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Research papers

A tropical forest of the middle Miocene of Fujian (SE China) reveals Sino-Indian biogeographic affinities

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ABSTRACT

The middle Miocene Fotan flora of Zhangpu County, South Fujian, China has been considered to represent tropical rainforest based on the occurrence of distinctive winged fruit fossils of the Dipterocarpaceae. However, this paleoclimatic interpretation has been challenged. In this study, we describe new tropical and subtropical elements of this flora that co-occurred with Dipterocarpaceae based on newly collected fossil leaves from the Fotan flora. The fossils were identified through detailed comparison with leaves of living plants. Six new species belonging to six different families are described: *Artocarpus basirotundatus* sp. nov. (Moraceae), *Bauhinia fotana* sp. nov. (Leguminosae), *Boehmeria fujianensis* sp. nov. (Urticaceae), *Calophyllum striatum* sp. nov. (Calophyllaceae), *Flacourtia serrulata* sp. nov. (Salicaceae), and *Macaranga stellata* sp. nov. (Euphorbiaceae). They represent the first fossil records of these genera in China, with the exception of *Bauhinia*. These elements provide further evidence for the recognition of tropical forest in South Fujian during the middle Miocene. They show more affinities with Indian Neogene floras than with other Chinese palaeofloras. It suggests that, during the Mid-Miocene Climatic Optimum, the border between the tropical and subtropical vegetation moved north to South Fujian. The Fotan palaeoflora is the first record of Miocene floristic affinities between Indian and South Chinese floras. In contrast, the southwestern Chinese Miocene palaeofloras have a different floristic composition without clear Indian affinities. We propose that the route of exchange between the Indian and South Chinese Miocene floras passed through South-East Asia.

1. Introduction

The distribution of tropical rainforest is very limited today in China. This vegetation type occurs on Hainan Island and in southern, southeastern, and southwestern Yunnan, southwestern Guangxi, southeastern Tibet, and southern Taiwan (Zhu, 2006, 2013). A true Southeast Asian tropical forest has been recognized in Xishuangbanna, Yunnan, on the basis of the occurrence of Dipterocarpaceae in this area during the 1970s (Zhu, 2006). However, how and when the tropical forest appeared in China is still debated. Palaeovegetation reconstructions of China during the Neogene indicate the continuous presence of evergreen forest in southern China during the Neogene (Sun and Wang, 2005; Jacques et al., 2011a, 2013). The palaeoclimatic reconstructions of south China demonstrate that the temperature during the coldest month was over 14 °C during the middle Miocene (Yao et al., 2011), and could have been suitable for a tropical forest. Palaeovegetation reconstruction based on palynology indicates that the tropical rainforest was almost or completely absent from mainland China during the Late Glacial Maximum (Ni et al., 2010), but little is known about the occurrence of rainforest in China during the early Neogene.

Recently, winged fruits belonging to two genera of the Dipterocarpaceae as well as fossil resins of the family were reported from the middle Miocene Fotan group in Fujian Province, southeastern China (Shi and Li, 2010; Shi et al., 2014a, b), complementing prior evidence for this family from palynological study (Zheng, 2000). The presence of *Dipterocarpus* and *Shorea* led Shi and Li (2010) to conclude that a 'classic' Asian tropical rainforest was present in the South Fujian during the middle Miocene. This time period coincides with the Mid-Miocene Climatic Optimum (Zachos et al., 2001; Mosbrugger et al., 2005). The palaeovegetation reconstruction based on the palynological record indicates the presence of an evergreen forest in this region (Jacques et al., 2011a, 2013). However, their conclusion was challenged because Dipterocarpaceae are not limited to tropical rainforests (Ghazoul, 2011).

The modern distribution pattern of Dipterocarpaceae has been explained by the out-of-India hypothesis (Ashton, 1982; Ashton and Gunatilleke, 1987). This hypothesis, which states that they arrived to

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Asia from India, after the collision of the Indian tectonic plate and Asia in the Eocene, is also used to explain the biogeography of other plant and animal groups (Conti et al., 2002; Karanth, 2006). This hypothesis is supported by the phylogeny of the Dipterocarpaceae and the early Eocene fossil resins derived from Dipterocarpaceae that were found in India (Rust et al., 2010; Dutta et al., 2011). However, the megafossils of Dipterocarpaceae that were reported in the Neogene sediments of India and Nepal (e.g. Awasthi and Prasad, 1990; Prasad, 1990, 1994; Prakash et al., 1994; Khan et al., 2011) are absent from the Paleogene of India but present in the Paleogene of South-East Asia (Bande and Prakash, 1986; Srivastava and Mehrotra, 2010; Shukla et al., 2013). The occurrence of Dipterocarpaceae from the middle Miocene of China raises the question of the route of exchange between Chinese and Indian palaeofloras. Based on southwestern Chinese palaeofloras, no floristic link could be made between Miocene vegetation of China and India (Mehrotra et al., 2005). However, our investigation on newly uncovered fossils from the Fotan flora will help to clarify the biogeographic link between this flora and the Indian palaeofloras.

In this article, we describe six new species from the Fotan flora, discuss their affinities, and elucidate whether they are consistent with the presence of a tropical forest. In addition, we discuss the biogeographical implications.

2. Materials and methods

2.1. Geological settings

More than 1000 fossil specimens were collected during spring 2011 from the Fotan group in Lindai village (24°12′N, 117°53′E), Zhangpu county, Fujian Province (Fig. 1). The locality is well known for yielding Dipterocarpaceae fruits (Shi and Li, 2010; Shi et al., 2014a, b).

The stratigraphy of the Fotan group has been extensively studied (Zheng, 1984; Bureau of Geology and Mineral Resources of Fujian Province, 1985; Zheng and Wang, 1994; Shi and Li, 2010). This group belongs to the Langhian stage, middle Miocene (14.8 ± 0.6 Ma), based on $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ radiometric dating (Ho et al., 2003).

Fossils have been found in two horizons: a layer of light brown diatomite and an underlying layer of blue-grey mudstone (Fig. 2; Shi and Li, 2010). All of the fossil species described here occur in the light brown diatomite layer. Some of them are also represented by specimens from the blue-grey mudstone layer.

2.2. Cleared leaves

For comparison with the fossils, cleared leaves were made from living specimens collected in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. They were prepared following the methods used by Hickey (1973).

2.3. Cuticle preparation

Fossil cuticles were cleaned by soaking for 1 h in hydrochloric acid, and then overnight in 40% hydrofluoric acid. They were then macerated in Schulze's solution followed by 5% potassium hydroxide. Finally, the samples were stained with safranin T (Shi et al., 2012). Modern cuticles were macerated in a 1:1 glacial acetic acid and 30% hydrogen peroxide solution. They were then stained with safranin T.

All slides were observed and photographed under a Leica DM750 microscope coupled with a digital camera.

2.4. Classification

The systematic classification as revealed by most recent phylogenetic research (APG III, 2009) was used in this study. Affinities between the fossils described here and modern species are based only on morphological similarities and may not represent natural or phylogenetic relationships at the specific level. Such relationships should be established through a cladistics analysis. Because the studied fossils are from the middle Miocene, it is not appropriate to include them in a modern species: the average duration of a fossil angiosperm species is ca. 3.5 Ma (Niklas, 1997), a much shorter time than the 11.6 Ma separating the middle Miocene from the present. To have a detailed systematic study of all fossil species occurring around the world for the genera found in the Fotan flora is beyond the scope of this paper. Because the fossils described here were found in Asia, we thought they had higher probabilities to be closer to other Asian fossils than to fossil from other part of the world. Therefore, we limited our species comparison to the fossil species occurring in Asia.

2.5. Modern distribution

The modern distribution of the genera that are reported in the Fotan fossil assemblage was drawn based on the data from the Chinese Virtual Herbarium (http://www.cvh.org.cn), consulted in December 2012. Data

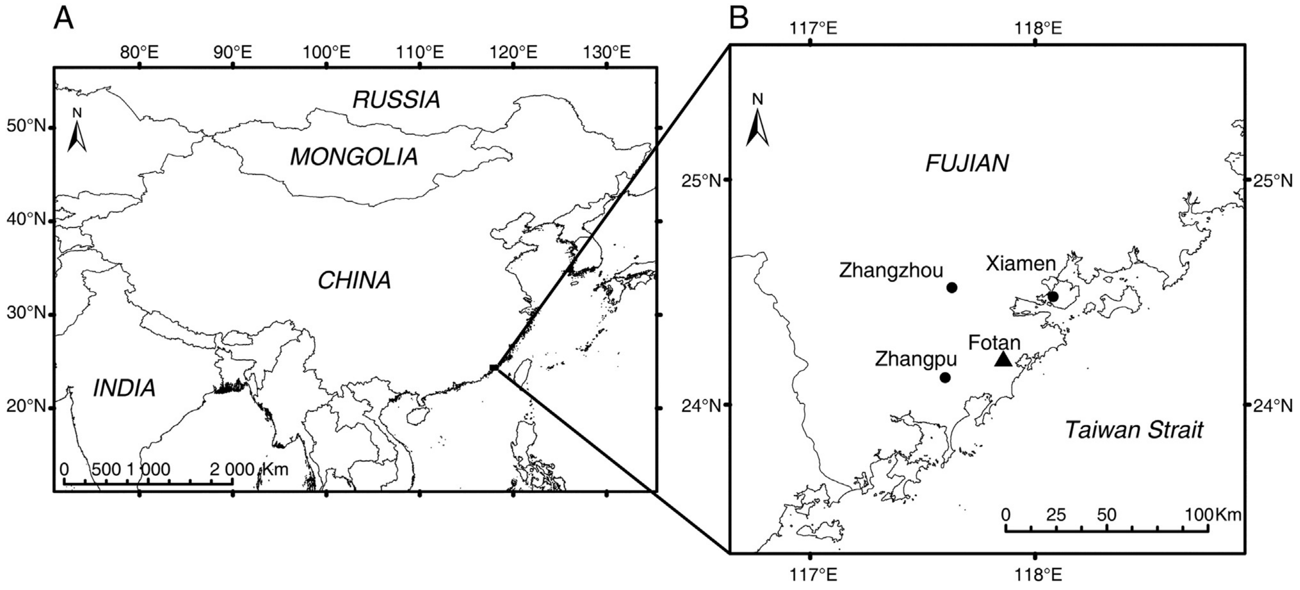


Fig. 1. Situation map of the Fotan assemblage. A. Regional map of Eastern Asia. B. Local map of South Fujian.

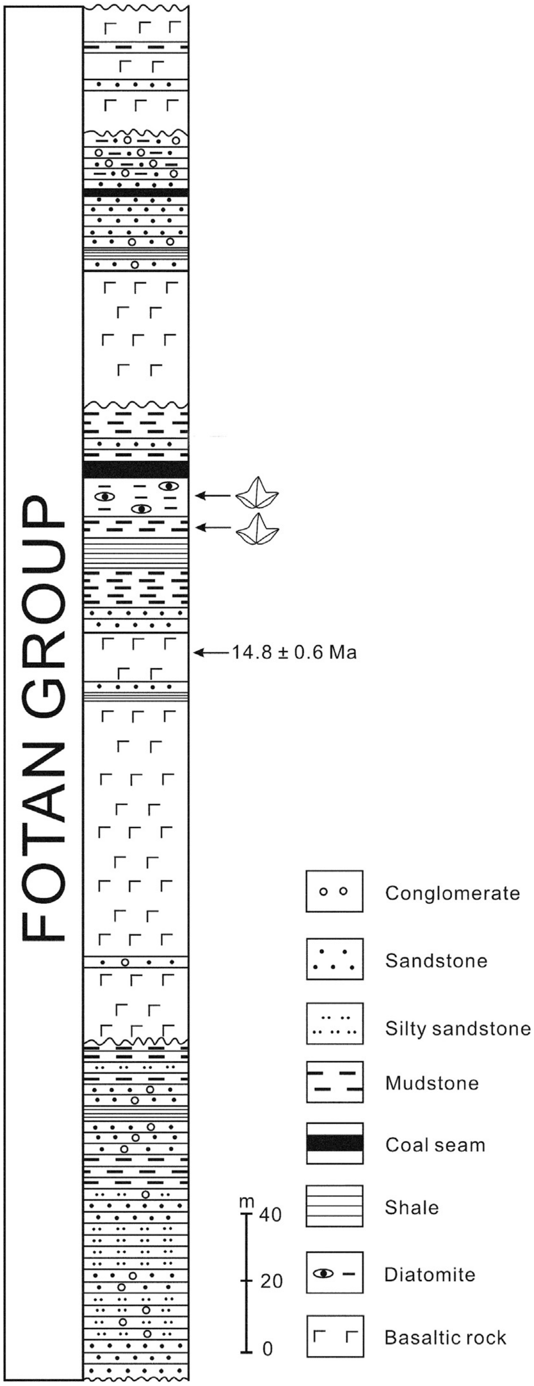


Fig. 2. Geological log of the Fotan section in Zhangpu County. Positions of the fossil-bearing layers are indicated, as well as the position of the radiometric dating.

were then plotted at the county level on a Chinese map using ArcGIS 9.3 (Environmental Systems Research Institute, Inc.). Detailed occurrences are given in appendix.

3. Systematics

Order Fabales Bromhead
Family Leguminosae Jussieu
BAUHINIA L.
Bauhinia fotana F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3A; Plate I, 1, 2)

Diagnosis: Leaf round to elliptic, bilobed, 6.2–8.3 cm long, 3.3–6.5 cm wide; lobes attached over half of the leaf length; base cordate, symmetrical; apex acute; margin entire; venation basal actinodromous, three to four main veins per lobe; the secondary veins usually stronger on the external side of primary veins.

