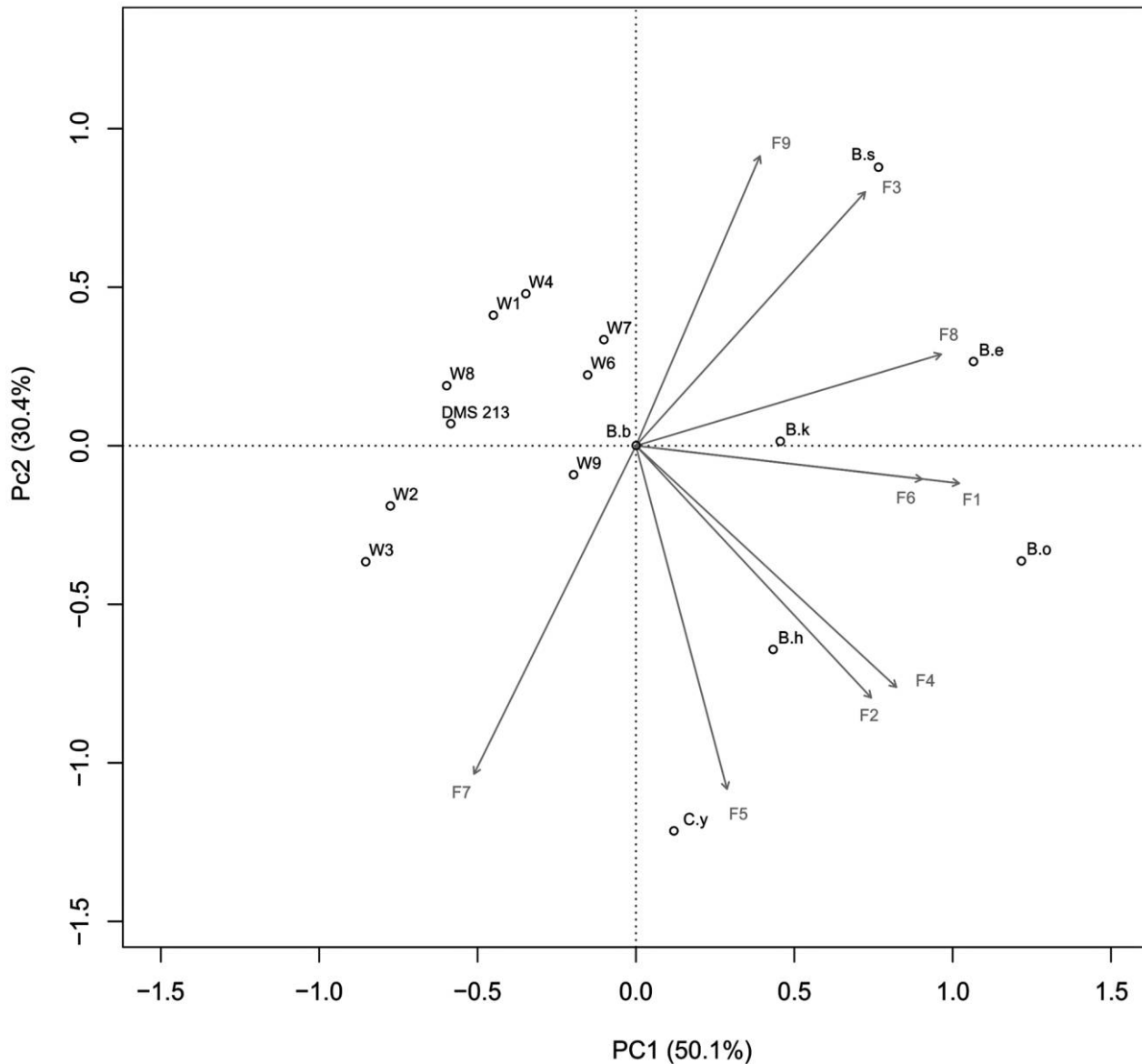




**Fig. 5** Fossil and extant *Burretiodendron* leaf micromorphology. *A–C*, Fossil *Burretiodendron miocenicum* paratype leaf lower cuticle DMS 3816. *A*, General view. *B*, Elongated vein cells. *C*, Trichome base and elongated vein cells. *D–F*, Extant *Burretiodendron hsienmu* leaf lower cuticle. *D*, General view. *E*, Gland. *F*, Trichome base. Scale bars = 50  $\mu\text{m}$ .

