

Late Miocene Pods and Leaves of *Albizzia* (Leguminosae: Mimosoideae) from Yunnan, SW China and Their Phytogeographic Implications

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Abstract: *Albizzia* is a leguminous genus belonging to the subfamily Mimosoideae with approximately 150 modern species, widely distributed in the tropical and subtropical regions of Asia, Africa, Australia and America. Among them, 17 species are mainly distributed in southern and southwestern China. Abundant fossils of the subfamily Mimosoideae, including leaves, pods, flowers and wood, have been reported from the Cretaceous and Paleogene strata of the Northern Hemisphere. However, Neogene records of Mimosoideae are relatively scarce. In this study, fossil pods and leaves belonging to the genus *Albizzia* from the Bangmai Formation of Yunnan, China were described. They were assigned to three species, including *Albizzia scalpelliformis* Guo, Li and Xie Emended, *Albizzia* cf. *kalkora* (Roxb.) Prain and *Albizzia* sp. The occurrence of *Albizzia* fossils from Lincang not only gives important information on the Neogene plant diversity from Yunnan—a worldwide famous biological hotspot—but also provides additional evidence for its phytogeographic history.

Key words: *Albizzia*, Mimosoideae, morphology, Late Miocene, Lincang

1 Introduction

Leguminosae are the third largest family after Compositae and Orchidaceae in the angiosperms, consisting of approximately 650 genera and 18000 species (Schrire et al., 2005). They have trees, shrubs, subshrubs and climbing herbs and are widely distributed throughout the world. In China, there are ca. 120 genera and 1000 species (Institute of Botany, the Chinese Academy of Sciences, 1955). The subdivision of this family into three subfamilies, including Mimosoideae, Caesalpinioideae and Faboideae, was proposed by some investigators (e.g., Polhill et al., 1981). The subfamily Mimosoideae includes approximately 56 genera and 2800 species, mainly distributed in the tropical and subtropical regions of the world, with a small number in the temperate regions. Central and southern America is the center of distribution and diversity for modern Mimosoideae species.

The genus *Albizzia* (Leguminosae: Mimosoideae) is composed of approximately 150 species, distributed in Asia, Africa, Oceania and American tropical and

subtropical regions. There are approximately 17 species in the southwest, south and southeast of China. This genus is morphologically characterized by glandular petiole and rachis, small leaflets in numerous pairs or larger ones in few pairs, flattened ovary, long and slender style, and minute stigma (Delectis Flora Reipublicae Popularis Sinicae Agenda Academiae Sinicae Edita, 1988). Their fruits are broadly linear or oblong, straight, plano-compressed, indehiscent or dehiscent along both sutures. The seeds are ovoid or orbicular and compressed with filiform funicle. The fossil record of Leguminosae, represented by fruits, flowers, leaves, woods and roots, was well preserved in the Paleogene and Neogene strata of the world (Herendeen et al., 1992). Among them, the fossils of the subfamily Mimosoideae occurred in Asia, Europe and North America. The earliest fossil leaves of Mimosoideae were found in the Lower Cretaceous (Fontaine, 1889). They were also reported in the upper Cretaceous (Lesquereux, 1892; Berry, 1914). The Middle Eocene has abundant records, represented by leaves (Berry, 1916, 1930), fruits (Bowerbank, 1840; Berry, 1916, 1930), seeds (Bowerbank, 1840) and flowers (Berry,

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1930). The reports from Late Eocene are also worldwide, preserved as leaves, fruits, seeds and wood (e.g., Lesquereux, 1878; Knowlton, 1898; Nikitin, 1935). However, during the Neogene period, little was known about the Mimosoideae.

In this study, Late Miocene *Albizzia* fossils preserved as leaflets and pods from Yunnan, China were described and illustrated. These fossils are assigned to three fossil species, including *Albizzia scalpelliformis* Guo, Li and Xie Emended, *Albizzia* cf. *kalkora* (Roxb.) Prain and *Albizzia* sp. Additionally, according to the fossil record of *Albizzia* and its current distribution, plant geography concerning its origin and migration was discussed.

2 Geography and Geological Setting

Lincang is located in the southwest of Yunnan Province and the south of the Hengduan Mountains; the Lancang River and the Nu River go respectively through the eastern and western ends, and this situation is similar to Baoshan at the northern Lincang, where numerous plant fossils were yielded (He Yuli et al., 2014). To the south of Lincang is Myanmar and Laos (Fig. 1b), which consist of

mountainous areas with deep canyons and low hills and basins in alternative distributions due to the Cenozoic uplift of the Tibet Plateau (Wu Zhenhan et al., 2007). There are many small intermontane basins in Lincang, e.g., Bangmai, Mengtuo, Mengwang and Linxiang, deposited in a series of terrestrial coal-bearing sediments of Neogene (Tao Junrong and Chen Minghong, 1983) as well as those basins on the northeastern of the Tibetan Plateau (e.g., Xu Zenglian et al., 2015).

Fossil specimens studied here were collected from the Bangmai Formation near the Bangmai Village of Lincang, Yunnan. The overlying Quaternary of yellow sand, gravel was in angular unconformable contact with the upper part of the Bangmai Formation, and the underlying Middle Triassic granite with grayish coarse biotite was also in angular unconformable contact with the lower part of the Bangmai Formation (Zhang Shuling et al., 1987; Ge Hongru and Li Daiyun, 1999; Fig. 1c). According to the lithostratigraphy, this formation can be divided into three members. The lower part is mainly composed of sandstone and conglomerate, the middle section is the coal-bearing member, containing plant and fish fossils, and the upper part is mudstone, with diatom and abundant plant fossils