Holotype: PB21577 (Plate I, 1; designated here).

Paratypes: PB21578 (Plate I, 2).

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *fotana* refers to Fotan group where the fossils occur.

Discussion: This species is represented by ten specimens in the fossil assemblage. The bilobed shape associated with the palmate venation is typical of the genus *Bauhinia* (Plate I, 3). *Bauhinia* is a member of the tribe Cercideae in family Leguminosae, groups around 300 species worldwide, including 47 species present in China. Because the fine venation of *B. fotana* is not well preserved, its morphological affinities with modern species are difficult to establish.

Comparison with other Asian fossils: Four fossils of *Bauhinia* have been reported in China: *B. larsenii* D.X. Zhang and Y.F. Chen from the Ningming Formation of Guangxi, South China (Chen and Zhang, 2005), *B. gracilis* J.R. Tao from the Paleocene of Heilongjiang, North-East China (Tao et al., 2000), *B. ningmingensis* Wang et al. and *B. cheniae* Wang et al. from the Oligocene Ningming Formation in Guangxi (Wang et al., 2014). They are all different from *B. fotana*: *B. larsenii* has a round base, *B. gracilis* has teeth, *B. ningmingensis* has bifoliate leaves, *B. cheniae* is deeply bifid 2/3 to 4/5 of laminar length.

Bauhinia ramthiensis Antal and Awasthi has been reported from the Siwalik of Darjeeling, India (Antal and Awasthi, 1993); it has many secondary veins joining the primaries, whereas secondary veins of *B. fotana* are only visible on the external side of the primaries and obscure between the primaries. *B. nepalensis* Awasthi and Prasad (1990) from the Siwalik of western Nepal has five primary veins per lobe, different from *B. fotana* the three to four main veins per lobe. *B. siwalika* Lakhanpal and Awasthi occurs in Bihar, India (Lakhanpal and Awasthi, 1984). *B. kachchhensis* Lakhanpal and Guleria reported from the early Miocene of Kachchh, India (Lakhanpal and Guleria, 1982) has four to six primary veins per lobe, more than these observed in *B. fotana*; the lamina is shorter than that of *B. fotana* (5.0 cm and more than 6.2 cm, respectively).

Because the *Bauhinia* leaves found in the Fotan flora are different from previously described Asian fossil *Bauhinia* leaves, we decided to describe them as a new species, *B. fotana*.

Biogeography: Fossil leaves of *Bauhinia* are found in China, India, and Nepal. *B. thonningi* Schumach. has been recorded from the Miocene of Uganda (Pickford et al., 1994). There are also several other older records of *Bauhinia* leaves being found in various places around the world such as Austria, Bolivia, Croatia, Czech Republic, Ecuador, Germany, Greece, Greenland, United States, and Vietnam (Unger, 1845, 1850, 1867; Newberry, 1895; Berry, 1908, 1916b, 1945; Knowlton, 1919; Chaney, 1933; Seward and Conway, 1935; Brown, 1956).

Fossil woods with affinities to *Bauhinia* are common in India: *B. miocenica* Mehrotra et al. from the Miocene of Assam (Merhrotra et al., 2011), *B. deomalica* Awasthi and Prakash from the Mio-Pliocene of Arunachal Pradesh (Awasthi and Prakash, 1986), *B. tertiara* Awasthi and Mehrotra from the Neogene of Nagaland (Awasthi and Mehrotra, 1990). *Bauhinium miocenicum* Trivedi and Panjwani and *B. palaeomalabaricum* Prakash and Prasad both come from the Siwalik of Uttar Pradesh (Prakash and Prasad, 1984; Trivedi and Panjwani, 1986).

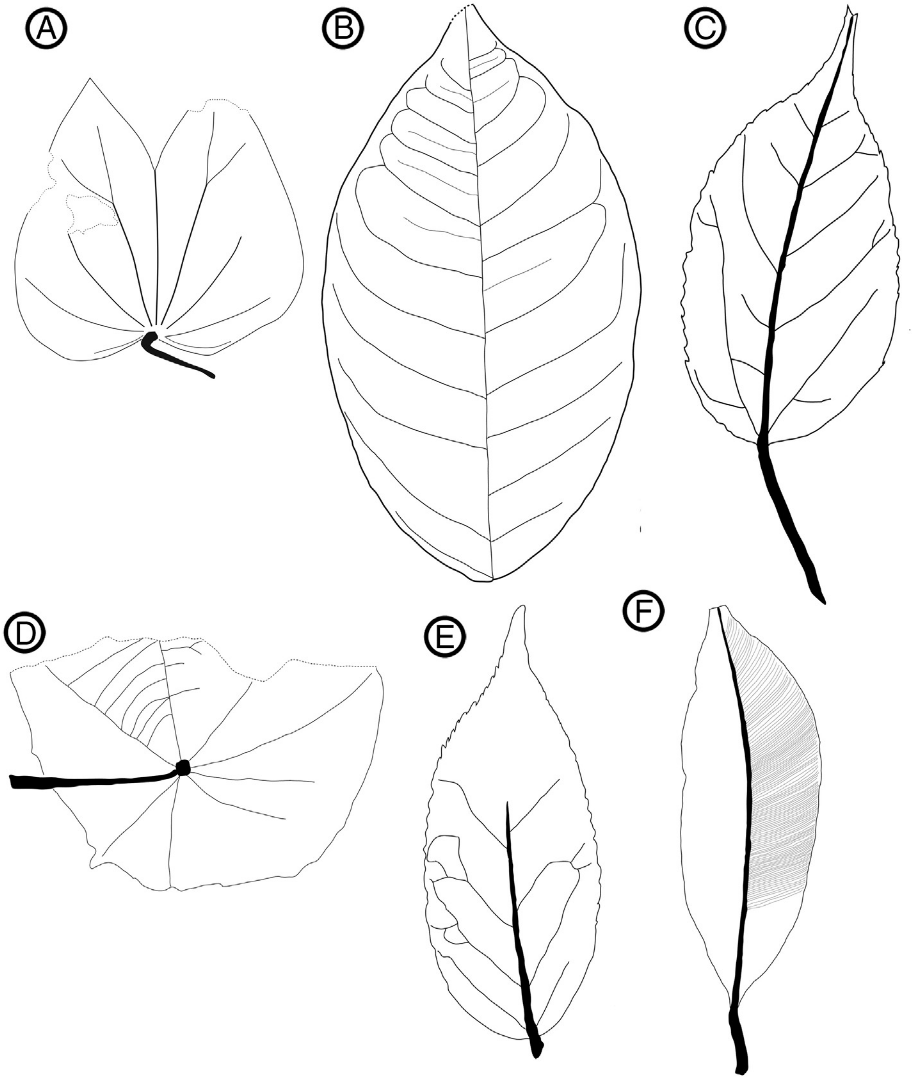


Fig. 3. Drawings of the fossil leaves. (A) *Bauhinia fotana*. (B) *Artocarpus basirotundatus*. (C) *Boehmeria fujianensis*. (D) *Macaranga stellata*. (E) *Flacourtia serrulata*. (F) *Calophyllum striatum*.

The present distribution of *Bauhinia* is mainly in tropical and subtropical regions with some species in more temperate areas.

Order Rosales Perleb

Family Moraceae Gaudichaud

ARTOCARPUS J. R. Forst. & G. Forst.

Artocarpus basirotundatus F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3B; Plate I, 4, 5)

Diagnosis: Leaf simple, elliptic, symmetrical, 4.2–11.3 cm long, 2.6–6.6 cm wide; base obtuse–round, symmetrical; apex shortly acuminate; margin entire; venation pinnate with more than 10 secondary veins on each side, eucamptodromous to brochidodromous towards the apex; secondary veins forming a 55–75° angle with the midvein; secondary veins more or less subopposite; intersecondaries sometimes present, irregular reticulate tertiary fabric; freely ending veinlets one branched to dichotomously branched; petiole strong.

Holotype: PB21587 (Plate I, 4; designated here).

Paratypes: PB21588, PB21589, PB21590a–b, PB21591, PB21592, PB21593, PB21594, PB21595, PB21596 (Plate I, 5), PB21597.

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

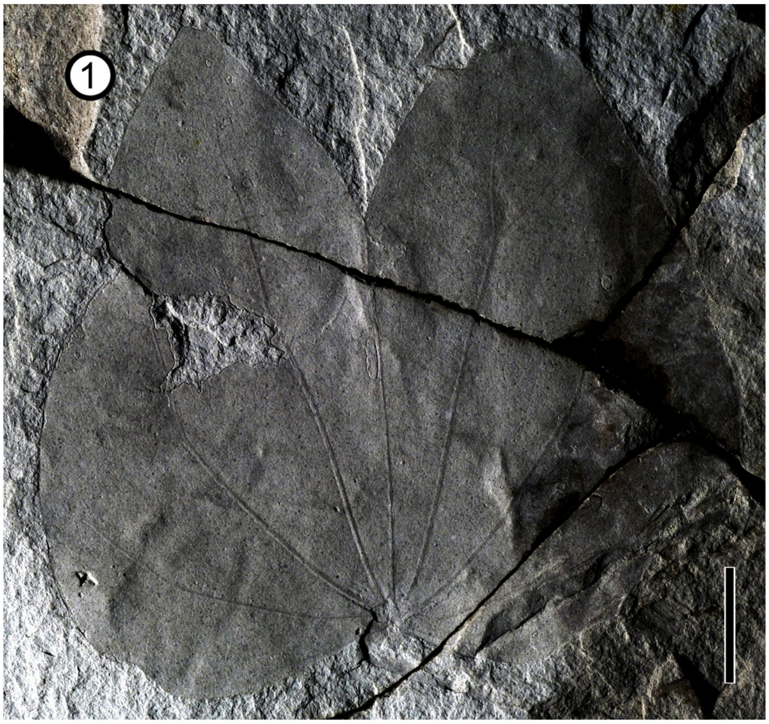
Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *basirotundatus* refers to the round base of the fossil leaves.

Plate I. 1, 2. *Bauhinia fotana* sp. nov.

1.	Full view of the holotype. PB21577. Scale bar = 1 cm.
2.	Details showing stronger secondary veins on the external side of primary veins. PB21578. Scale bar = 5 mm.
3.	*Bauhinia acuminata* L., extant species. Scale bar = 1 cm.
4, 5.	*Artocarpus basirotundatus* sp. nov.
4.	Full view of the holotype. PB21587. Scale bar = 1 cm.
5.	Details showing the finest venation. PB21596. Scale bar = 2 mm.
6.	*Artocarpus heterophyllus* Lam., extant species. Scale bar = 1 cm.
7.	Details showing the finest venation of *Artocarpus heterophyllus*, enlarged from 6. Scale bar =2 mm.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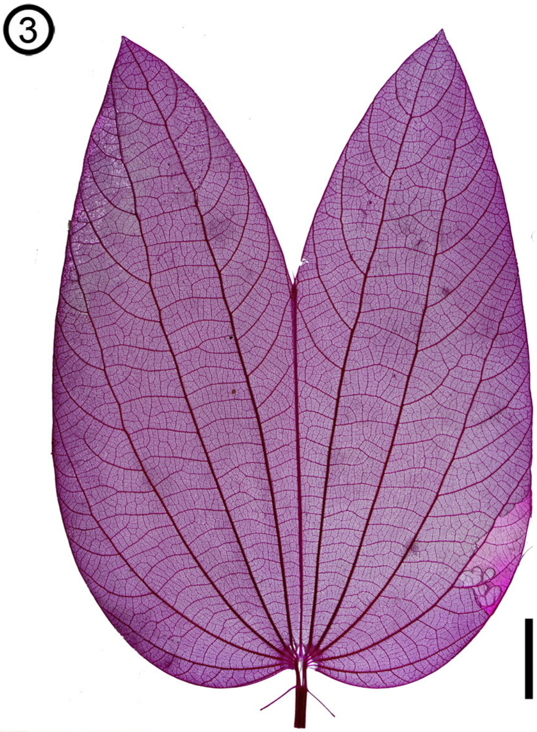
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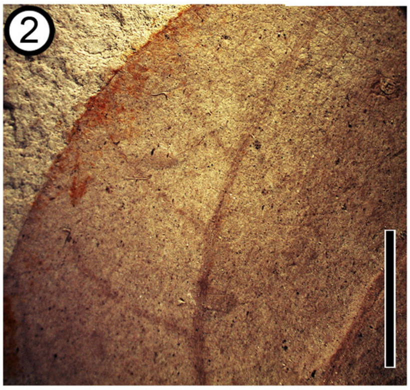
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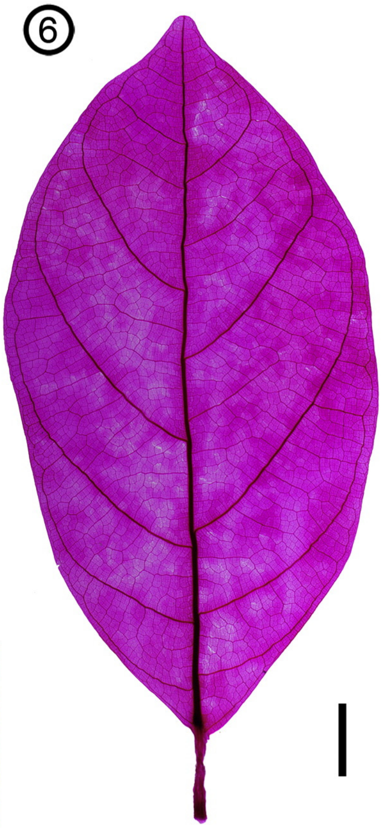
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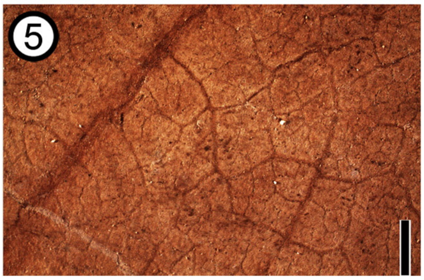
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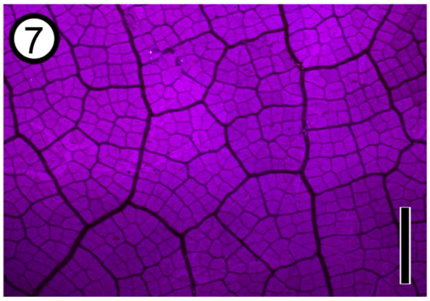
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Discussion: This species is represented by 11 specimens. The strong petiole, and the eucamptodromous venation becoming brochidodromous towards the apex are characteristic of *Artocarpus* (Plate I, 6). The irregular reticulate tertiary fabric is found both in the fossil (Plate I, 5) and in extant *Artocarpus* (Plate I, 7). *A. basirotundatus* differs from *A. heterophyllus* by a round base (Plate I, 4). *Ficus* L., another genus of Moraceae, can be excluded because the typical ternate venation near the base is lacking. *Artocarpus* groups 50 species worldwide, including 14 species growing in China.