ward the hair (fig. 5C). These characteristics are also observed in the lower cuticle of extant leaves; the vein cells are similar in their rectangular, linear, and elongated outlines with straight walls (fig. 5D–5F). Moreover, the hair and gland bases are

also found only on the veins (fig. 5E, 5F). Finally, the cell number surrounding the hair and gland bases is six to seven (fig. 5E, 5F). Therefore, the micromorphology further corroborates the determination of the fossil leaves as *Burretiodendron*.



**Fig. 6** Fruit *Burretiodendron* principal component analysis results. DMS 213 is the holotype of *Burretiodendron parvifructum*; the other fossils are named starting with the letter W. B.h = *Burretiodendron hsiennmu*; B.o = *Burretiodendron obconicum*; B.e = *Burretiodendron esquirolii*; B.s = *Burretiodendron siamense*; B.b = *Burretiodendron brilletii*; B.k = *Burretiodendron kydiifolium*; C.y = *Craigia yunnanensis*. *Burretiodendron brilletii* has coordinates of (0, 0) because the fruit is still unknown. Arrows represent the eigenvector scatter.

Thus, *Burretiodendron miocenicum* is confidently assigned to the extant genus on the basis of the untoothed margin, 3-actinodromous primary venation, the first pair of major secondary veins occurring in the middle of the lamina, brochidodromous minor secondary venation, and the absence of intersecondary venation. Moreover, when areoles are observed, they are well developed, while free ramifying veinlets are absent. Finally, when observing the lower cuticle, the vein cell shape and the presence of trichome bases on the vein confirm the identification. Yet, *B. miocenicum* is readily distinguished from the extant species by its smaller size (table 3).

The presence of fossil fruits and leaves of the genus *Burretiodendron* in the same strata in Wenshan suggests that both

organs could belong to the same species. However, they have never been found attached. This would be an unlikely situation, even in extant species, because fruits are shed in June and July (Wang et al. 1986; Tang et al. 2005a), whereas leaves are shed the following spring after the new leaves unfold (Zhuge 1990). Therefore, not finding fruits attached to leaves does not exclude the possibility that both belong to the same species.

#### *Burretiodendron in the Fossil Record*

The fossil fruits of *Burretiodendron* are the first to be described, but there is a possibility that some of the numerous