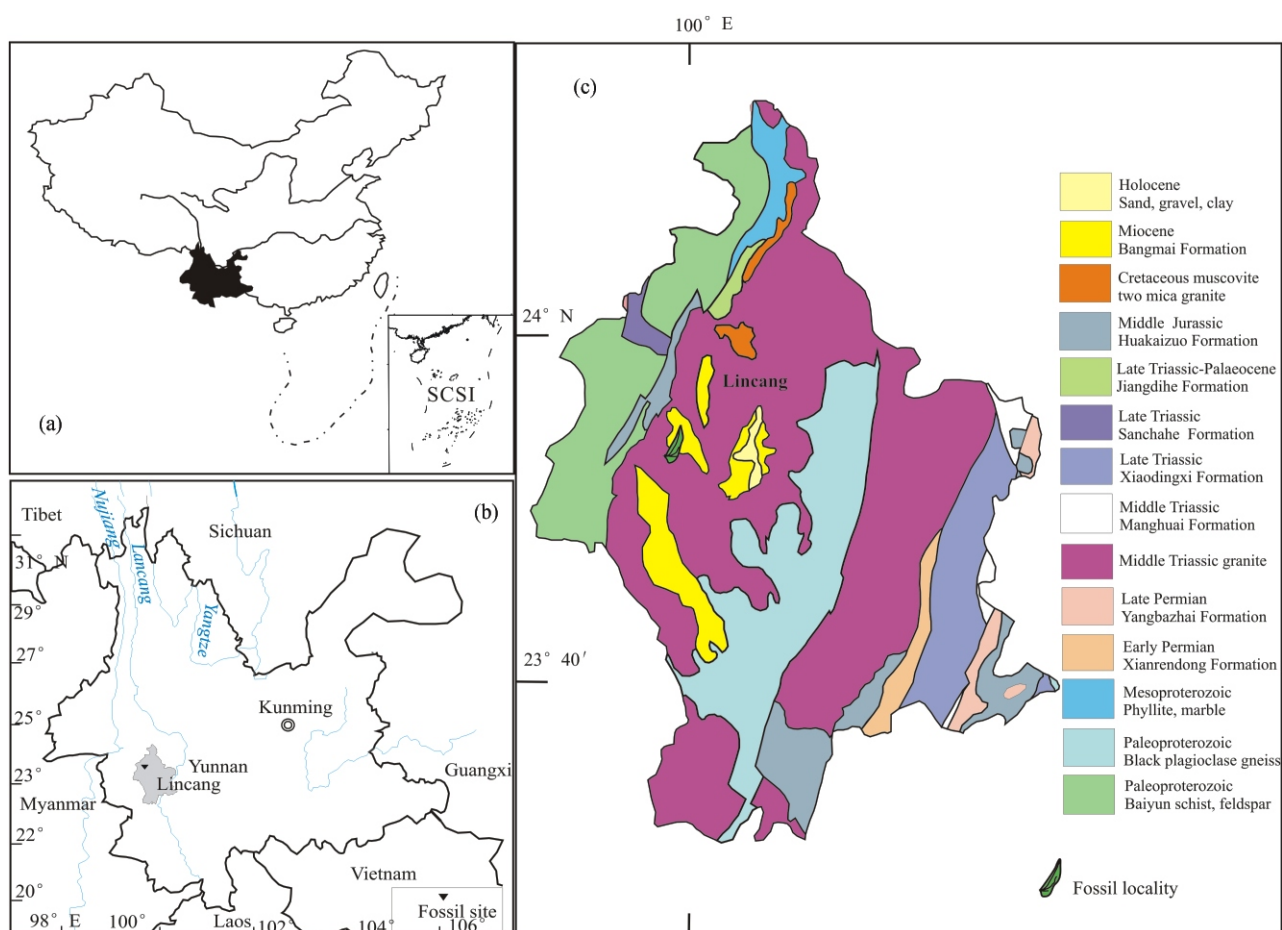


Fig. 1. Simplified geological map of Lincang and fossil locality in Yunnan Province, China. (a), showing Yunnan location in China; (b), showing Lincang location in Yunnan; (c), showing fossil locality and geological map of Lincang.

(Xie et al., 2014). On the basis of lithofacies, the Bangmai Formation consists of fluvial, swampy and lacustrine strata from bottom to top (Ge Hongru and Li Daiyun, 1999; Tao Junrong et al., 2000). This formation recently yielded numerous plant fossils, e.g., *Fraxinus* fruits (Wang Lei et al., 2012), *Dalbergia* pods (Jia Gaowen et al., 2013), ferns (Wen Wenwen et al., 2013; Xie et al., 2016), *Citrus* leaves (Xie et al., 2013), *Firmiana* capsules (Xie et al., 2014), *Ventilago* samaras (Liu Kenan et al., 2015) and *Acer* leaves and samaras (Wang Yunfeng et al., 2015).

3 Materials and Methods

Eight fossil specimens, including five pod fossils and three leaf fossils, were investigated here. Fossil specimens were photographed with a Panasonic DMC-LX5 camera. Morphological characteristics of the fossils were observed and measured directly by the aid of Adobe Photoshop CS3 software. Fossil specimens are housed in the Institute of Paleontology and Stratigraphy, School of Earth Sciences, Lanzhou University, Gansu Province, China. The images of extant species for comparison were photographed from the Institute of Botany, Chinese Academy of Sciences. Illustrations in this study were made using CorelDRAW 12.0 (Corel Corporation, Ottawa, Ontario, CA). The description terminology of *Albizzia* leaf morphology referred to the manual of leaf architecture for angiosperms (Ellis et al., 2009). The terminology of pod morphology followed Delectis Flora Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita (1988).

4 Discussion

4.1 Systematic paleontology

Family Leguminosae Juss., 1789

Genus *Albizzia* Durazz., 1772

Albizzia scalpelliformis Guo, Here Emended

(Fig. 2a–d, Fig. 3a–b)

Specimens No. MCD090216–003, LDGSW20151602, MCD090217–014, MCD090209–008, MCD090209–011.

Emended description: Leaf morphology: Compound leaves are pinnate, with opposite leaflets, with 5–8 pairs visible along the rachis (Fig. 2b–c), and the axial angle is between 30–70 degrees. The leaflets are entire, falcate in shape and strongly asymmetric (Fig. 2a). The size is 1.2–1.4 cm long and 4.3–6.0 mm wide. The apex is obtuse; the base has pillow structure (Fig. 2a), a vital diagnosis characteristic could be observed in extant species (Fig. 2g), without petiole. Midrib is near the upper edge of the blade (i.e., relatively straight edge; Fig. 2a, c), which is identical to the extant species (Fig. 2e–g). Lateral veins extend to the inside of the bend edge, without reaching the

margin, and the angle between lateral veins and midrib is acute (Fig. 2a), comparable to that of extant one (Fig. 2e). Tertiary veins and higher-order venation are invisible (Fig. 2a).