Comparison with other Asian fossils: *Artocarpus garoensis* Bhattacharyya occurs in the Eocene of Meghalaya, India (Bhattacharyya, 1983). It differs from *A. basirotundatus* by its lobed leaves. *Artocarpus nepalensis* Prasad and Awasthi was reported from the Siwalik sediments of Nepal (Prasad and Awasthi, 1996; Prasad and Dwivedi, 2007); it differs from *A. basirotundatus* by its acute base.

Because the *Artocarpus* leaves from the Fotan flora are different from previously described Asian species, we describe them as a new species *A. basirotundatus*.

Biogeography: Several *Artocarpus* leaves are reported from the Cretaceous and Paleogene of North America, but are mostly lobed leaves (Berry, 1916a). Other fossil leaves that have been attributed to this genus are unlobed and entire-margined, also occur in North America (Collinson, 1989). *Artocarpus* fossil leaves have also been recorded from the Paleocene of Kazakhstan (Takhtajan, 1982). Fossil leaves with affinities to *Artocarpus* have been reported from the Cenozoic of Brazil (Krasser, 1903).

Fossil woods with affinities to *Artocarpus* have been reported from India. *Artocarpoxylon kartikcherraensis* Prakash and Lalitha occurs in the Neogene of Kerala, India (Srivastava, 1998), and in the Miocene Tipam sandstone of northeast India (Prakash et al., 1994). *Artocarpoxylon deccanensis* Mehrotra et al. was reported from the Deccan Intertappean beds of Mandla, India (Mehrotra et al., 1984).

This is the first fossil record of *Artocarpus* in China. The distribution of extant *Artocarpus* includes tropical and subtropical Asia and the Pacific Islands.

Family Urticaceae Jussieu

BOEHMERIA Jacq.

Boehmeria fujianensis F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3C; Plate II, 1–3)

Diagnosis: Leaf simple, elliptic, symmetrical, not peltate, 5.6 cm long, 2.5 cm wide; apex longly acuminate; base round and symmetrical; margin serrate; venation basal actinodromous with three major veins, 3–4 pairs of secondary veins towards the apex; the two lateral primary veins going up to the middle of the leaf; agrophic veins present, filling only a small part on the lamina; secondary veins brochidodromous; basal lateral primary veins forming a 30–35° angle with the primary veins, other secondary veins forming a 40–50° angle with the midvein; margin serrate; teeth small; teeth near the base smaller and more distantly spaced than the teeth close to the apex; petiole slender, over 2.4 cm long.

Holotype: PB21598 (Plate II, 1–3; designated here).

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *fujianensis* refers to Fujian Province where the fossil was found.

Discussion: This species is represented by only one complete specimen. The long slender petiole, the actinodromous venation, the symmetrical base and serrate margin indicates an urticaceous affinity. Within the Urticaceae, the Fujian fossil has more affinities with *Boehmeria* (Plate II, 4, 5) than with *Debregeasia* because of its elliptic shape. The fossil has also some similarities with *Pipturus*, but the petioles are generally short in this genus. *Boehmeria* groups 65 species worldwide, including 25 species growing in China. Amongst the extant Chinese species, *B. fujianensis* shows closer morphological affinities with *B. zollingeriana* Weddell.

Biogeography: *Boehmeria* has an extensive fossil record in the Cenozoic of Europe and Russia, its seeds have been retrieved from Germany, Lithuania, Belorussia, and Siberia (Dorofeev, 1963; Takhtajan, 1974; Mai and Walther, 1988; Mai, 2001; Nikitin, 2006).

Debregeasia fangi Tao from Lijiang, South-West China (Tao et al., 2000), is the only reported Urticaceae macrofossil in China. *Boehmeria fujianensis* is the first fossil record of *Boehmeria* in China.

Boehmeria has a mainly tropical to subtropical distribution; however, some species occur in temperate areas.

Order Malpighiales Martius

Family Euphorbiaceae Jussieu

MACARANGA Thouars

Macaranga stellata F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3D; Plate II, 6, 7).

Diagnosis: Leaf simple, symmetrical, peltate, 5.3 cm wide; base round; venation palmate brochidodromous, primary veins 10, secondary veins forming circles around the petiole insertion point, tertiary veins perpendicular to the secondary veins with a radial orientation; margin entire; petiole long, over 3.8 cm long.

Holotype: PB21599 (Plate II, 6, 7; designated here).

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *stellata* refers to the venation resembling a star.

Discussion: This species is represented by one specimen. The peltate leaf with the very characteristic venation pattern confirms the assignment to *Macaranga* (Plate II, 8). *Macaranga* leaves are difficult to discriminate from the leaves of *Mallotus* (Lee et al., 2010). Because peltate leaves are common in *Macaranga* but rare in *Mallotus* and because the fossil species has a strong petiole, the fossil leaf has a closer affinity with *Macaranga* (García Massini et al., 2010). *Macaranga* groups 260 species around the world, with 10 species occurring in China.

Comparison with other Asian fossils: Lee et al. (2010) erected a new fossil genus, *Malloranga* D. E. Lee et al., for fossils that are difficult to assign either to *Macaranga* or *Mallotus*. The diagnosis of this organ genus clearly refers to a subpeltate state; because *Macaranga stellata* is clearly peltate, it cannot be included into this genus. Nucete et al. (2012) made a comprehensive review for the fossil records of *Macaranga*. A putative *M. thompsonii* Merr. has been reported from the Neogene on the Mariana Islands (Fosberg and Corwin, 1958), but the specimen is only poorly preserved. *M. siwalika* Anatal and Awasthi has been reported from the Miocene of India (Antal and Awasthi, 1993), it has a craspedodromous venation whereas *M. stellata* has a brochidodromous venation. *M.* cf. *denticulata* has been recorded in the Siwalik of Arunachal Pradesh (Khan et al., 2011), but has teeth on the contrary to *M. stellata*.

Because the *Macaranga* leaf from the Fotan flora is different from all previously described Asian fossil of this genus, we assigned it to a new species, *M. stellata*.

Biogeography: Besides the Asian records, *Macaranga* sp. has been reported from the Oligocene of Ethiopia (García Massini et al., 2010; Currano et al., 2011). *Macaranga* leaves have also been reported from the Paleogene of northwestern North America (Wolfe, 1968; Wolfe, 1972).

This is the first fossil record of *Macaranga* in China. The distribution of extant *Macaranga* includes tropical Africa, Asia, Madagascar, Australia, and the Pacific Islands.

Family Salicaceae Mirbel

FLACOURTIA Comm. ex L'Hér.

Flacourtia serrulata F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3E; Plate III, 1, 2).

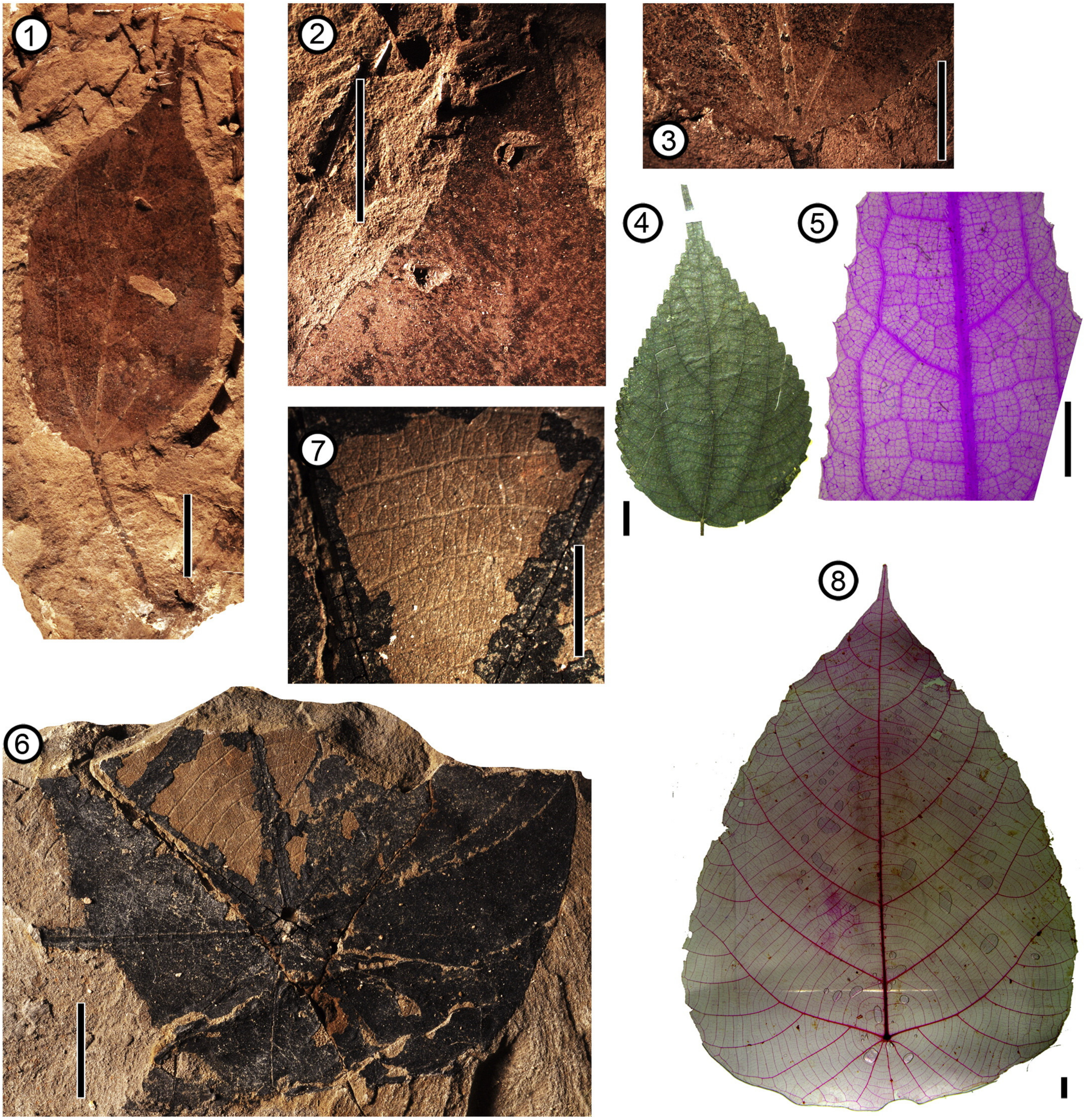

Plate II. 1, 2. *Boehmeria fujianensis* sp. nov. PB21598.

1. Full view of the holotype. Scale bar = 1 cm.
2. Details showing the acuminate apex and teeth, enlarged from 1. Scale bar = 5 mm.
3. Details of the lamina base showing the ternate basal venation and the smaller teeth, enlarged from 1. Scale bar = 5 mm.
4. *Boehmeria zollingeriana* Weddell, extant species, G.D. Tao 19755 (HITB). Scale bar = 1 cm.
5. *Boehmeria longispica* Steud., extant species. Scale bar = 2 mm.

6, 7. *Macaranga stellata* sp. nov. PB21599.

6. Full view of the holotype. Scale bar = 1 cm.
7. Details showing the tertiary venation, from 6. Scale bar = 5 mm.
8. *Macaranga kurzii* Pax & K.Hoffm., extant species. Scale bars = 1 cm.

Diagnosis: Leaf simple, symmetrical, elliptic, not peltate, 6.8–6.9 cm long, 2.7 cm wide; apex acuminate; acumen 1.1 cm long; base round; margin serrulate; teeth regular and spherulate; 4.5 teeth per cm; venation pinnate, semicraspedodromous; secondary veins opposite at the base to alternate upwards, decurrent; secondary veins form a 35–45° angle with the midvein; agrophic veins absent; petiole short, 0.1–0.2 cm long.

Holotype: PB21600 (Plate III, 1; designated here).

Paratype: PB21601 (Plate III, 2).

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *serrulata* refers to the serrulate margin of the fossil leaves.