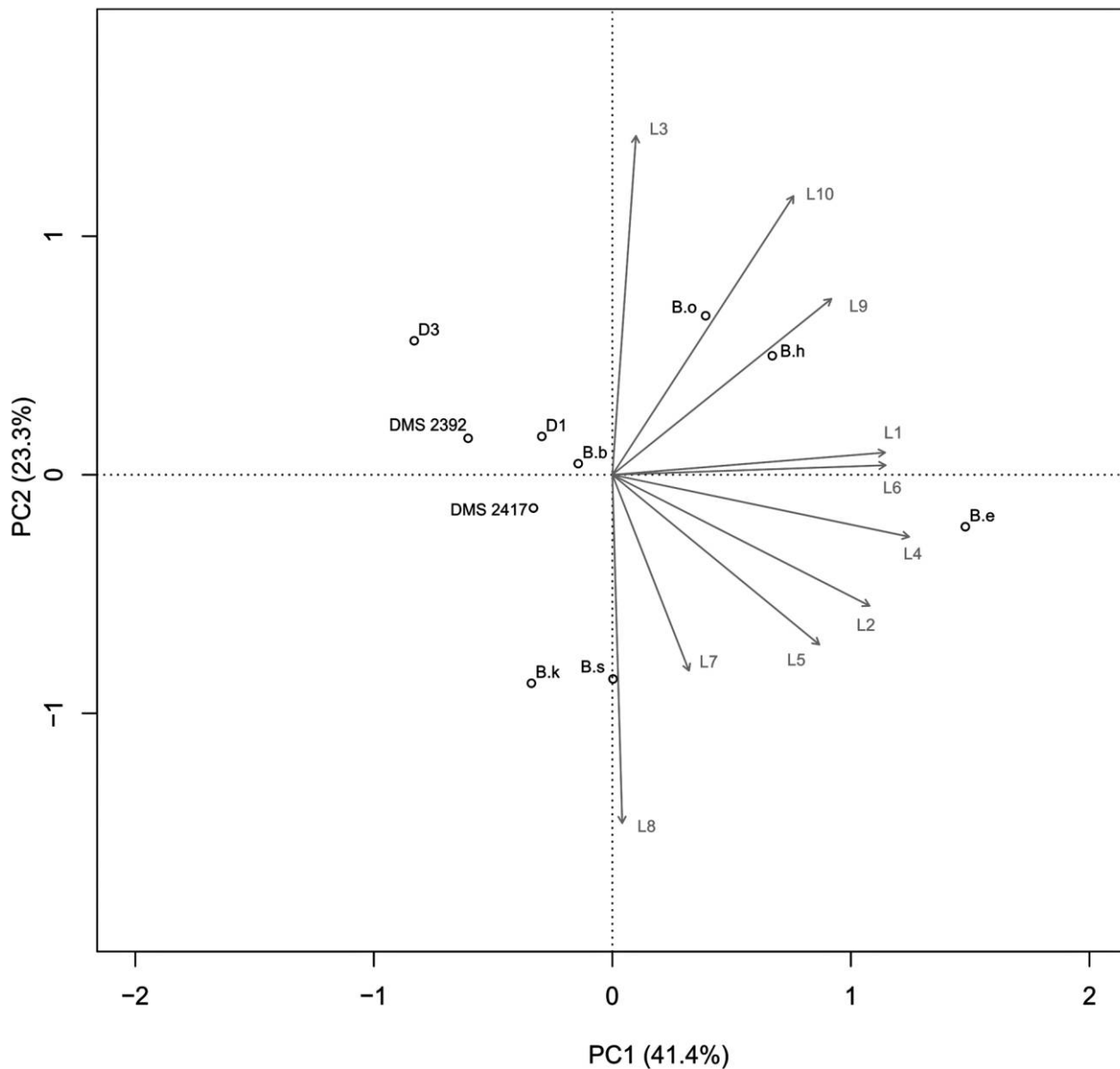


Fig. 7 Leaf *Burretiodendron* principal component analysis results. DMS 2417 is the holotype for *Burretiodendron miocenicum*. DMS 2392 is a fossil possessing venation similar to *Burretiodendron*. The fossils are named starting with D. B.h = *Burretiodendron hsienmu*; B.o = *Burretiodendron obconicum*; B.e = *Burretiodendron esquirolii*; B.s = *Burretiodendron siamense*; B.b = *Burretiodendron brilletii*; B.k = *Burretiodendron kydiifolium*. Arrows represent the leaf *Burretiodendron* eigenvector scatter.

fossil fruits that have been described as *Craigia* (Bůžek et al. 1989; Kvaček et al. 1991, 2002, 2005; Jin et al. 2009; Liu et al. 2012) might instead be *Burretiodendron*. The isolated capsule valves of *Craigia* can appear somewhat similar to *Burretiodendron* but can be readily distinguished by the fusiform oblong shape of the locule area in *Craigia* (while it is obovate in *Burretiodendron*) and the presence of elongated areoles formed by the veins of the wings in *Craigia* (while these elongated areoles are absent from the wing venation in *Burretiodendron*). These two genera are sympatric today, for example, in Hekou county, southeast Yunnan (L. Jia, personal com-

munication 2014). We think it is likely that there are more fossil *Burretiodendron* fruits in the fossil record than is currently known.