Pod morphology: Pod specimens (Fig. 3a–b) are preserved as impressions. The pod is linear in shape, and the base and the apex are not fully preserved (Fig. 3a). The preserved part was 7.4–12.4 cm in length and 1.4–2.2 cm in width. The pod is flat, glabrous, with a straight margin and an obvious irregular constriction near the base (Fig. 3a) or both straight margin (Fig. 3b). Seeds have 6–10, oval or elliptic, flat, perpendicular to the edge of the pod (Fig. 3a–b). Size of seeds is in 1–1.5×0.6–0.7 cm, with an average distance 0.3–0.7 cm each other (Fig. 3a–b).

Comparison and discussion: The fossil pods here (Fig. 3a–e) have some characters distinguishing them from other similar genera (Table 1), but identical to that of *Albizzia*. The main difference between *Leucaena* and the fossil specimens is the way of the dehiscence. *Leucaena* presents the two petals' dehiscence, while the fossil pods have no dehiscence (Fig. 3a–e). The pod of *Acacia* are oblong or linear in shape, while the fossil pods here are ribbon or flat. The fossil specimens and *Cassia* differed in the pod shape, the way of dehiscence, and seeds shape (Fig. 3a–e, Table 1). The difference between *Bauhinia* and the current fossil pods are the way of dehiscence and seeds direction. *Bauhinia* is often dehiscent, with seeds in the middle or near one side of the pod edge (Fig. 3a–e, Table 1). At the species level, the difference between fossil pods here and *Albizzia miokalkora* from the Miocene of Shandong, China (Hu and Chaney 1940) and from the Miocene of Korea (Kim, 2005), exists in the shape of pods and seeds. The fossil pods here are near basally constricted, with oval and flat-shaped seeds, contrasting to the pods without basal constriction and suborbicular seeds in *Albizzia miokalkora*. Among extant species, the current fossils (Fig. 3a–b) are most similar to extant *Albizzia julibrissin* (Fig. 4a–b) in morphology, except the seeds size. Seeds in extant one are 1–1.6 cm long and 0.5–1 cm wide, with a spacing 0.3–0.8 cm (Fig. 4a–b), slightly larger than that in fossils (Fig. 3a–b).

The fossil leaves, here, are morphologically similar to the previous reported *Albizzia scalpelliformis* preserved as a single leaflet (Guo Shuangxing, 2011). The *Albizzia scalpelliformis* was in a poorly preserved condition (Guo Shuangxing, 2011), however, considering they are from the same basin, we adopted the previous reported name but revised the characters here to represent both the leaves and pods. Although the pod and leaf fossils were not associated together, the morphology of fossil leaves and pods here respectively resemble that observed in extant *Albizzia julibrissin* (Fig. 2e–g, Fig. 4a–b). Therefore, the

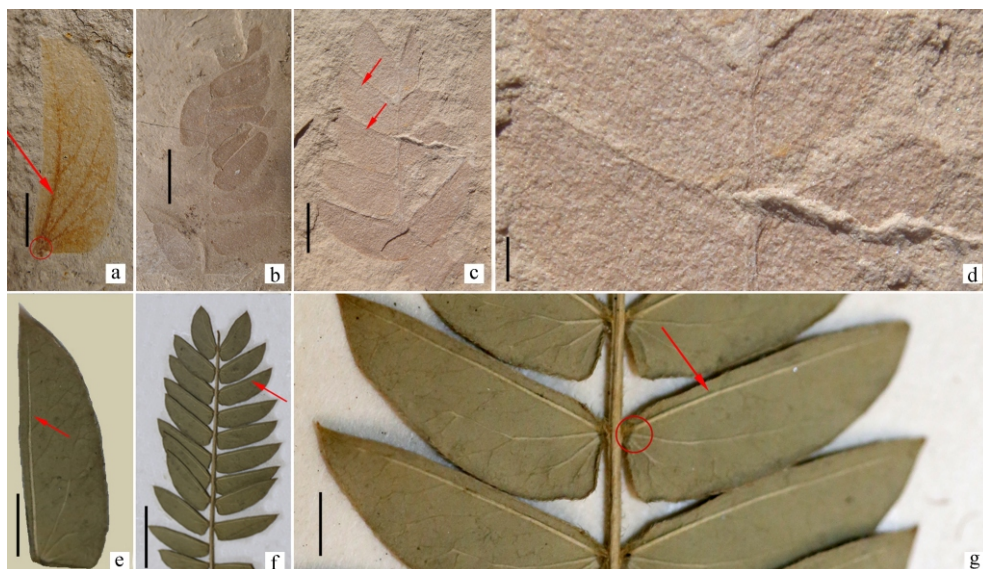


Fig. 2. Leaf morphology of *Albizzia scalpelliformis* Guo, Li and Xie Emended and extant *Albizzia julibrissin* for comparison

(a–c), *Albizzia scalpelliformis* Guo, Li and Xie Emended, specimen No. MCD090216–003, LDGSW20151602, MCD090217–014; arrows in A and C indicate midribs close to the upper edge of the blade, the circle in A is showing the pillow structure at the base. (d), Close-up of C, showing the detail of leaflets. (e–g), *Albizzia julibrissin* Durazz., barcode: PE00322114; arrow in F indicate the midrib for comparison, circle in G is showing the pillow structure comparable to that observed in fossils. Scale = 0.3 cm in a–c, e and f, scale = 0.1 cm in d and g.



Fig. 3. Pods morphology of fossil *Albizzia*.

(a–b), *Albizzia scalpelliformis* Guo, Li and Xie Emended, specimen No. MCD090209–008, MCD090209–011. (c), *Albizzia* cf. *kalkora* (Roxb.) Prain, specimen No. LDGSW20151279. (d–e), *Albizzia* sp., specimen No. LDGSW20151314, LDGSW20151307. Scale = 0.5 cm in a–e.

fossil leaves and pods similar to *Albizzia julibrissin* were assigned to the same species.

Albizzia cf. *kalkora* (Roxb.) Prain

(Fig. 3c)

Specimens No. LDGSW20151279.