Discussion: This species is represented by two specimens. The pinnate venation associated with spherulate glands on the teeth indicates a salicaceous affinity (Plate III, 2, 4). The tooth gland of the fossil appears to be outside of the margin (Plate III, 2) whereas the gland is inside the margin in the extant specimen (Plate III, 4); we think this difference might be due to the preservation. The teeth are otherwise similar with a long convex basal flank and a very short apical flank. The genus *Flacourtia* is the most probable because the first secondaries are basal and there is no agrophic vein (Plate III, 3). *Flacourtia* is a small genus of 15 to 17 species, with five of them occurring in China. The modern distribution is in tropical Africa and tropical Asia. *Flacourtia serrulata* has morphological affinities with *F. ramontchi* L'Héritier but differs in having a higher number of veins per centimetre, a longer acumen, a more round base, and a less elongate brochidodromy. Members of the former Flacourtiaceae family have been included in the Salicaceae based on molecular evidence (Chase et al., 2002).

Comparison with other Asian fossils: *Flacourtia nepalensis* Awasthi and Prasad was described from the Siwalik sediments of western Nepal (Awasthi and Prasad, 1990). The authors suggested its affinity with extant *F. ramontchi* (Awasthi and Prasad, 1990). However, this fossil can be easily distinguished from the Fujian fossils by its round apex. *F. tertiara* Prasad and Awasthi has also been described from the Siwalik sediments of Nepal (Prasad and Awasthi, 1996); it has an acute base, differing from the round base of *F. serrulata*. Therefore, the *Flacourtia* leaves of the Fotan flora have been described as a new species.

Biogeography: Besides the Asian record, leaves formerly belonging to the Flacourtiaceae family have been described in the Cretaceous–Paleogene of North America (Johnson, 2002; Wilf et al., 2006), and the Siwalik of India (Antal and Awasthi, 1993). Fossil seeds belonging to the former Flacourtiaceae (genus *Oncoba*) have been reported from the London Clay (Chandler, 1961). Fossil woods belonging to the former Flacourtiaceae family have been reported from the Cenozoic of Assam (Prakash and Tripathi, 1972). *F. serrulata* is the first record of *Flacourtia* in China, and the first record of the former Flacourtiaceae in this country.

Family Calophyllaceae J. Agardh

CALOPHYLLUM L.

Calophyllum striatum F. M. B. Jacques, G. L. Shi & Z. K. Zhou sp. nov. (Fig. 3F; Plate III, 5–7; Plate IV, 1, 2).

Diagnosis: Leaf simple, symmetrical, elliptic, not peltate, 3.3–8.2 cm long, 1.4–5.2 cm wide; margin entire, apex acuminate, base cuneate; venation pinnate, secondary veins excurrent, parallel, regularly spaced, unbranched, close to each other and uniting in a marginal vein; angle between the secondaries to midvein decreasing towards apex: from 65–80° near the base to 45–55° near the apex; tertiary veins not visible, petiolate striate; leaf amphistomatic; epidermal cells jigsaw-puzzle-like, with anticlinal wall Ω-shaped undulate, regular, stomata anisocytic, 24–27 μm long, 22–24 μm wide.

Holotype: PB21602a, b (part and counterpart; Plate III, 5; designated here).

Paratypes: PB21603, PB21604, PB21605, PB21606, PB21607, PB21608, PB21609, PB21610, PB21611, PB21612, PB21613, PB21614, PB21615 (Plate IV, 1, 2), PB21616, PB21617, PB21618, PB21619, PB21620, PB21621, PB21622 (Plate III, 6, 7), PB21623, PB21624, PB21625, PB21626, PB21627.

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.

Type Locality: Lindai Village (24°12′N, 117°53′E), Zhangpu County, Fujian Province, China.

Stratigraphy: Middle part of the Fotan group, Langhian stage (middle Miocene).

Etymology: The Latin epithet *striatum* is chosen in reference to the striate petiole.

Discussion: This species is common in the fossil assemblage with 26 specimens, including a few which are almost complete. The very special venation, with all the lamina filled by secondaries with obscure tertiaries is characteristic of *Calophyllum* (Plate III, 8, 9). The cuticle structure of the fossils confirms this assignment (Plate IV, 1–4). This genus has almost 200 species worldwide, with only four occurring in China today, all restricted to the tropical regions of China. The fossils mostly resemble *Calophyllum polyanthum* Wallich ex Choisy amongst extant Chinese species because of the cuneate base and acuminate apex. However, the genus is too large to check morphological affinities with all extant species worldwide.

Comparison with other Asian fossils: *Calophyllum suraikholaensis* Awasthi and Prasad has been reported from the Siwalik of Nepal (Awasthi and Prasad, 1990), the Siwalik of Arunachal Pradesh, India (Khan et al., 2011), the Siwalik of the Darjeeling District, India (Antal and Awasthi, 1993), the Palaeocene of Cherrapunji, India (Ambwani, 1991), and the Oligocene of Makum Coalfield in Assam, India (Awasthi and Mehrotra, 1995); it differs from *Calophyllum striatum* by a less cuneate base and an obtuse apex. *Calophyllum nathorsti* Geyler and *Calophyllum* sp. occur in the Cenozoic of Sumatra (Geyler, 1887; Kräusel, 1929), but have an obtuse base differencing them from *C. striatum*.

Because the *Calophyllum* leaves from the Fotan flora are different from all other described Asian *Calophyllum* fossils, we describe them as a new species, *Calophyllum striatum*.

Biogeography: Besides the Indian, Nepalese and Indonesian record, fossil leaves of *Calophyllum* have been recorded in Brazil, and Columbia. *Calophyllum pliocenicum* Krasser occurs in the Pliocene of Ouricanga, Brazil (Krasser, 1903), and it differs from the Fotan fossils in general shape. *Calophyllites mesaensis* Pons has been recorded from the Cenozoic of Columbia (Pons, 1978), but is smaller and has less secondaries than the Fotan fossils. *Calophyllum* leaves have also been reported from the Upper Eocene of Texas (Berry, 1916a).

Fossil woods with affinity to *Calophyllum* have also been recorded. *Calophylloxylon indicum* Lakhanpal and Awasthi has been reported from the Cenozoic of South India (Lakhanpal and Awasthi, 1964). *Calophylloxylon gogalacherraensis* Prakash et al. and *Calophylloxylon eoniphyllum* Prakash occur in the Miocene of Tipam, India (Prakash et al., 1994). *Calophyllum* woods have also been reported from the Neogene of Indonesia (Kramer, 1974) and Ethiopia (Lemoigne, 1978).

Calophyllum striatum is the first fossil record of the genus in China, contrasting with its long fossil history in India. Extant *Calophyllum* has a pantropical distribution. This genus is sometimes an important component of dipterocarp forests (Ayyapan and Parthasarathy, 1999; Sambas and Siregar, 1999; Pascal et al., 2004; Rajkumar and Parthasarathy, 2008).

4. Discussion

4.1. Palaeoenvironmental significance

Eight genera have been described from the Fotan palaeoflora based on macro-remains: *Artocarpus*, *Bauhinia*, *Boehmeria*, *Calophyllum*, *Dipterocarpus*, *Flacourtia*, *Macaranga*, and *Shorea*. Amongst them, *Dipterocarpus*, *Shorea*, *Flacourtia* and *Calophyllum* are distributed only in tropical regions (Fig. 4; Table 1). Other components occur mainly in tropical areas, but with some representatives in subtropical regions and a very few in temperate areas (Fig. 4). However, their occurrence in the same fossil assemblage favours the reconstruction of a tropical flora: at present day, the only Chinese regions where the six genera of

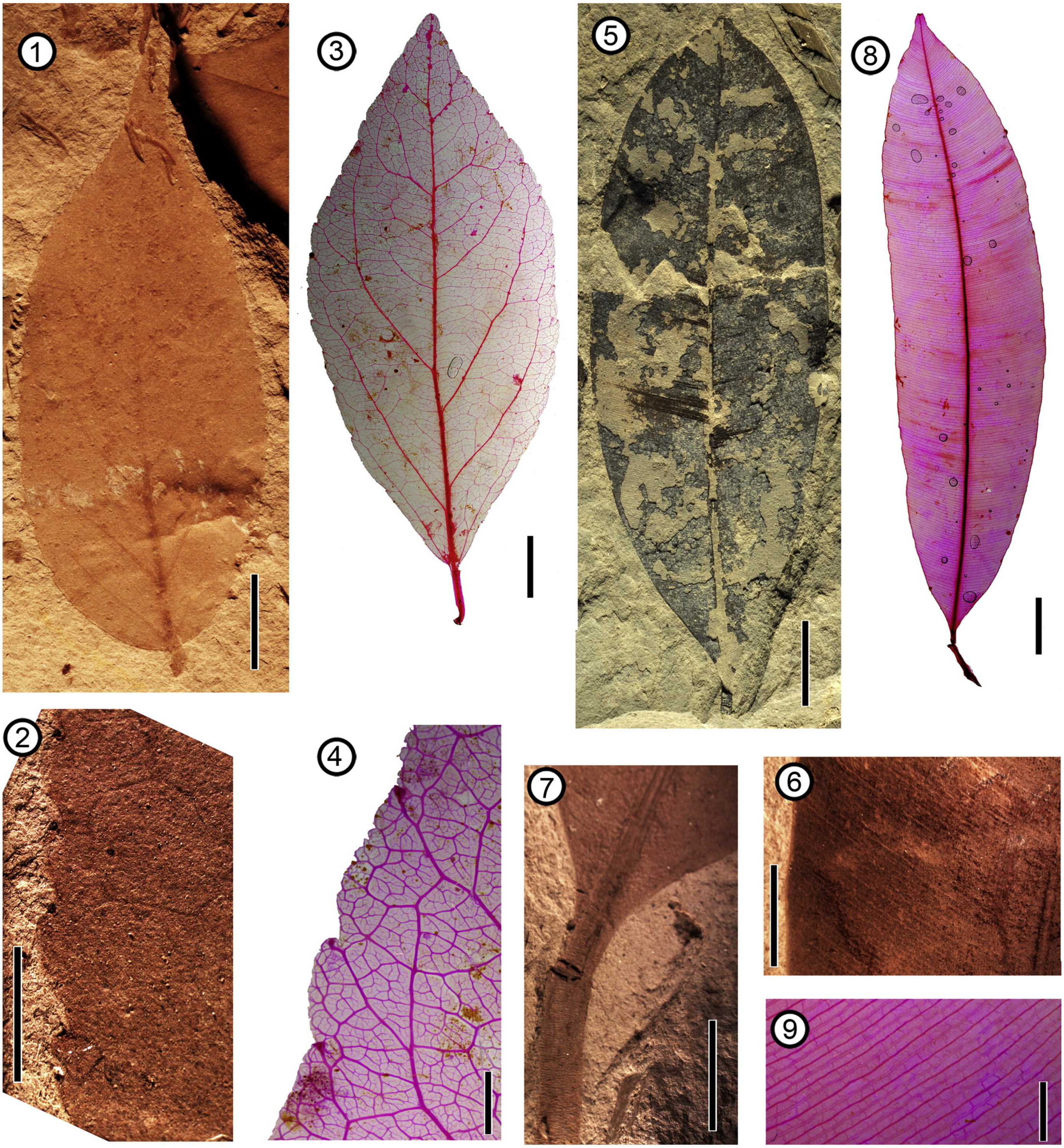

Plate III. 1, 2. *Flacourtia serrulata* sp. nov.

1. Full view of the holotype. PB21600. Scale bar = 1 cm.
2. Details showing the salicoid teeth. PB21601. Scale bar = 3 mm.
3. *Flacourtia ramontchi* L'Hér., extant species. Scale bar = 5 mm.
4. *Flacourtia ramontchi*, details showing the salicoid teeth from 3. Scale bar = 2 mm.

5, 6. *Calophyllum striatum* sp. nov.

5. Full view of the holotype. PB21602a. Scale bar = 1 cm.
6. Details showing the secondary venation filling the whole lamina. PB21606. Scale bar = 5 mm.
7. Details showing the striate petiole. PB21622. Scale bar = 5 mm.

8, 9. *Calophyllum polyanthum* Wall, extant species.