There are two mentions of potential fossil *Burretiodendron* leaves. Pavlyutkin (2007) described a fragment of a leaf dating from the middle Miocene and retrieved from Novokachalinsk (Primory'e, Russia) as an *Excentrodendron*. The venation, although not complete, seems to correspond to our fossil and to extant *Burretiodendron*: the venation is 3-actinodromous, the minor secondary venation is likely to be brochidodromous (but the venation is damaged), the intersecondary veins are ab-

Table 1

Climatic Parameters of Extant *Burretiodendron*

	MAT (°C)	MTWM (°C)	MTCM (°C)	MAP (mm)	PWETM (mm)	PDRYM (mm)	PCQ (mm)	PWQ (mm)
Range	15.0–27.5	22.7–35.6	2.3–20.3	886–2067	158–424	4–48	42–279	255–1146
Mean $\pm$ SD	21.7 $\pm$ 2.9	31.3 $\pm$ 2.5	10.3 $\pm$ 4.7	1476 $\pm$ 256	280 $\pm$ 54	18 $\pm$ 10	95 $\pm$ 56	701 $\pm$ 203

Note. MAT, mean annual temperature; MTWM, maximum temperature of warmest month; MTCM, minimum temperature of coldest month; MAP, mean annual precipitation; PWETM, precipitation of wettest month; PDRYM, precipitation of driest month; PCQ, precipitation of coldest quarter; PWQ, precipitation of warmest quarter.

sent, and the tertiary veins are subperpendicular to the major secondary veins. While the areoles are not visible on the illustration, Pavlyutkin (2007) confirms their presence but does not specify whether they contain free ramifying veinlets. *Burretiodendron* leaves are similar to *Mallotus* Lour. (Euphorbiaceae) leaves but differ in the presence of free ramifying veinlets in *Mallotus*. Therefore, we cannot exclude the possibility that the fossil described by Pavlyutkin belongs to *Mallotus*. Pavlyutkin (2007) also mentions a similar leaf from the Kraskino flora of Primory'e dating from the Oligocene, but there is neither formal description nor illustration. This same leaf is again referenced by Pavlyutkin (2011) but without formal description or illustration. Therefore, detailed description is necessary before placing these fossils confidently in *Burretiodendron*. Thus, our fossil leaves represent the first confirmed occurrence of *Burretiodendron* leaves in the fossil record.

## Taxonomic Implications

Rehder (1936) first described the genus *Burretiodendron*, and Chang and Miao (1978) separated the species into two genera: *Burretiodendron* sensu stricto and *Excentrodendron* based on floral characteristics. They distinguished *Excentrodendron* by its possession of bisexual flowers and evergreen habit. Tang et al. (2006) reexamined *Burretiodendron hsienmu* flowers and concluded that they were unisexual, which seemed to support the merging of the two taxa. Tang (1998), Tang et al. (2005b, 2006, 2007), and Gao et al. (2006) support the maintenance of two genera, on the basis of differences in microspores, microgametogenesis, megasporogenesis, pollen, and wood anatomy. In this context, it is interesting to interpret our PCA results. In figures 6 and 7, both fruits and leaves representing *Excentrodendron* taxa do not group with the *Burretiodendron* taxa. This lends support to the separation of the two groups. However, our sample size for each species is quite low because measurable specimens are rare. Molecular analysis on plastid DNA was also inconclusive (Won 2009); the branch of the tree indicates that the divergence between *Burretiodendron* and *Excentrodendron* has a bootstrap maximum likelihood value under 50% but a Bayesian posterior probability of 0.83. Therefore, the division between the two taxa is still unresolved.