The pod characteristics: The pod is flat and indehiscent (Fig. 3c). The top of the pod was not well preserved, but the wavy suture could be observed. The margin of the pod is undulate and constricted once every 1

or 2 seeds (Fig. 3c). The constriction reaches its maximum near the base (Fig. 3c). The length of the preserved part is approximately 8 cm, and the width of the pod is 1.3–2.3 cm (Fig. 3c). Four seeds chambers can be observed (Fig. 3c). Seeds are oval in shape, perpendicular to the edge of the pod, 0.6–1 cm in length and 0.4–0.6 cm in width. The spacing of seeds was between 0.5–1.1 cm (Fig. 3c).

Comparison and discussion: The fossil pod (Fig. 3c) is different from *Albizzia scalpelliformis* Guo, Li and Xie Emended in the length and the distance of seeds (Fig. 3a–

b). Compared to above fossil species (Fig. 3a–b), the length of the seed is longer, and the distance between the seed is larger. In addition, the wavy suture of *Albizzia* cf. *kalkora* (Fig. 3c) is more significant. Among extant species, the fossil (Fig. 3c) here mostly resembles extant *Albizzia kalkora* (Roxb.) Prain (Fig. 4c) in gross morphology. The pod of extant *Albizzia kalkora* is 1.5–2.9 cm wide, associated with seeds 0.8–1×0.6–0.8 cm in size and 0.5–0.8 cm in spacing, slightly larger than that of fossil specimen. The obvious expansion of wavy suture could be seen both in fossil species (Fig. 3c) and extant one (Fig. 4c), except the seed center is exerted in extant species (Fig. 4c). Therefore, the fossil was assigned as *Albizzia* cf. *kalkora* (Roxb.) Prain.

Albizzia sp.

(Fig. 3d–e)

Specimens No. LDGSW20151314, LDGSW20151307.

The pod characteristics: The pod is flat cylindrical and beaded, with acuminate apexes and bases (Fig. 3d–e). The pod is approximately 5 cm in length and 0.8–1.3 cm in width. The surface is glabrous and the margin is undulate. Seeds retain two, ellipse in shape, perpendicular to the edge of the pod. The length of seeds is 0.6–0.7 cm; the width is approximately 0.5 cm; the distance between seeds is approximately 2 cm.

Comparison and discussion: The fossils (Fig. 3d–e) are most similar to extant *Albizzia chinensis* (Osbeck) Merr (Fig. 4d). The pods of extant species (Fig. 4d) are approximately 6 cm in length and 0.6–1.2 cm in width. The length of seeds is approximately 0.8 cm, and the width is approximately 0.5 cm. The distance between seeds is approximately 1.8 cm. The shrink of the apex and the base in extant species (Fig. 4d) is more distinguished than those in the current fossil species (Fig. 3d–e). We assigned the fossil pods here as *Albizzia* sp., considering the coexistence of its characteristics in different extant species.

4.2 Phytogeography

The fossil record of the genus *Albizzia* was reviewed in this investigation (Table 2; Fig. 5). The earliest record of this genus so far was from the Eocene of Africa, represented by pods *Albizzia* sp. (Caccavari, 1996). Another Eocene record was from the southeast of North America (Herendeen and Dilcher, 1990). The earliest occurrence of the genus in Asia was reported from the upper Eocene of Sichuan, China (Chen Minghong et al., 1983). Neogene records of *Albizzia* in Asia were more prevalent (Fig. 5); e.g., *Albizzia miokalkora*, represented by leaflets and pods, was widely distributed in the Miocene of Asia, including Shandong of China (Hu and

Table 1 Selected pod characters distinguishing *Albizzia* from similar genera in the family Leguminosae

Genera	Shape	Dehiscence	Seed number	Seed position	Seed direction	Seed shape
<i>Albizzia</i>	Ribbon, flat	Dehiscence or no dehiscence	2–13	Middle	Vertical to the pod edge	Round or ovate
<i>Leucaena</i>	Ribbon, straight, flat, smooth	Two petals dehiscence	6–25	Middle	Vertical to the pod edge	Oval, flat
<i>Acacia</i>	Oblong or linear	Dehiscence or no dehiscence	2–12	Middle	Vertical to the pod edge	Flat and smooth
<i>Cassia</i>	Cylindrical or flat	Two petals dehiscence or no dehiscence	4–60	Middle	Vertical or parallel to the pod edge	Septa presence between seeds
<i>Bauhinia</i>	Oblong, ribbon or linear	Dehiscence, rare not dehiscence	2–25	Middle or near one side of the pod edge	Vertical to the pod edge	Round or ovate

Based on (Delectis Flora Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edit, 1988).

Table 2 Fossil records of the genus *Albizzia*

Species	Ages	Occurrence site	Preserved type	Reference
<i>Albizzia</i> sp.	Pleistocene	Japan	leaf	Onoe, 1971
<i>Albizzia</i> sp.	Pliocene	Shanxi, China	leaf	Tao Junrong et al., 2000
<i>Albizzia</i> sp.	Pliocene	Sichuan, China	leaf	Tao Junrong et al., 2000
<i>Albizinium eolebbeckianum</i>	Late Miocene	Himachal Pradesh	wood	Prakash, 1975
<i>Albizzia gummifera</i>	Late Miocene	Ethiopia	wood	Jolly-Saad et al., 2011
<i>Albizzia miokalkora</i>	Miocene	Shangdong, China	leaf	Hu and Chaney, 1940
<i>Albizzia miokalkora</i>	Miocene	Korea	pod	Kim, 2005
<i>Albizzia miokalkora</i>	Miocene	Japan	leaf	Hayashi, 1975; Tanai, 1978
<i>Albizzia bracteata</i>	Miocene	Kaiyuan, Yunnan	leaf	WGCP, 1978
<i>Albizzia miokalkora</i>	Miocene	Lincang, Yunnan	leaf	Tao Junrong et al., 2000
<i>Albizzia juligreissii</i>	Miocene	Tengchong, Yunnan	leaf	Tao Junrong et al., 2000
<i>Albizzia scalpelliformis</i>	Miocene	Lincang, Yunnan	leaf	Guo Shuangxing, 2011
<i>Albizzia miokalkora</i>	Miocene	Kaiyuan, Yunnan	leaf	Tao Junrong et al., 2000
<i>Albizzia bracteata</i>	Miocene	Kaiyuan, Yunnan	leaf	Tao Junrong et al., 2000
<i>Albizinium pondicherriense</i>	Neogene	India	wood	Awasthi and Mehrotra, 1997
<i>Albizinium arunachalensis</i>	Neogene	Arunachal Pradesh	wood	Mehrotra et al., 1999
<i>Albizzia</i> sp.	Late Eocene	Sichuan, China	leaf	Chen Minghong et al., 1983
<i>Albizzia</i> sp.	Eocene	Southeastern North America	pollen	Herendeen and Dilcher, 1990
<i>Albizzia</i> sp.	Eocene	Africa	pollen	Caccavari, 1996



Fig. 4. Pods morphology of extant *Albizzia* species for comparison.