8. Scale bar = 1 cm.
9. Details showing the secondary venation, from 8. Scale bars = 2 mm.

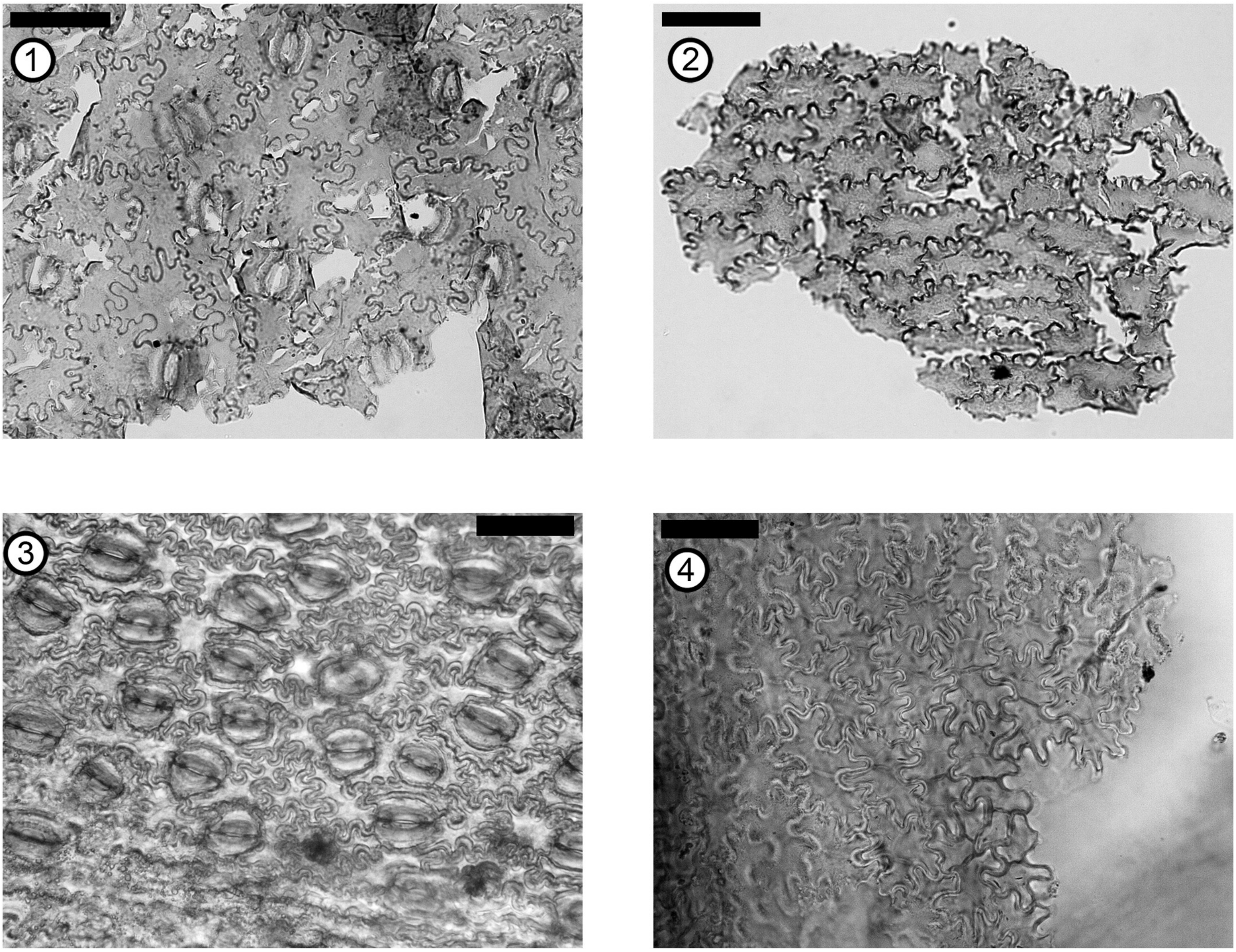

Plate IV. 1, 2. *Calophyllum striatum* sp. nov. from PB21615.

1. Upper cuticle. 2. Lower cuticle.
3, 4. *Calophyllum polyanthum* Wall, extant species, cultivated in XTBG.
3. Upper cuticle. 4. Lower cuticle. Note that the fossil species has a lower stomatal density than the extant species. All scale bars = 50 μm.

the new fossil species described here co-occur are in the tropical regions (Fig. 4H), which mostly corresponds to the modern distribution of *Dipterocarpus* in China (Fig. 4G). This floristic assemblage corresponds to the modern tropical rainforest: *Dipterocarpus*, *Calophyllum*, and *Artocarpus* are main components of the canopy of the giant evergreen forest of the Andaman Islands (Rajkumar and Parthasarathy, 2008), *Dipterocarpus* and *Calophyllum* are important components of the canopy of rainforests in Western Ghats, India, and Singkep Island in Indonesia (Ayyapan and Parthasarathy, 1999; Sambas and Siregar, 1999; Pascal et al., 2004), and *Flacourtia* is an important component of the middle storey of Western Ghats, India (Ayyapan and Parthasarathy, 1999). The presence of a tropical forest in South Fujian during the middle Miocene previously suggested by the Dipterocarpaceae fruits is, therefore, corroborated by these six new elements.

The Fotan flora indicates that a tropical climate was occurring in South Fujian during the Mid-Miocene Climatic Optimum (Zachos et al., 2001; Mosbrugger et al., 2005). Even if not all taxa occurring in the Fotan flora have been identified, the occurrence of several taxa with nearest living relatives requiring tropical climates clearly points towards a tropical climate. The global climate during the Miocene, warmer than present, is characterized by a weaker meridional temperature gradient (Bruch et al., 2006; Steppuhn et al., 2006, 2007; Utescher et al., 2011). Temperature anomalies during the Cenozoic were most significant at high latitudes in the Northern Hemisphere (Utescher et al., 2011). However, the Fotan palaeoflora demonstrates that the climate at low latitudes also changed: the limit between tropical and subtropical belts moved a few degrees northwards, at least north to South Fujian.

4.2. Biogeographic implications

The Fotan flora is unique amongst Chinese Neogene palaeofloras. Five of the genera reported in this paper, ie. *Artocarpus*, *Boehmeria*, *Macaranga*, *Flacourtia*, and *Calophyllum*, were not known previously from the Chinese fossil records. *Dipterocarpus zhengae* was also the first macrofossil record of Dipterocarpaceae in China (Shi and Li, 2010). *Shorea* is known from *Shorea fujianensis* Shi et al. in the Fotan flora (Shi et al., 2014a, 2014b), its only other known occurrence in China is *Shorea maomingensis* Feng et al. recently described from the late Eocene of South China (Feng et al., 2013). However, with the exception of *Boehmeria*, all these elements occur in fossil floras of India (Table 1). Such affinities raise the hypothesis of a floristic link between South Chinese and Indian palaeofloras. Sharing several components, some of them presumably dominant components, the Fotan palaeoflora and the Indian palaeofloras demonstrate that vegetation exchanges between the Indian Gondwanan land and Laurasia were strong at that time.

According to the out-of-India hypothesis, the uniqueness of the Indian flora was diluted by the floristic interchange with Asia after the collision started (Karanth, 2006). Based on the Fotan palaeoflora, we

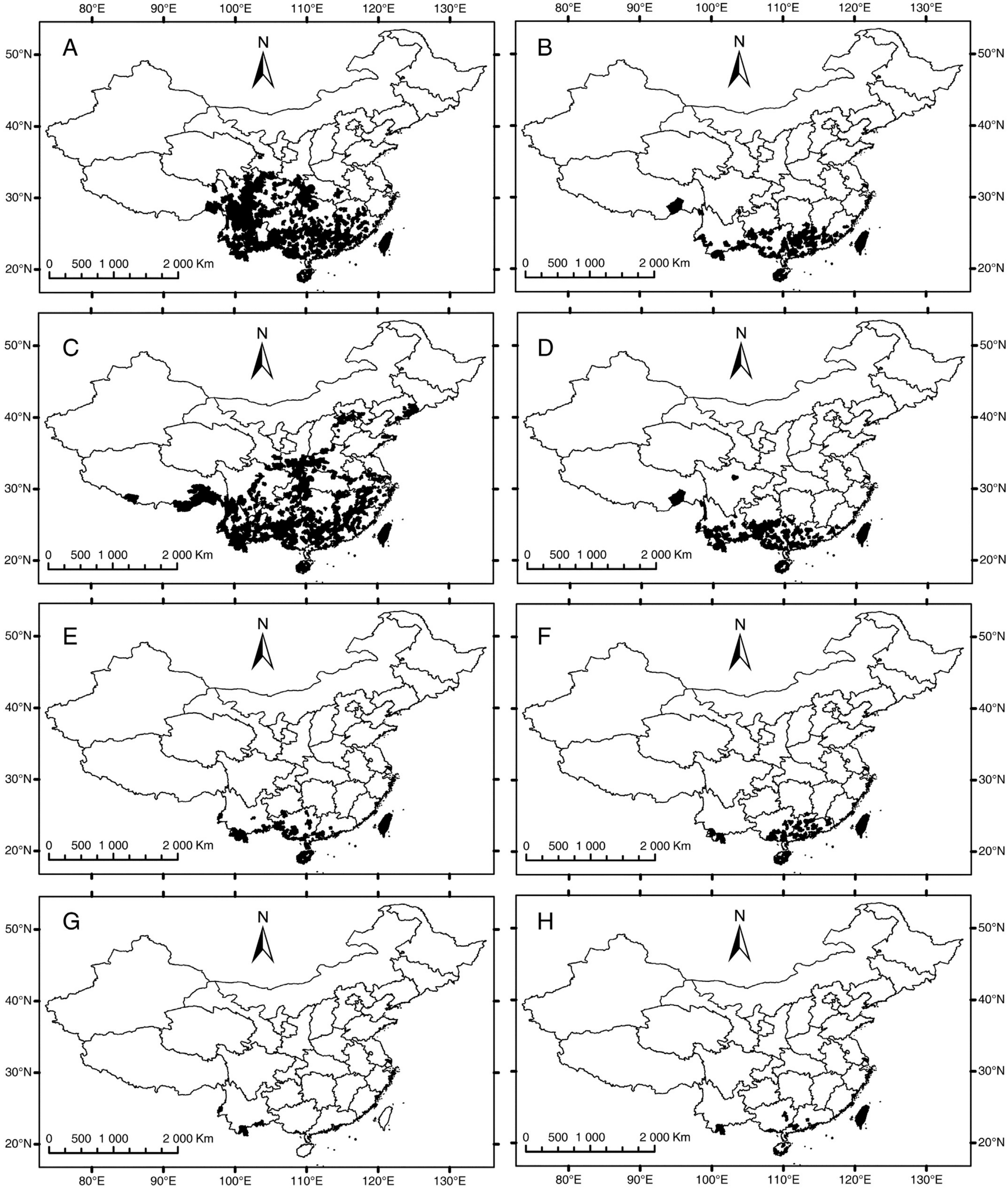

Fig. 4. Distribution of extant species in China at the county level (black areas). Distribution in Taiwan is only represented at the island level, and not at the county level. Not all islands of the South China Sea are represented. (A) *Bauhinia*. (B) *Artocarpus*. (C) *Boehmeria*. (D) *Macaranga*. (E) *Flacourtia*. (F) *Calophyllum*. (G) *Dipterocarpus*. (H) Intersection of the distributions of *Bauhinia*, *Artocarpus*, *Boehmeria*, *Macaranga*, *Flacourtia* and *Calophyllum*.

Table 1
Modern and fossil distributions of the elements of the Fotan flora.

Genus	First fossil occurrence in China	Present in Indian or Nepalese palaeofloras	Modern distribution
Dipterocarpus	Yes	Yes	Tropical South and South-East Asia
Shorea	No	Yes	Tropical South and South-East Asia
Bauhinia	No	Yes	Pantropical with some temperate elements
Boehmeria	Yes	No	Tropical, subtropical, and rarely temperate
Artocarpus	Yes	Yes	Tropical and subtropical Asia
Macaranga	Yes	Yes	Africa, tropical Asia, Australia, Madagascar, Pacific Islands
Flacourtia	Yes	Yes	Tropical Africa and Asia
Calophyllum	Yes	Yes	Pantropical, mainly in Asia

suggest that, under the out-of-India hypothesis, this dilution was already important at the time of the middle Miocene. However, our results do not imply that the out-of-India is true, but only imply a floristic link between Chinese and Indian palaeofloras. Exchanges from China to India, India to China, along both directions or originating from a third region could explain the observed link.

Mehrotra et al. (2005) compared the Tertiary flora of southwest China and northeast India. They concluded that these palaeofloras were quite different. The southwestern Chinese palaeofloras are characterized by temperate and subtropical elements, whereas the Indian palaeofloras are typically tropical (Mehrotra et al., 2005). Indeed, late Miocene macrofloras of Yunnan, like Lincang, Xiaolongtan, and Xianfeng, have no typically tropical elements and have cold month temperatures incompatible with a tropical forest (Xia et al., 2009; Jacques et al., 2011b, 2011c; Xing et al., 2012). The Fotan palaeoflora gives a totally new picture. The tropical character of this southeast Chinese flora is conspicuous. It also shows clear affinities with the Indian palaeofloras. Pollen of Dipterocarpaceae, *Bauhinia*, and *Calophyllum* has also been retrieved from the middle Miocene Chiang Muan basin, Thailand (Songtham et al., 2004). *Dipterocarpus* and *Calophyllum* have also been found in the Cenozoic of Sumatra and Borneo (Geyler, 1887; Kräusel, 1929). All of these regions have tropical flora. The evergreen rainforest expanded in South-East Asia in the later part of the early Miocene (Morley, 2000). The Fotan flora demonstrates that the rainforest in the middle Miocene was even more widespread in Asia than it is at present day. Other elements, such as Fagaceae, Lauraceae, and *Liquidambar*, are present in the Fotan flora (unpublished data), but they are not clear biogeographic markers.