## Biogeographic and Paleoclimatic Implications

Today, the Dombeyoideae subfamily is mainly distributed in the Old World Tropics, North Australia, Saint Helena, Madagascar, and Mascarenes (Stevens 2012). The genus *Burret-*

*iodendron*, however, has a much more restricted distribution. Along the Sino-Vietnamese border, five species are found, and another species has a disjunct distribution in the North Malay Peninsula in Thailand and Myanmar (fig. 1). Zhuge (1990) hypothesized that this genus originated along the Sino-Vietnamese border, because it is the current center of biodiversity of this genus. Both fossil sites are located within the biodiversity center and would corroborate this hypothesis.

The very restricted distribution of this genus makes it particularly suitable to assess the paleoclimate in Wenshan and Maguan during the late Miocene. From the results in table 1, the presence of *Burretiodendron* in Wenshan and Maguan might indicate a high mean annual temperature and winter temperature above freezing and precipitation seasonality with a dry winter and a wet summer. This corroborates the climatic reconstruction from pollen analysis, which estimates that the mean temperature of the coldest was 7.5°–10.3°C, the mean annual temperature was 16.6°–17.5 °C, the mean annual precipitation was 1432–1598 mm, and the precipitations were seasonal, with precipitation during the warm quartile being much higher than precipitation during the cold quartile (515–721 mm vs. 89–192 mm; Li et al. 2015). Moreover, the *Burretiodendron* fossils have small leaves and a large seed, supporting the possibility that this genus was growing in a seasonally dry climate, as Liu et al. (2014) show that monsoon tropical limestone forest communities are characterized by a significantly smaller leaf area, denser wood, and higher seed mass than tropical Fagaceae and mixed forests.

## Biodiversity Conservation Implications

The current restricted distribution of *Burretiodendron* makes it vulnerable to habitat loss and human overexploitation and led to a dramatic decrease in population numbers (Wang et al. 1986; Tang et al. 2005a). Moreover, limestone forests, where *Burretiodendron* are growing, are particularly vulnerable to species loss because these forests have been demonstrated to have a lower functional richness and low resistance ability (Liu and Slik 2014). Limestone forests have lower species richness compared to other forest types due to extreme environmental conditions, such as water and nutrient limitation (Liu and Slik 2014). On the other hand, these forests have a high number of endemic species and a unique species composition (Zhu et al. 2003; Fu et al. 2012; Liu et al. 2014), which makes them important to conserve. Besides, limestone forest restoration is very difficult because the species are slow growing and because the soil in limestone forest is very thin and erodes as soon as the vegetation is cleared (Zhu et al. 2003; Tang et al. 2005a). In this

Table 2  
Comparison of Fossil and Extant *Burretiodendron* Fruits with *Craigia*