(a–b), *Albizzia julibrissin* Durazz, No. PE01466453, PE01466449. (c), *Albizzia kalkora* (Roxb.) Prain, from LZU campus. (d), *Albizzia chinensis* (Osbeck) Merr, No. PE00490337. Scale = 0.5 cm in a–d.

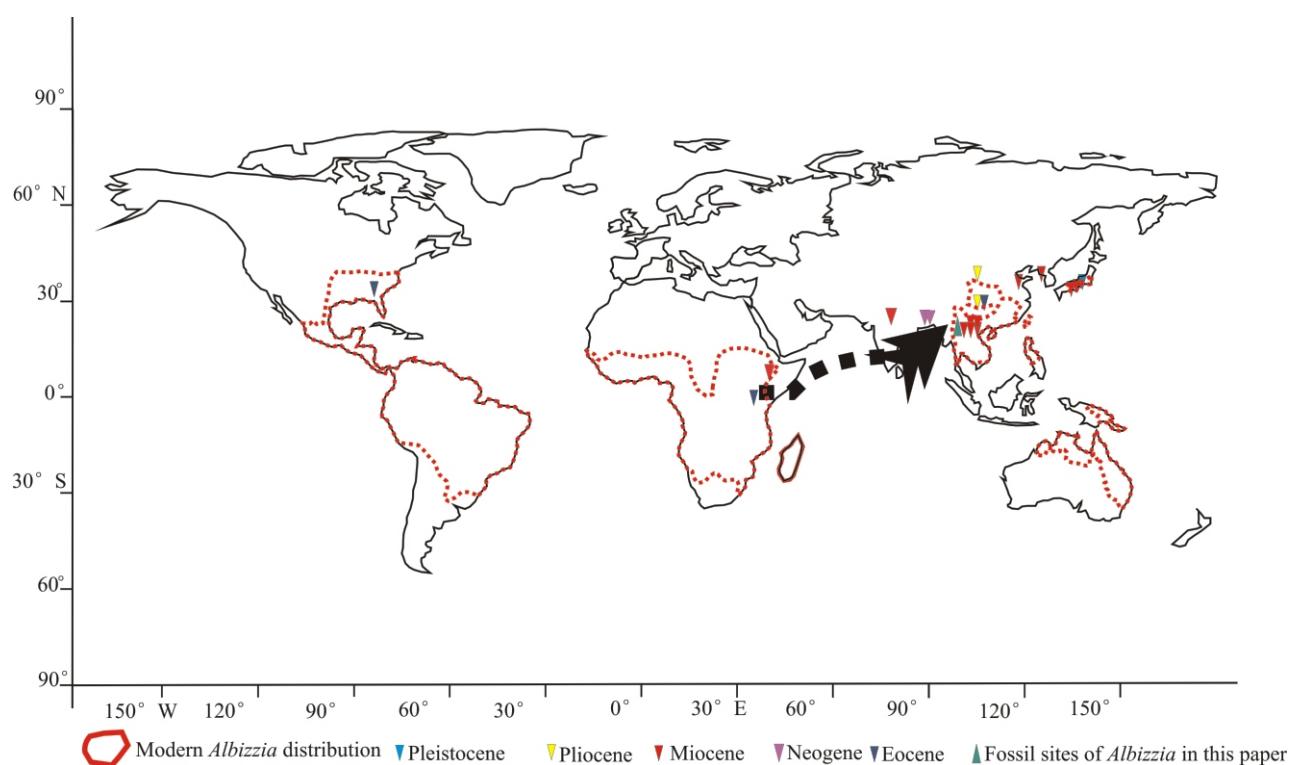


Fig. 5. Historical geographic distribution of *Albizzia*.

Modern *Albizzia* data from Global Biodiversity Information Facility: <http://www.gbif.org/>.

Chaney, 1940; WGCP, 1978), Tengchong, Lincang and Kaiyuan of Yunnan Province, China (Tao Junrong et al., 2000), Yeonil of Korea (Kim, 2005) and Japan (Hayashi,

1975; Tanai, 1978). Additional fossil species represented by leaves, e.g., *Albizzia juligreissin* (Tao Junrong et al., 2000), *Albizzia scalpelliformis* (Guo Shuangxing, 2011),

and *Albizzia bracteata*. (Tao Junrong et al., 2000), also occurred in the Miocene of Yunnan, China. *Albizzia*-like or *Albizzia* fossil woods were reported from Africa and India, e.g., *Albizinium eolebbeckianum* from the lower Siwalik beds from the Middle Miocene to lower Pleistocene of Himachal Pradesh (Prakash, 1975), *Albizinium pondicherriense* found in the Neogene of India (Awasthi and Mehrotra, 1997), *Albizinium arunachalensis* from the Neogene deposit of Arunachal Pradesh (Mehrotra et al., 1999), and *Albizzia gummifera* from the late Miocene Adu-Asa Formation of the Middle Awash, located in the Afar Rift of Ethiopia (Jolly-Saad et al., 2011). Pliocene record was constricted in Shanxi and Sichuan of China (Tao Junrong et al., 2000). Quaternary document was only found in the Pleistocene of Japan known by *Albizzia* sp. (Onoe, 1971).

The legumes might have originated from the humid tropical regions of the world in the late Cretaceous (Sprent, 2007). Due to the earliest credible fossils that were found in the African continent (Late Cretaceous or Paleocene) (Herendeen, 1992a; Herendeen and Jacobs, 2000), the leguminous plants were considered to be originated in the tropics of West Gondwana. Guinet et al. (1987) and Kedves (1971) studied the pollen of Mimosoideae and concluded that the earliest ancestor of this subfamily might have also originated from the West Gondwana. On the basis of the molecular phylogeny of legumes, Lavin et al. (2005) concluded that many clades of the subfamily Mimosoideae, including the genus *Albizzia*, had an evolutionary history of 42.4 ± 2.6 Ma. According to above studies, it can be inferred that *Albizzia* probably originated in Africa, consistent with the fossil record (Fig. 5).