We suggest that during the Mid-Miocene Climatic Optimum (Zachos et al., 2001; Mosbrugger et al., 2005) the tropical rainforest could have moved northwards up to South Fujian. However, this tropical rainforest was not recorded in the middle Miocene in most parts of Yunnan, maybe due to the local topography: exhumation of Diancang mountains and Ailaoshan mountains started before the middle Miocene (Schoenmbohm et al., 2004; Cao et al., 2011). During the Mid-Miocene, there were already floristic exchanges between India and China. The migration route was probably through South-East Asia and linked India with southeast China and not southwest China (Fig. 5). The collision between the Indian plate, a Gondwanan land, and the Eurasian plate started in Paleocene or Eocene (Yin, 2010; Chatterjee et al., 2013). Therefore, India and Eurasia were already linked during the middle Miocene, when the Fotan flora shows affinities with Indian palaeofloras. The sinistral motion of the Red River Fault, which extruded Indochina, stopped at around 15 Ma (Replumaz and Tapponnier, 2003), just before the middle Miocene. Therefore, South-East Asia was about at its present position during the middle Miocene. Mid-Miocene

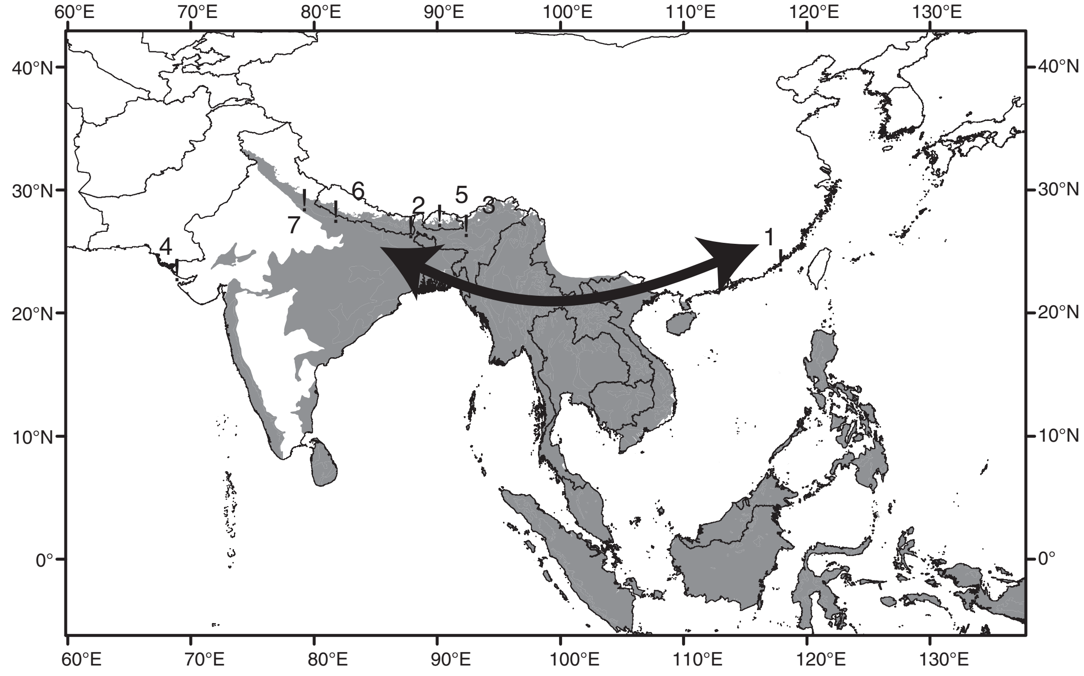

Fig. 5. Geography of Asian tropical forest. Modern distribution of tropical forest is indicated in grey; data of global ecological zones from www.fao.org (consulted on 06.29.2013); tropical rainforest, tropical moist deciduous forest, tropical dry forest and tropical mountain system were considered as tropical forests. Neogene tropical fossil sites indicated by points: 1, Fotan floras (this study); 2, Oodlabari (Antal and Awasthi, 1993); 3, Papumpare (Khan et al., 2011); 4, Kachchh (Lakhanpal and Guleria, 1982); 5, Makum (Awasthi and Mehrotra, 1995); 6, Surai Khola (Awasthi and Prasad, 1990); and 7, Kathgodam (Prasad, 1994). The double-head arrow indicates a possible route to explain the biogeographic affinities between the Fotan flora and the Indian palaeofloras.

palaeogeography is consistent with a biogeographic link between India and South-East China. Moist forests were present in Indochina at least from the early Miocene (Morley, 2000), and Dipterocarpaceae were prominent in Thailand since that time (Morley, 2000). South-East Asia is, thus, a good candidate to explain the floristic link between India and South China. Our results suggest that there could have been strong floristic links between India, South-East Asia and South China during the middle Miocene, with a continuous tropical forest zone (Fig. 5).

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Appendix A. Modern distribution of the studied genera in China

Artocarpus:

Anlong, Baisha, Baoting, Boluo, Cangwu, Cangyuan, Ceheng, Changjiang, Chengmai, Chongyi, Conghua, Daguan, Dabu, Daxin, Dayu, Danzhou, Deqing, Dongfang, Donglan, Dongxing, Du'an, Fangchenggang, Fengshun, Fengkai, Dongfang, Gaoyao, Gaozhou, Gongcheng, Gongshan, Guangning, Guangzhou, Guiping, Hepu, Heping, Hekou, Heyuan, Hezhou, Honghe, Hua'an, Huaiji, Huanjiang, Huichang, Huiyang, Jiaoling, Jinping, Jinxiu, Jinghong, Jingxi, Lechang, Ledong, Liannan, Lianping, Lianshan, Lianzhou, Lingao, Lingshui, Longling, Longmen, Longzhou, Longlin, Luxi, Luoding, Malipo, Maguan, Maoming, Menghai, Mengla, Meetog, Napo, Napo, Nan'ao, Nandan, Nanjing, Nanning, Nanxiong, Ningming, Pingle, Pingnan, Pingyuan, Pingbian, Pubei, Qinzhou, Qingyuan, Qionghai, Qiongzhong, Raoping, Renhua, Rong, Ruyuan, Ruili, Sanjiang, Sanya, Xiamen, Shenzhen, Shixing, Shuangjiang, Taiwan, Taishan, Tian'e, Tianlin, Wanning, Wenshan, Wengyuan, Wuzhou, Wuhua, Xichou, Xinfeng, Xinyi, Xingning, Xuwen, Xunwu, Sanya, Yanshan, Yangchun, Yangjiang, Yangshan, Yizhang, Yingde, Yongtai, Yongxing, Yulin, Yuanjiang, Yunfu, Yunxiao, Zengcheng, Zhaoping, Zhenfeng, Zhenkang, Zhuhai, Zixing.

Bauhinia:

Aba(Ngawa), Anfu, Hanbin, Anlong, Anning, Anyuan, Anyue, Badong, Batang, Bose, Baoting, Binchuan, Bobai, Boluo, Butuo, Cangxi, Cangyuan, Ceheng, Zayuu, Qamdo, Changjiang, Chengdu, Chengkou, Chengjiang, Chengmai, Chishui, Wuyishan, Chongyi, Chongzuo, Chuxiong, Cili, Conghua, Daguan, Dali, Dabu, Daxin, Dayao, Dayu, Dazhu, Danba(Rongzhag), Danzhou, Dawu, Dao, Daocheng(Dabba), Deerong, Dechang, Dehua, Deeqeen, Deqing, Dianbai, Ding'an, Dingnan, Dongfang, Donglan, Dongxiangzu, Dongkou, Du'an, Doumen, Dushan, Panzhihua, Ebian, Emeishan, Eshan, Enshi, Eryuan, Fangchenggang, Fengshun, Fengkai, Fenggang, Fengqing, Fengshan, Fengjie, Fusui, Fugong, Fuzhou, Fuchuan, Fumin, Funing, Ganluo, Garzee, Dongfang, Gao'an, Gaoyao, Gejiu, Gengma, Gongcheng, Dujiangyan, Guanyang, Guangze, Guangchang, Guanghan, Guangnan, Guangning, Guangzhou, Guigang, Guixi, Guigang, Guiyang, Guilin, Haikou, Hanyuan, Hechuan, Hepu, Heping, Hechi, Hekou, Heyuan, Hezhou, Hefeng, Heqing, Heishui, Hengshan, Hua'an, Huaning, Huaping, Huaiji, Huanjiang, Huangping, Huichang, Huidong, Huili, Huize, Huidong, Huilai, Huiyang, Ji'an, Jianshi, Jianshui, Jianchuan, Jiange, Jiangcheng, Jiangchuan, Jianghua, Jiangjin, Jiangkou, Jiangyong, Jiaoling, Jiexi, Jinchuan(Quqeen), Jinping, Jinxiu, Jinyang, Jinggangshan, Jingdong, Jinggu, Jinghong, Jingxi, Jiulong(Gyaisi), Junlian, Kaiyuan, Kaili, Kangding(Dardo), Kunming, Laifeng, Lanzhou, Langao, Lancang, Le'an, Lechang, Ledong, Leibo, Lichuan, Li, Lijiang, Lichuan, Libo, Liannan, Lianping, Lianshan, Lianzhou, Lingui, Linwu, Lingchuan, Lingyun, Lingshui, Yongzhou, Liucheng, Liuzhou, Longchuan, Longling, Longmen, Longnan, Longshan, Longsheng, Longzhou, Longlin, Luding(Jagsamka), Lushui, Luchuan, Lufeng, Luchuan, Luxi, Luodian, Luoding, Huiyang, Luuchun, Malipo, Barkam, Maguan, Maguan, Mangkam, Maoming, Mao, Mengzi, Menghai, Mengla, Menglian, Miyi, Mianning, Mojiang, Muli, Muchuan, Napo, Nanchuan, Nandan, Nanfeng, Nanjiang, Nanjing, Nanning, Nanping, Jiuzhaigou, Nanxiong, Ninglang, Ningming, Ningyuan, Pengshui, Pingguo, Pinghe, Pingle, Pingnan, Pingyang, Pingyuan, Pingxiang, Pingbian, Pingshan, Pingxiang, Qidong, Qiaojia, Qinzhou, Qionghai, Qiongshan, Qiongzhong, Quannan, Quanzhou, Raoping, Renhua, Rong, Rongjiang, Rongshui, Ruyuan, Ruili, Sanjiang, Sanya, Sangzhi, Sha, Xiamen, Shantou, Shanglin, Shangrao, Shangsi, Shangyou, Shaoyang, Shenzhen, Shennongjia, Shicheng, Shimian, Shiping, Shiqian, Shixing, Shuangbai, Shuangjiang, Songpan(Sungqu), Songtao, Suichuan, Suining, Taiwan, Taiwan, Taishan, Taiwan, Sanming, Taihe, Taining, Taoyuan, Teng, Tian'e, Tianquan, Tianlin, Tianyang, Taiwan, Tongdao, Tonghai, Tongren, Wanning, Wanyuan, Wangmo, Weixin, Weixi, Wenshan, Wen, Wenchuan, Wengyuan, Wushan, Wuxi, Wuzhou, Wufeng, Wuhua, Wuding, Wudu, Wugang, Wuhan, Wuming, Xichang, Xichou, Xilin, Xianfeng, Xiangcheng(Qagcheeng), Hong Kong, Xiaojin, Xinfeng, Xinhui, Xinning, Xinping, Taiwan, Xinyi, Xing'an, Xingguo, Xingning, Xingren, Xingshan, Xingwen, Xingyi, Xuwen, Xuyong, Xuan'en, Xunwu, Sanya, Yajiang(Nyagquka), Yanbian, Yanjin, Yanting, Yanyuan, Yanshan, Yangchun, Yangjiang, Yangshan, Yangshuo, Yangbi, Yao'an, Yichang, Yifeng, Yizhou, Yizhang, Yiliang, Yimen, Yinjiang, Yingde, Yingjiang, Yongning, Yong'an, Yongchun, Yongfu, Yongren, Yongshan, Yongsheng, Yongshun, Yongxin, Yongxing, Yuxi, Yuanjiang, Yuanmou, Yuanyang, Yuanling, Yuexi, Yunfu, Yun, Yunxiao, Zhaoping, Shaoyang, Zhaoqing, Zhenfeng, Zhenkang, Zhenping, Zhenxiong, Zhijiang, Zhongdian, Zhuhai, Zixi, Zigui, Zijin, Ziyang.

Boehmeria:

Anfu, Hanbin, Anlong, Anyuan, Badong, Bama, Baisha, Bose, Baoxing, Baojing, Baoting, Benxi, Bijie, Binchuan, Bomi(Bowo), Boluo, Butuo, Cangwu, Cangyuan, Ceheng, Zayuu, Changjiang, Changli, Changping, Changshu, Juchao, Chengdu, Chengbu, Chengkou, Chengjiang, Chengmai, Chishui, Wuyishan, Chongyi, Chuzhou, Chuxiong, Chun'an, Conghua, Cona, Daguan, Dali, Dabu, Daxin, Zhangjiajie, Dayu, Dandong, Dandong, Danfeng, Dantu, Danyang, Danzhou, Dao, Daozhen, Debao, Dechang, Ruili, Dejiang, Deeqeen, Deqing, Dexing, Ding'an, Dingnan, Dongfang, Donglan, Dongxing, Dongkou, Du'an, Dushan, Ebian, Emeishan, Eshan, Enshi, Eryuan, Fangchenggang, Fengkai, Fengcheng, Fengqing, Fengshan, Fengjie, Foping, Fusui, Fuliang, Fugong, Fuping, Fuchuan, Fumin, Funing, Ganyu, Gaoyao, Gengma, Gongcheng, Gongshan, Guzhang, Guangchang, Guangfeng, Guangshui, Guangzhou, Guixi, Guigang, Guiyang, Guilin, Beijing, Hanzhong, Hangzhou, Heping, Hechi, Hekou, Hezhou, Hefeng, Heqing, Hengshan, Hu, Huaning, Hua, Huayin, Huaiji, Huairou, Huanjiang, Huanren, Huangshan, Huixian, Huichang, Huitong, Huize, Huidong, Huiyang, Huoshan, Gyirong, Jiyuan, Jixi, Ji, Taiwan, Jianning, Jianshi, Jianshui, Jianyang, Jiangkou, Jiangning Qu, Jiangpu, Jiangyin, Jiangle, Jiaoling, Jinping, Jinxiu, Jinyang, Jinzhai, Jincheng, Jinggangshan, Jingdezhen, Jingdong, Jinggu, Jinghong, Jing'an, Jingxi, Jiujiang, Jurong, Danjiangkou, Kaihua, Kaili, Kang, Kuandian, Kunming, Laifeng, Laiyuan, Lanping, Langao, Lantian, Lancang, Lechang, Ledong, Leping, Leye, Leishan, Lichuan, Lijiang, Liandu, Lichuan, Libo, Liyang, Liancheng, Liannan, Lianping, Lianshan, Lianzhou, Lianyungang, Lianhua, Lianghe, Nyingchi, Linzhou, Lin'an, Lincang, Lingui, Lingbao, Lingyun, Lingshu, Luhe, Longling, Longmen, Longnan, Longquan, Longsheng, Longzhou, Long'an, Longlin, Lushi, Lushan, Jiujiang, Luding(Jagsamka), Lushui, Luxi, Lushan, Lufeng, Luxi, Luanchuan, Luocheng, Luodian, Luoding, Luoping, Luuchun, Luueyang, Malipo, Maguan, Mashan, Maoming, Mao, Mei, Meigu, Menghai, Mengla, Menglian, Mile, Mian, Mojiang, Meetog, Yantai, Muli, Napo, Nan'ao, Nanchuan, Nandan, Nanfeng, Nanhai, Nanjing, Nanjing, Nankang, Nanning, Nanping, Nanxiong, Nanyang, Hengshan, Neiqiu, Neixiang, Nyalam, Ningbo, Ningdu, Jinggangshan, Ningming, Ningqiang, Ningshan, Ningyuan, Panzhihua, Pan, Pingguo, Pingle, Pingli, Pinglu, Pingnan, Pingyuan, Pingxiang, Pingbian, Pingshan, Pingxiang, Pu'an, Pu'er, Qixia, Qidong, Qimen, Yanshan, Longnan, Hongjiang, Qinyang, Qingdao, Qingzhen, Qionghai, Qiongzhong, Quanzhou, Raoping, Renhua, Rongcheng, Rong, Rongjiang, Rongshui, Ruyang, Ruyuan, Rui'an, Ruichang, Ruijin, Sandu, Sanjiang, Sangzhi, Xiamen, Shanyang, Shangcheng, Shangnan, Shangzhou, Shangzhou, Shanghang, Shanglin, Shangrao, Shangsi, Shangyou, Shaowu, Shenzhen, Shennongjia, Shizong, Shibing, Shicheng, Shilin, Shimian, Shiqian, Shiquan, Shizhu, Shixing, Shucheng, Shuangbai, Shuangjiang, Shunchang, Simao, Songtao, Songxi, Song, Suzhou, Suichang, Suichuan, Taiwan, Taishan, Taibai, Taining, Tengchong, Teng, Tian'e, Tianquan, Tianshui, Tiantai, Tiandong, Tianlin, Tianyang, Tongcheng, Tonghai, Tongshan, Tongshi, Tongbai, Tonggu, Huangshan, Wanning, Wanyuan, Wanzai, Wangmo, Weixi, Weinan, Yu, Wenling, Wenshan, Wen, Wenchuan, Wengyuan, Weng'an, Wushan, Wuxi, Wuzhong, Wuzhou, Wugang, Wulong, Wuming, Wuning, Wuyishan, Wuyi, Xichou, Xilin, Ximeng, Xixia, She, Xianfeng, Hong Kong, Xiangzhou, Xinbin, Xinfeng, Xinning, Xinping, Xin, Xinxing, Taiwan, Xindu, Xinyang, Xinyi, Xingzi, Xing'an, Xingguo, Xinglong, Xingshan, Xingyi, Xiuning, Xiushui, Xiuwen, Xuan'en, Xunyang, Xundian, Xunwu, Yanhe, Yanbian, Yanjin, Yanshan, Yangcheng, Yangchun, Yangjiang, Yangshan, Yangshuo, Yang, Yangbi, Yihuang, Yiliang, Yixing, Yizhang, Yimen, Yi, Yin, Yingde, Yingjing, Yingjiang, Yongning, Yong'an, Yongfu, Yongshun, Yongxin, Yongxiu, Youyang, Yudu, Yulin, Yushan, Yunan, Yuanjiang, Yuanmou, Yuanyang, Yuexi, Yuexi, Yunfu, Yun, Zhashui, Zhangjiakou, Zhangping, Zhaoping, Zhen'an, Ningbo, Zhenjiang, Zhenkang, Zhenxiong, Zhengding, Zhijiang, Zhongdian, Zhouzhi, Zhuhai, Zhuji, Zhuxi, Zhuanghe, Zhuolu, Zixi, Ziyuan, Ziyang.

Calophyllum:

Baisha, Baoting, Bobai, Boluo, Chengmai, Deqing, Ding'an, Dongfang, Dongxing, Enping, Fangchenggang, Fengshun, Fengkai, Dongfang, Gaoyao, Guangzhou, Heyuan, Heng, Huaiji, Huidong, Jinxiu, Jinghong, Lancang, Lechang, Ledong, Lianjiang, Lingshui, Longmen, Luchuan, Mei, Mengla, Pingnan, Taiwan, Qinzhou, Qingyuan, Qionghai, Qiongshan, Qiongzhong, Sanya, Shangsi, Shenzhen, Taishan, Wanning, Wenchang, Wengyuan, Wuzhou, Xinhui, Xinyi, Sanya, Yangchun, Yingde, Yongning, Yulin, Yunfu, Zhaoping, Zhuhai.

Dipterocarpus:

Hekou, Jinping, Jinghong, Hekou, Mengla, Pingbian, Yingjiang.

Flacourtia:

Baisha, Bose, Baoting, Bobai, Changjiang, Chengmai, Daxin, Danzhou, Debao, Enping, Fangchenggang, Fusui, Funing, Dongfang, Guangzhou, Haikou, Hepu, Hekou, Jinping, Jinxiu, Jinning, Jinghong, Jingxi, Lancang, Ledong, Leizhou, Lingao, Lingui, Lingshui, Longzhou, Luodian, Maguan, Maoming, Mengshan, Menghai, Mengla, Menglian, Napo, Nanning, Ningming, Pingnan, Qionghai, Qiongshan, Qiongzhong, Ruili, Sanya, Simao, Taiwan, Tian'e, Wanning, Wenchang, Wenshan, Wuming, Xichou, Xinxing, Xinyi, Xuwen, Sanya, Yangchun, Yangjiang, Yingjiang, Yongning.

Macaranga:

Anlong, Bama, Baisha, Bose, Baoting, Beiliu, Binyang, Boluo, Cangwu, Cangyuan, Ceheng, Changjiang, Chengjiang, Chengmai, Dabu, Daxin, Danzhou, Debao, Ding'an, Donglan, Du'an, Enping, Fangchenggang, Fengshun, Fengshan, Fusui, Fugong, Fumin, Funing, Dongfang, Gaoyao, Gaozhou, Gengma, Gongshan, Guanyang, Guangzhou, Guiping, Hepu, Hechi, Hekou, Heyuan, Hezhou, Heng, Huaiji, Huanjiang, Huidong, Jinping, Jinxiu, Jingdong, Jinggu, Jinghong, Jingxi, Kunming, Ledong, Leye, Li, Libo, Lianjiang, Lingao, Lingyun, Lingshui, Longling, Longzhou, Longlin, Longchuan, Lushui, Luocheng, Luoping, Luuchun, Malipo, Maguan, Maoming, Mengshan, Menghai, Mengla, Menglian, Mojiang, Meetog, Napo, Nandan, Nanjing, Ningming, Pingguo, Pingnan, Pingbian, Taiwan, Pubei, Qinzhou, Qingyuan, Qionghai, Raoping, Rongshui, Ruili, Sanya, Shanglin, Shangsi, Shenzhen, Shuangbai, Shuangjiang, Simao, Taiwan, Taiwan, Taishan, Tian'e, Tianlin, Tianyang, Wanning, Wenshan, Wuming, Xichou, Xiangzhou, Xinyi, Xing'an, Sanya, Yanshan, Yangchun, Yangjiang, Yingde, Yingjiang, Yongde, Yongfu, Yuanjiang, Yun, Zhangzhou, Zhenfeng, Zhenkang, Zhuhai.

References

Ambwani, K., 1991. Leaf impressions belonging to the Tertiary age of North-East India. Phytomorphology 41, 139–146.

Antal, J.S., Awasthi, N., 1993. Fossil flora from the Himalayan foot-hills of Darjeeling District, West Bengal and its palaeoecological and phytogeographical significance. Palaeobotanist 42, 14–60.

APG, I.I.I., 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161, 105–121.

Ashton, P.S., 1982. Dipterocarpaceae. In: van Steenis, C.G.G.J. (Ed.), Flora Malesiana, Series 1. Spermatophyta vol. 9. Martnius-Nijhoff Publications, The Hague, The Netherlands, pp. 237–552.

Ashton, P.S., Gunatilleke, C.V.S., 1987. New light on the plant geography of Ceylon. I. Historical plant geography. J. Biogeogr. 14, 249–285.

Awasthi, N., Mehrotra, R.C., 1990. Some fossil woods from the Tipam sandstone of Assam and Nagaland. Palaeobotanist 38, 277–284.

Awasthi, N., Mehrotra, R.C., 1995. Oligocene flora from Makum Coalfield, Assam, India. Palaeobotanist 44, 157–188.

Awasthi, N., Prakash, Y., 1986. Fossil woods of *Kingiodendron* and *Bauhinia* from the Namsang beds of Deomali, Arunachal Pradesh. Palaeobotanist 35, 178–183.

Awasthi, N., Prasad, M., 1990. Siwalik plant fossils from Surai Khola area, western Nepal. Palaeobotanist 38, 298–318.

Ayyapan, N., Parthasarathy, N., 1999. Biodiversity inventory of trees in a large-scale permanent plot of tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. Biodivers. Conserv. 8, 1533–1554.

Bande, M.B., Prakash, U., 1986. The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-Malayan region. Rev. Palaeobot. Palynol. 49, 203–233.

Berry, E.W., 1908. A new Cretaceous *Bauhinia*. Torreya 8, 218–219.

Berry, E.W., 1916a. The lower Eocene floras of southeastern North America. U. S. Geol. Surv. Prof. Pap. 91, 1–481.

Berry, E.W., 1916b. The Upper Cretaceous floras of the world. Maryland Geological Survey Special Publicationpp. 183–313.

Berry, E.W., 1945. Fossil floras of southern Ecuador. Johns Hopkins Univ. Stud. Geol. 14, 93–150.

Bhattacharyya, B., 1983. Fossil plants from the Tura Formation (Eocene) in the Garo Hills, Meghalaya. Indian J. Earth Sci. 10, 1–10.

Brown, R.W., 1956. New items in Cretaceous and Tertiary floras of western United States. J. Wash. Acad. Sci. 46, 103–108.

Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I., Ivanov, D.A., 2006. Late Miocene climate in the circum-Alpine realm — a quantitative analysis of terrestrial palaeofloras. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 270–280.

Bureau of Geology, Mineral Resources of Fujian Province, 1985. Regional Geology of Fujian Province. Geology Publishing House, Beijing, China (in Chinese).

Cao, S.Y., Neubauer, F., Liu, J.L., Genser, J., Leiss, B., 2011. Exhumation of the Diancang Shan metamorphic complex along the Ailao Shan-Red River belt, southwestern Yunnan, China: Evidence from ^{40}Ar/^{39}Ar thermochronology. J. Asian Earth Sci. 42, 525–550.

Chandler, M.E.J., 1961. The lower Tertiary floras of Southern England I. Paleocene Floras. British Museum (Natural History), London, United Kingdom.

Chaney, R.W., 1933. A Tertiary flora from Uganda. J. Geol. 41, 706.

Chase, M.W., Zmarzty, S., Lledó, M.D., Wurdack, K.J., Swensen, S.M., Fay, M.F., 2002. When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid *rbc*L DNA sequences. Kew Bull. 57, 141–181.

Chatterjee, S., Goswami, A., Scotese, C.R., 2013. The longest voyage: tectonic, magmatic, and paleoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. Gondwana Res. 23, 238–267.

Chen, Y.F., Zhang, D.X., 2005. *Bauhinia larsenii*, a fossil legume from Guangxi, China. Bot. J. Linn. Soc. 147, 437–440.

Collinson, M.E., 1989. The fossil history of the Moraceae, Urticaceae (including Cecropiaceae), and Cannabaceae. In: Crane, P.R., Blackmore, S. (Eds.), Evolution, Systematics, and Fossil History of the Hamamelidae. 'Higher' Hamamelidae Vol. 2. Clarendon Press, Oxford, United Kingdom, pp. 319–339.

Conti, E., Eriksson, T., Schönenberg, J., Systma, K.J., Baum, D.A., 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. Evolution 56, 1931–1942.

Currano, E.D., Jacobs, B.F., Pan, A.D., Tabor, N.J., 2011. Inferring ecological disturbance in the fossil record: a case study from the late Oligocene of Ethiopia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 309, 242–252.

Dorofeev, P.I., 1963. Tertiary Floras of Western Siberia. Izdat. Akad. Nauk, Moscow/Leningrad, Russia (in Russian).

Dutta, S., Tripathi, S.M., Mallick, M., Mathews, R.P., Greenwood, P.F., Rao, M.R., Summons, R.E., 2011. Eocene out-of-India dispersal of Asian dipterocarps. Rev. Palaeobot. Palynol. 166, 63–68.

Feng, X.X., Tang, B., Kodrul, T.M., Jin, J.H., 2013. Winged fruits and associated leaves of *Shorea* (Dipterocarpaceae) from the Late Eocene of South China and their phytogeographic and paleoclimatic implications. Am. J. Bot. 100, 574–581.

Fosberg, F.R., Corwin, G., 1958. A fossil flora from Pagan, Mariana Islands. Pac. Sci. 12, 3–16.

García Massini, J.L., Jacobs, B.F., Tabor, N.J., 2010. Palaeobotany and sedimentology of late Oligocene terrestrial strata from the Northwestern Ethiopian plateau. Palaeontol. Electron. 13.1 (6A), 1–51.

Geyler, H.T., 1887. Über fossil Pflanzen von Labuan. Vega Exped. Vertenskaper Arbor. 4, 475–507.