	Fruit outline				Endocarp				Wing venation		
	Shape	Length (mm)	Width (mm)	L:W	Shape	Length (mm)	Width (mm)	L:W	Framework	Elongated areoles	
<b>Fossil species:</b>											
<i>B. parvifractum</i> sp. nov.	Obovate	14.3–18.8	8.4–10.6	1.4–1.9	Obovate	5.7–8.5	3.6–6.2	1.0–1.9	Craspedodromous	Absent	
<i>C. bromii</i>	Elliptic to obovate	10.7–26.2	9.3–23.6	1.1–1.2	Oblong	7.3–12.7	3.9–8.5	1.5–1.9	Craspedodromous	Present	
<i>C. oregonensis</i>	Elliptic to obovate	14.4–31.8	8.1–28.3	1.1–1.8	Oblong	7.7–19.8	3.2–10.0	2.0–2.4	Craspedodromous	Present	
<i>C. hainanensis</i>	Elliptic	11.7–12.1	13.6–14.2	.9	Oblong	5.7–6.3	3.0–3.1	1.9–2.0	Craspedodromous	Present	
<b>Extant species:</b>											
<i>B. hsienmu</i>	Obovate	34.1–35.8	20.7–21.4	1.6–1.7	Obovate	11.8–14.9	6.0–6.9	2.0–2.2	Craspedodromous	Absent	
<i>B. obconicum</i>	Obovate to elliptic	42.5–45.1	18.8–21.5	2.0–2.4	Obovate	16.7–17.7	6.7–7.6	2.2–2.6	Craspedodromous	Absent	
<i>B. esquirolii</i>	Elliptic, rarely obovate	29–49.9	11.0–23.4	2.5–3.1	Obovate to elliptic	12.0–13.5	4–5.2	2.5–3.0	Craspedodromous	Absent	
<i>B. siamense</i>	Obovate to elliptic	33.4–38.9	12.9–15.2	2.4–2.5	Obovate	7.9–8.3	4.5–5.0	1.6–1.7	Craspedodromous	Absent	
<i>B. kydiifolium</i>	Obovate to elliptic	30.5–38.0	16.9–19.3	1.8–2.0	Obovate	9.8–11.3	5.6–6.7	1.7–1.8	Craspedodromous	Absent	
<i>C. yunnanensis</i>	Elliptic	28.3–31.0	22.5–24	1.2–1.3	Oblong	12.7–14.0	6–10.8	1.2–2.3	Craspedodromous	Present	

Note. L:W, ratio of length divided by width. There is no measurement of *Burretiodendron brilletii* because the fruit is still unknown.

**Table 3**  
**Comparison of Fossil and Extant Species of *Burretiodendron* Leaves**

Lamina	Fossil species			Extant species				
	<i>B. mioenicum</i> sp. nov.	<i>B. hsiennu</i>	<i>B. obconicum</i>	<i>B. esquirolii</i>	<i>B. siamense</i>	<i>B. brilletii</i>	<i>B. kydtifolium</i>	
Outline	Ovate	Ovate to elliptic	Ovate	Elliptic to ovate	Ovate to elliptic	Ovate to elliptic	Ovate to elliptic	
Margin	Entire	Entire	Entire	Toothed	Toothed	Entire	Toothed	
Length (cm)	4-4.6	7.8-12.8	10.7-17.6	10.4-21.0	8.0-11.9	9.5-13.7	5.6-7.2	
Width (cm)	2.2-3.3	3.3-8.2	5.5-6.9	7.0-14.7	6.3-10.2	5.8-10.2	3.8-5.7	
L:W	1.6	1.6-2.4	1.9-2.5	1.3-1.5	1.2-1.3	1.3-1.6	1.0-1.3	
Primary vein no.	3	3	3	3-5	5	3-5	5	
Major secondary pair no.	4	3-5	4-5	4-6	3-4	4	3-4	
Minor secondary no.	5-6	7-13	6-12	6-8	5	5-7	5	

Note. L:W, ratio of length divided by width.

context, the Institute of Botany of the Chinese Academy of Science declared the genus *Burretiodendron* endangered and initiated a program of in situ and ex situ conservation (Wang et al. 1986; Tang et al. 2005a). Discovery of the fossil *Burretiodendron* in the area where the biodiversity of this genus is the highest today and where biodiversity hotspots have been identified (Zhang and Ma 2008) reinforces the suggestion that the best location for its conservation in situ lies at the Sino-Vietnamese border.

### Conclusion

In this study, we describe two new fossil species of the genus *Burretiodendron* s.l. These constitute the first fossil record of the fruit and the first confirmed record of a fossil leaf of *Burretiodendron*, a rare genus growing primarily in limestone forests on the Sino-Vietnamese border and in Thailand. This find suggests a warm climate during the late Miocene with seasonal precipitations. It also corroborates the hypothesis that the genus originated at the Sino-Vietnamese border, where its biodiversity center lies today.

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