The fossil record shows that in the early stage of the evolution and diversification of the legume species, there was an exchange of plant flora between the Americas and Africa (Herendeen and Dilcher, 1990), as well as between Eurasia and Africa (Herendeen, 1992b). According to the fossil distribution of *Albizzia* (Fig. 5), it could be seen that *Albizzia* species in Eocene were distributed in southeastern Africa, North America and Sichuan of China. There is a widespread arid band throughout the Oligocene (Song Zhichen et al., 1983), and no *Albizzia* fossil records have been found in this time. Miocene records mainly occurred in South and East Asia and are widely distributed in Korea, Japan, and China (Table 2), probably implying a Neogene migration to Asia or a local diversification at Asia. Additionally, leguminous plants have a good ability of transoceanic dispersal (Raven and Polhill, 1981; Herendeen et al., 1992) and salt tolerance. It is possible that the migration pattern of the genus *Albizzia* was similar to that of its affinitive genus *Acacia*. That is, Eocene or

earlier *Albizzia* originated in Africa or North America. It is assumed that *Albizzia* originated in North America and arrived in Asia through the Bering land bridge (Davis et al., 2002; Nie et al., 2012), but since the Bering land bridge is situated at higher latitudes, which might restrict tropical or subtropical plants to migrate, there is little possibility of *Albizzia* plants being spread through the Bering land bridge (Meng et al., 2014). An alternative scenario is Eocene or earlier; *Albizzia* originated in Africa and afterwards, in favorable climatic conditions, e.g., The Paleocene-Eocene Thermal Maximum, where the Eocene climate was warmer than any other period of the Cenozoic (Quan et al., 2012), *Albizzia* plants spread to the Indian plate through long distance transportation across the ocean (Raven and Polhill, 1981; Herendeen et al., 1992). Until the continental collision between the Indian plate and the Eurasian plate, the genus *Albizzia* first reached neighboring India and then migrated into Southwest China and began to differentiate in Asia in favor of the warm and humid climate during the Miocene (Sun and Wang, 2005; Wang Haobo et al., 2015). By the Pliocene, the distribution of *Albizzia* fossil species reached their northern maximum range of extant species in East Asia, but no fossil record was reported in South America and Africa, which may be due to the regional extinction in these continents or insufficient fossil records. The exchanges of post-Pliocene in different continents finally resulted in the disjunctive distribution pattern of *Albizzia* in Asia, Africa, Oceania and tropical America (Fig. 5). This migration pattern between the Northern and Southern Hemisphere is different from the exchange within the Northern Hemisphere from the neighbor fossil flora (Dao Kequn et al., 2013; Wu Jingyu et al., 2015).

5 Conclusions

(1) The pods and leaves of *Albizzia* from the Bangmai Formation of Lincang, Yunnan, China were assigned to three species, including *Albizzia scalpelliformis* Guo, Li and Xie Emended, *Albizzia* cf. *kalkora* (Roxb.) Prain and *Albizzia* sp.

(2) A pattern concerning the origin, migration and extinction of the genus *Albizzia* was proposed, i.e., the genus *Albizzia* may have originated in Africa, and after that, with the collision of the Indian plate and the Eurasian plate, they migrated to Asia and subsequently differentiated in Asia. The wide range of the *Albizzia* distribution in East Asia during the Miocene may be related to the optimum climatic conditions.

(3) *Albizzia* fossils found in Lincang not only added fossil evidence for plant diversity but also provided information for investigation of its phylogeography.

Furthermore, more fossil evidence is needed to discuss its relationship with climatic changes and plate collisions.

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References

- Awasthi, N., and Mehrotra, R.C., 1997. Some fossil dicotyledonous woods from the Neogene of Arunachal Pradesh, India. *Palaeontographica Abteilung B-Palaophytologie*, 245: 109–121.
- Berry, E.W., 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *U.S. Geological Survey. Prof. Pap.* 84.
- Berry, E.W., 1916. The lower Eocene floras of southeastern North America. *U.S. Geological Survey. Prof. Pap.* 91.
- Berry, E.W., 1930. Revision of the lower Eocene Wilcox flora of the southeastern states. *U.S. Geological Survey. Prof. Pap.* 156.
- Ellis, B., Daly, D.C., Hickey, L.J., Johnson, K.R., Mitchell, J.D., Wilf, P., and Wing, S.L., 2009. *Manual of leaf architecture*. New York: Cornell University Press, 190.
- Bowerbank, J.S., 1840. *A history of the fossil fruits and seeds of the London Clay*. London: Jan Van Voorst, 144.
- Caccavari, M.A., 1996. Analysis of the South American fossil pollen record of Mimosoideae (Leguminosae). *Review of Palaeobotany and Palynology*, 94 (1–2): 123–135.
- Chen Minghong, Kong Zhaochen and Chen Ye, 1983. On the discovery of palaeogene flora from the western Sichuan plateau and its significance in phytogeography. *Acta Botanica Sinica*, 25(5): 483–484 (in Chinese with English abstract).
- Dao Kequn, Chen Junlin, Jin Peihong, Dong Chong, Yang Yi, Xu Xiaohui, Wu Jingyu, Xie Sanping, Lin Zhicheng and Sun Bainian, 2013. A new material of *Lindera* (Lauraceae) of the Late Pliocene from Tengchong, Yunnan and the Genus' biogeography significance. *Acta Geologica Sinica* (English Edition), 87(3): 690–706.
- Davis, C.C., Bell, C.D., Mathews, S., and Donoghue, M.J., 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences of the United States of America*, 99: 6833–6837.
- Delectis Flora Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita, 1988. *Flora Reipublicae Popularis Sinicae* (Tomus 39). Beijing: Science Press, 57–68.
- Fontaine, W.M., 1889. The Potomac or younger Mesozoic flora. *U.S. Geological Survey. Mono.* 15.
- Ge Hongru and Li Daiyun, 1999. *Cenozoic coal-bearing Basins and Coal-forming Regularity in West Yunnan*. Kunming: Yunnan Science and Technology Press, 15–19 (in Chinese with English abstract).
- Guinet, P., El Sabrouy, N., Soliman, H., and Oram, A.M., 1987. Etude des caracteres du pollen des Legumineuses-Mimosoideae des sediments tertiaires du nord-ouest de l'Egypte. *Memoires et Travaux, Ecole Pratique des Hautes Etudes de l'Institut de Montpellier*, 17: 159–171.
- Guo Shuangxing, 2011. The Late Miocene Bangmai Flora from Lincang County of Yunnan, Southwestern China. *Acta Palaeontologica Sinica*, 50(3): 353–408 (in Chinese with English abstract).
- Hayashi, T., 1975. Fossils from Chojabaru, Iki Island, Japan. *Science Institute of Island, Iki, Japan*, 120. (in Japanese).
- He Yuli, Li Na, Wang Zixi, Wang Haoqi, Yang Guolin, Xiao Liang, Wu Jingyu and Sun Bainian, 2014. *Quercus yangyiensis* sp. nov. from the Late Pliocene of Baoshan, Yunnan and its paleoclimatic significance. *Acta Geologica Sinica* (English Edition), 88(3): 738–747.
- Herendeen, P.S., 1992a. The fossil history of the leguminosae from the Eocene of southeastern North America. In: Herendeen, P.S., and Dilcher D.L. (eds.), *Advances in Legume Systematics, Part 4, the Fossil Record*. London: The Royal Botanic Kew Garden Press, 85–160.
- Herendeen, P.S., 1992b. A re-evaluation of the fossil genus *Podogonium* Heer. In: Herendeen, P.S., and Dilcher, D.L. (eds.), *Advances in Legume Systematics, Part 1, the Fossil Record*. London: The Royal Botanic Kew Garden Press, 3–18.
- Herendeen, P.S., Crepet, W.L., and Dilcher, D.L., 1992. The fossil history of the Leguminosae: Phylogenetic and biogeographic implications. In: Herendeen P.S., Dilcher D.L. (eds.), *Advances in Legume Systematics, Part 4. the Fossil Record*. London: The Royal Botanic Kew Garden Press, 303–316.
- Herendeen, P.S., and Jacobs B.F., 2000. Fossil legumes from the Middle Eocene (46.0Ma) Manenge Flora of Singida, Tanzania. *American Journal of Botany*, 87(9): 1358–1366.
- Herendeen, P.S., and Dilcher, D.L., 1990. Fossil mimosoid legumes from the Eocene and Oligocene of southeastern North America. *Review of Palaeobotany and Palynology*, 62 (3): 339–361.
- Hu, H.H., and Chaney, R.W., 1940. Part 1. *Instruction and systematic considerations*. In: Hu, H.H., and Chaney, R.W. (eds.), *A Miocene flora from Shantung Province, China*. Carnegie Institution of Washington Publication, 507: 1–84, pls. 1–50.
- Institute of Botany, Academia Sinica, 1955. *Flora Illustration of Chinese Plants (Leguminosae)*. Beijing: Sciences Press, 726 (in Chinese).
- Jia Gaowen, Liu Kenan, Wang Yunfeng, Xie Sanping, Yan Defei and Sun Bainian, 2013. Pod and leaflet fossils of *Dalbergia* (Leguminosae) from the upper Miocene of Lincang, Yunnan. *Acta Palaeontologica Sinica*, 52(2): 213–222 (in Chinese with English abstract).
- Kedves, M., 1971. Presence de types sporomorphes importants dans les sediments prequaternaires Egyptiens. *Acta Botanica Sinica*, 17(3–4): 371–378.
- Kim, J.H., 2005. Fossil *Albizia* legume (Mimosaceae) from the Miocene Duho Formation of the Yeonil Group in the Pohang

- area, Korea. *Journal of the Korean Earth Science Society*, 26: 166–171.
- Knowlton, F.H., 1898. A catalogue of the Cretaceous and Tertiary plants of North America. *U.S. Geological Survey. Bull.* 152.
- Lavin, M., Herendeen, P.S., and Wojciechowski, M.F., 2005. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. *Systematic Biology*, 54(4): 575–594.
- Lesquereux, L., 1878. *Contributions to the fossil flora of the Western Territories*. Part 2. The Tertiary flora. U.S. Geol. and Geog. Surv. Terr. Rept. 7.
- Lesquereux, L., 1892. *The flora of the Dakota group*. Monographs of the U.S. Geological Survey. 17.
- Liu Kenan, Xie Sanping, Manchester, S.R., Wang Yunfeng, Shao Yang and Li Binke, 2015. Samaras of *Ventilago* (Rhamnaceae) from the upper Miocene of Lincang, Yunnan, China and their phytogeographic implications. *Journal of Systematics and Evolution*, 53(3): 252–258.
- Jolly-Saad, M.C., Bonnefille, R., Duperon, J., and Duperon, M., 2011. 5.8 Myr old Mimosoideae fossil woods from Ethiopia and comparison with African *Albizia*. *Palaeontographica Abteilung B Stuttgart*, 288(5–6): 161–187.
- Mehrotra, R.C., Awasthi, N., and Dutta, S.K., 1999. Study of fossil woods from the Upper Tertiary sediments (Siwalik) of Arunachal Pradesh, India and its implication in palaeoecological and phytogeographical interpretations. *Review of palaeobotany and palynology*, 107: 223–247.
- Meng Honghu, Jacques, F.B., Su Tao, Huang Yongjiang, Zhang Shitao, Ma Hongjie and Zhou Zhekun, 2014. New Biogeographic insight into *Bauhinia* s.l. (Leguminosae): integration from fossil records and molecular analyses. *BMC Evolutionary Biology*, 14: 181.
- Nie, Z.L., Sun H., Manchester S.R., Meng Y., Luke Q., and Wen J., 2012. Evolution of the intercontinental disjunctions in six continents in the Ampelopsis clade of the grape family (Vitaceae). *BMC Evolutionary Biology*, 12: 17.
- Nikitin, A.A., 1935. *Nevaia drevesina iz verkhnego pliotse na vostochnoi Gruzii*. Trudy neftyanogo geologo-razvedochnogo. Inst. Ser. B, 51: 52–54.
- Onoe, T., 1971. A Pleistocene flora Ebino City, Miyazaki Prefecture, Japan. *Bulletin of Geological Survey of Japan*, 241: 1–46, pls. 1–12 (in Japanese).
- Polhill, R.M., Raven, P.H., and Stirton, C.H., 1981. Evolution of systematics of the legume. In: Polhill, R.M., and Raven, P.H. (eds.), *Advances in Legume Systematics, Part 4, the Fossil Record*. London: The Royal Botanic Kew Garden Press, 1–26.
- Prakash, U., 1975. Fossil woods from the Lower Siwalik beds of Himachal Pradesh, India. *Palaeobotanist*, 22: 192–210.
- Quan Cheng, Liu Yusheng and Utescher, T., 2012. Eocene monsoon prevalence over China: a paleobotanical perspective. *Palaeogeography Palaeoclimatology Palaeoecology* 365–366: 302–311.
- Raven, P.H., and Polhill, R.M., 1981. Biogeography of the Leguminosae. In: Polhill, R.M., and Raven, P.H. (eds.), *Advances in Legume Systematics*. London: The Royal Botanic Kew Garden Press, 27–34.
- Schrire, B.D., Lavin, M., and Lewis, G.P., 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. *Biologiske Skrifter*, 55: 375–422.
- Song Zhichen, Li Wenben and He Chengquan, 1983. Cretaceous and Palaeogene palynofloras and distribution of organic rocks in China. *Science in China Series B-Chemistry, Biological, Agricultural, Medical & Earth Sciences* 26(5): 538–549.
- Sprent, J.I., 2007. Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. *New Phytologist*, 174(1): 11–25.
- Sun Xiangjun and Wang Pinxian, 2005. How old is the Asian monsoon system? Palaeobotanical records from China. *Palaeogeography Palaeoclimatology Palaeoecology*, 222(3–4): 181–222.
- Tanai, T., 1978, *Angiosperm*. In: Huzioka, K. (ed.), *Paleontology, IV*. Tokyo: Asakura Shoten, 313–383 (in Japanese).
- Tao Junrong and Chen Minghong, 1983. Neogene flora of southpart of the watershed of Salween-Mountain-Yangtze rivers (the Lincang region) Yunnan. In: *Comprehensive Expedition in Xizang Plateau from Chinese Academy of Sciences: Exploration of Hengduan Mountains Expedition* (1). Kunming: Yunnan People's Publishing House, 74–89 (in Chinese with English abstract).
- Tao Junrong, Zhou Zhekun and Liu Yusheng, 2000. *The Evolution of Late Cretaceous-Cenozoic Floras in China*. Beijing: Science Press, 49–290 (in Chinese).
- Wang Haobo, Bondarenko, O.V., Jacques, F.M.B., Wang Yuehua and Zhou Zhekun, 2015. A New Species of *Tsuga* (Pinaceae) based on Lignified Wood from the Late Miocene of Central Yunnan, China, and Its Paleoenvironmental Implications. *Acta Geologica Sinica* (English Edition), 89(5): 1429–1439.
- Wang Lei, Xie Sanping, Liu Kenan, Wen wenwen, Zhang Lirui and Sun Bainian, 2012. Late Miocene samara of *Fraxinus* (Oleaceae) from the Lincang in Yunnan Province and its paleophytogeographical significance. *Journal of Jilin University* (Earth Sciences Edition), 42(2): 332–342 (in Chinese with English abstract).
- Wang Yunfeng, Shao Yang, Li Binke, Liu Kenan and Xie Sanping, 2015. *Acer* Leaves and Samaras from the Late Miocene of Lincang Yunnan Province. *Geological Journal of China Universities*, 21(1): 105–116 (in Chinese with English abstract).
- Wen Wenwen, Xie Sanping, Liu Kenan, Sun Bainian, Wang Lei, Li Hong and Dao Kequn, 2013. Two species of fern macrofossil from the late Miocene of Lincang, Yunnan, China and their paleoecological implications. *Palaeoworld*, 22(3): 144–152.
- WGCP (Writing Group of Cenozoic Plants of China), 1978. *Cenozoic Plants from China, Fossil Plants of China*, Vol. 3. Beijing: Science Press (in Chinese).
- Wu Jingyu, Zhao Zhenrui, Li Qijia, Liu Yusheng, Xie Sanping, Ding Suting and Sun Bainian, 2015. A New Species of *Rhodoleia* (Hamamelidaceae) from the Upper Pliocene of West Yunnan, China and Comments on Phytogeography and Insect Herbivory. *Acta Geologica Sinica* (English Edition), 89(5): 1440–1452.
- Wu Zhenhan, Wu Zhonghai, Hu Daogong, Ye Peisheng and Zhou Chunjing, 2007. Geological Evidences for the Tibetan Plateau Uplifted in Late Oligocene. *Acta Geologica Sinica*, 81(5): 577–588 (in Chinese with English abstract).
- Xie Sanping, Li Binke, Zhang Sihang, Shao Yang, Wu Jingyu and Sun Bainian, 2016. First megafossil record of *Neolepisorus* (Polypodiaceae) from the late Miocene of

- Yunnan, Southwest China. *PalZ*, 90(2): 413–423.
- Xie Sanping, Manchester, S.R., Liu Kenan, Wang Yunfeng and Shao Yang, 2014. *Firmiana* (Malvaceae: Sterculioideae) fruits from the Upper Miocene of Yunnan, Southwest China. *Geobios*, 47: 271–279.
- Xie Sanping, Manchester, S.R., Liu Kenan, Wang Yunfeng and Sun Bainian, 2013. *Citrus linczangensis* sp. n., a leaf fossil of Rutaceae from the late Miocene of Yunnan, China. *International Journal of Plant Sciences*, 174(8): 1201–1207.
- Xu Zenglian, Zhang Jianyu, Ji Junliang and Zhang Kexin, 2015. The Mid-Miocene pollen record of the Xunhua Basin, NE Tibetan Plateau: implications for global climate change. *Acta Geologica Sinica* (English Edition), 89(5): 1649–1663.
- Zhang Shuling, Wang Shuying and Yin Jinshuang, 1987. The study of germanium ore in uranium-bearing coal of the Bangmai basin, Lincang region, Yunnan province. *Uranium Geology*, 3(5): 267–275.

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