Ghazoul, J., 2011. The challenge of inferring palaeoclimates from extant plant distributions: an example from *Dipterocarpus*. Rev. Palaeobot. Palynol. 173, 80–81.

Hickey, L.J., 1973. Classification of the architecture of dicotyledonous leaves. Am. J. Bot. 60, 17–33.

Ho, K., Chen, J., Lo, C., Zhao, H., 2003. ^{40}Ar–^{39}Ar dating and geochemical characteristics of late Cenozoic basaltic rocks from the Zhejiang-Fujian region, SE China: eruption ages, magma evolution and petrogenesis. Chem. Geol. 197, 287–318.

Jacques, F.M.B., Shi, G.L., Wang, W.M., 2011a. Reconstruction of Neogene zonal vegetation in South China using the Integrated Plant Record (IPR) analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307, 272–284.

Jacques, F.M.B., Guo, S.X., Su, T., Xing, Y.W., Huang, Y.J., Liu, Y.S., Ferguson, D.K., Zhou, Z.K., 2011b. Quantitative reconstruction of the Late Miocene monsoon climates of southwest China: a case study of the Lincang flora from Yunnan Province. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 318–327.

Jacques, F.M.B., Su, T., Spicer, R.A., Xing, Y.W., Huang, Y.J., Wang, W.M., Zhou, Z.K., 2011c. Leaf physiognomy and climate: are monsoon systems different? Glob. Planet. Chang. 76, 56–62.

Jacques, F.M.B., Shi, G.L., Wang, W.M., 2013. Neogene zonal vegetation of China and the evolution of the winter monsoon. Bull. Geosci. 88, 175–193.

Johnson, K.R., 2002. Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: vegetational response to climate change, the Cretaceous–Tertiary boundary event, and rapid marine transgression. Geol. Soc. Am. Spec. Pap. 361, 329–391.

Karanth, K.P., 2006. Out-of-India Gondwanan origin of some tropical Asian biota. Curr. Sci. 90, 789–792.

Khan, M.A., Ghosh, R., Bera, S., Spicer, R.A., Spicer, T.E.V., 2011. Floral diversity during Plio-Pleistocene Siwalik sedimentation (Kimin Formation) in Arunachal Pradesh, India, and its palaeoclimatic significance. Palaeobiodivers. Palaeoenviron. 91, 237–255.

Knowlton, F.H., 1919. A catalogue of the Mesozoic and Cenozoic plants of North America. U. S. Geol. Surv. Bull. 606, 1–815.

Kramer, K., 1974. Die Tertiären Hölzen Südost-Asiens (unter Ausschluβ der Dipterocarpaceae). 2. Palaeontogr. Abt. B 145, 1–150.

Krasser, R., 1903. Konstantin Ettingshausen's Studien über die fossile Flora von Ouriçanga in Brasilien. Sitzungsbericht der Akademie der Wissenschaften zu Wien 112 pp. 852–860.

Kräusel, R., 1929. Fossil Pflanzen aus dem Tertiär von Süd Sumatra. Verhandelingen der Geologie en Mijnbouw Genootschap voor Nederland en KolonienGeologie Serie 9 pp. 1–44.

Lakhanpal, R.N., Awasthi, N., 1964. Fossil woods of *Calophyllum* from the Tertiary of South India. Palaeobotanist 13, 328–336.

Lakhanpal, R.N., Awasthi, N., 1984. A late Tertiary florule from near Bikhnathoree in west Champaran District, Bihar. Symposium on Evolutionary Botany and Biostratigraphy, pp. 587–596.

Lakhanpal, R.N., Guleria, J.S., 1982. Plant remains from the Miocene of Kachchh, Western India. Palaeobotanist 30, 279–296.

Lee, D.E., Bannister, J.M., Raine, J.I., Conran, J.G., 2010. Euphorbiaceae: Acalyphoideae fossils from early Miocene New Zealand: *Mallotus–Macaranga* leaves, fruits, and inflorescence with *in situ Nyssapollenites endobalteus* pollen. Rev. Palaeobot. Palynol. 163, 127–138.

Lemoigne, Y., 1978. Flores tertiares de la haute vallée de l'Omo (Ethiopie). Palaeontogr. Abt. B 165, 89–157.

Mai, D.H., 2001. Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. III. Fundstellen und Palaeobiologie. Palaeontogr. Abt. B 258, 1–85.

Mai, D.H., Walther, H., 1988. Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie 7, 55–297.

Mehrotra, R.C., Prakash, U., Bande, M.B., 1984. Fossil woods of *Lophopetalum* and *Artocarpus* from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh, India. Palaeobotanist 32, 310–320.

Mehrotra, R.C., Liu, X.Q., Li, C.S., Wang, Y.F., Chauhan, M.S., 2005. Comparison of the Tertiary flora of southwest China and northeast India and its significance in the antiquity of the modern Himalayan flora. Rev. Palaeobot. Palynol. 135, 145–163.

Merhrotra, R.C., Bera, S.K., Basumatary, S.K., Srivastava, G., 2011. Study of fossil wood from the Middle–Late Miocene sediments of Dhemaji and Lakhimpur districts of Assam, India and its palaeoecological and palaeophytogeographical implications. J. Earth Syst. Sci. 120, 681–701.

Morley, R.J., 2000. Origin and Evolution of Tropical Rain Forest. John Wiley & Sons, Chichester, UK.

Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. Proc. Natl. Acad. Sci. 102, 14964–14969.

Newberry, J.S., 1895. The flora of Amboy Clay. U. S. Geol. Surv. Monogr. 26, 11–260.

Ni, J., Yu, G., Harrison, S.P., Prentice, I.C., 2010. Palaeovegetation in China during the late Quaternary: biome reconstructions based on a global scheme of plant functional types. Palaeogeogr. Palaeoclimatol. Palaeoecol. 289, 44–61.

Nikitin, V.P., 2006. Palaeocarpology and Stratigraphy of the Paleogene and the Neogene Strata in Asian Russia. Izd. SO RAN, Filial Geo, Novosibirsk, Russia (In Russian).

Niklas, K.J., 1997. The Evolutionary Biology of Plants. University of Chicago Press, Chicago, Illinois, USA.

Nucete, N., van Konijnenburg-van Cittert, J.H.A., van Welzen, P.C., 2012. Fossils and palaeontological distributions of *Macaranga* and *Mallotus* (Euphorbiaceae). Palaeogeogr. Palaeoclimatol. Palaeoecol. 353–355, 104–115.

Pascal, J.P., Ramesh, B.R., De Franceschi, D., 2004. Wet evergreen forest types of the southern western Ghats, India. Trop. Ecol. 45, 281–292.

Pickford, M., Mein, P., Senut, B., 1994. Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. S. Afr. J. Sci. 90, 227–230.

Pons, D., 1978. *Calophyllites mesaensis* nov. gen. nov. sp., Guttiferae fossile de Falan (Formation Mesa, Colombie). Congrès National des Sociétés Savantes de Nancy 103 pp. 201–209.

Prakash, U., Prasad, M., 1984. Wood of *Bauhinia* from the Siwalik beds of Uttar Pradesh, India. Palaeobotanist 32, 140–145.

Prakash, U., Tripathi, P.P., 1972. Fossil woods from the Tertiary of Assam. Palaeobotanist 21, 305–316.

Prakash, U., Vaidyanathan, L., Tripathi, P.P., 1994. Plant remains from the Tipam sandstones of Northeast India with remarks on the palaeoecology of the region during the Miocene. Palaeontogr. Abt. B 231, 113–146.

Prasad, M., 1990. Some more leaf-impressions from the Lower Siwalik sediments of Koilabas, Nepal. Palaeobotanist 37, 299–305.

Prasad, M., 1994. Siwalik (Middle Miocene) leaf impressions from the foothills of the Himalayas, India. Tertiary Res. 15, 53–90.

Prasad, M., Awasthi, N., 1996. Contribution to the Siwalik flora from Surai Khola sequence, western Nepal and its palaeoecological and phytogeographical implications. Palaeobotanist 43, 1–42.

Prasad, M., Dwivedi, H.D., 2007. Systematic study of the leaf impressions from the Churia Formation of Koilabas area, Nepal and their significance. Palaeobotanist 56, 139–154.

Rajkumar, M., Parthasarathy, N., 2008. Tree diversity and structure of Andaman giant evergreen forests, India. Taiwania 53, 356–368.

Replumaz, A., Tapponnier, P., 2003. Reconstruction of the deformed collision zone between India and Asia by backward motion of lithospheric blocks. J. Geophys. Res. 108, 2285.

Rust, J., Singh, H., Rana, R.S., McCann, T., Singh, L., Anderson, K., Sarkar, N., Nascimbene, P.C., Stebner, F., Thomas, J.C., Solórzano Kraemer, M., Williams, C.J., Engel, M.S., Sahni, A., Grimaldi, D., 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proc. Natl. Acad. Sci. 107, 18360–18365.

Sambas, E.N., Siregar, M., 1999. Floristic composition of Gunung Muncung forest, Singkep Island, Riau. Buletin Kebun Raya Indonesia 9 pp. 7–17 (In Indonesian with English abstract.).

Schoenmbohm, L.M., Whipple, K.X., Burchfiel, B.C., Chen, L., 2004. Geomorphic constraints on surface uplift, exhumation, and plateau growth in the Red River region, Yunnan Province, China. GSA Bull. 116, 895–909.

Seward, A.C., Conway, V.M., 1935. Additional Cretaceous plants from western Greenland. Kungliga Svenska vetenskapsakademiens handlingar 15 pp. 1–41.

Shi, G.L., Li, H.M., 2010. A fossil fruit wing of *Dipterocarpus* from the middle Miocene of Fujian, China and its palaeoclimatic significance. Rev. Palaeobot. Palynol. 162, 599–606.

Shi, G.L., Zhou, Z.Y., Xie, Z.M., 2012. A new Oligocene *Calocedrus* from South China and its implications for transpacific floristic exchanges. Am. J. Bot. 99, 108–120.

Shi, G.L., Dutta, S., Paul, S., Wang, B., Jacques, F.M.B., 2014a. Terpenoid compositions and botanical origins of Late Cretaceous and Miocene amber from China. PLoS ONE 9, e111303. http://dx.doi.org/10.1371/journal.pone.0111303.

Shi, G.L., Jacques, F.M.B., Li, H.M., 2014b. Winged fruits of *Shorea* (Dipterocarpaceae) from the Miocene of Southeast China: evidence for the northward extension of dipterocarps during the Mid-Miocene Climatic Optimum. Rev. Palaeobot. Palynol. 200, 97–107.

Shukla, A., Mehrotra, R.C., Guleria, J.S., 2013. Emergence and extinction of Dipterocarpaceae in western India with reference to climate change: fossil wood evidences. J. Earth Syst. Sci. 122, 1373–1386.

Songtham, W., Ratanasthien, B., Mildenhall, D.C., 2004. New species of algae *Actinastrum lagerheim* and *Closterium nitzsch* ex. Ralfs from middle Miocene sediments of Chiang Muan basin, Phayao, Thailand, with tropical pollen composition. Sci. Asia 30, 171–181.

Srivastava, R., 1998. Fossil wood of *Artocarpus* from Warkalli Formation of Kerala coast, India. Phytomorphology 48, 391–397.

Srivastava, G., Mehrotra, R.C., 2010. Tertiary flora of Northeast India vis-à-vis movement of the Indian Plate. Mem. Geol. Soc. India 75, 123–130.

Steppuhn, A., Micheels, A., Geiger, G., Mosbrugger, V., 2006. Reconstructing the Late Miocene climate and oceanic heat flux using the AGCM ECHAM4 coupled to a mixed-layer ocean model with adjusted flux correction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 399–423.

Steppuhn, A., Micheels, A., Bruch, A.A., Uhl, D., Utescher, T., Mosbrugger, V., 2007. The sensitivity of ECHAM4/ML to a double CO$_2$ scenario for the Late Miocene and the comparison to terrestrial proxy data. Glob. Planet. Chang. 57, 189–212.

Sun, X.J., Wang, P.X., 2005. How old is the Asian monsoon system? Palaeobotanical records from China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 222, 181–222.

Takhtajan, A., 1974. Magnolophyta Fossilia URSS I. Nauka, Leningrad, Russia (in Russian).

Takhtajan, A., 1982. Fossil Flowering Plants of the USSR II. Nauka, Leningrad, Russia (in Russian).

Tao, J.R., Zhou, Z.K., Liu, Y.S., 2000. The Evolution of the Late Cretaceous–Cenozoic Floras in China. Science Press, Beijing, China.

Trivedi, B., Panjwani, M., 1986. Fossil wood of *Bauhinia* from the Siwalik beds of Kalagargh. U.P. Geophytology 16, 66–69.

Unger, F., 1845. Plantarum fossilium. Apud. Leopoldum Voss, Leipzig, Germany.

Unger, F., 1850. Genera et species Plantarum fossilium. Apud Wilhelmum Braumüller, Vienna, Austria.

Unger, F., 1867. Die fossile Flora von Kumi auf der Insel Euboea. Denkschrift der Kaiserlichen Akademie der Wissenschaften, Wien 27 pp. 1–66.

Utescher, T., Bruch, A.A., Micheels, A., Mosbrugger, V., Popova, S., 2011. Cenozoic climate gradients in Eurasia — a palaeo-perspective on future climate change? Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 351–358.

Wang, Q., Song, Z.Q., Chen, Y.F., Shen, S., Li, Z.Y., 2014. Leaves and fruits of *Bauhinia* (Leguminosae, Caesalpinioideae, Cercideae) from the Oligocene Ningming Formation of Guangxi, South China and their biogeographic implications. BMC Evol. Biol. 14, 88.

Wilf, P., Labandeira, C.C., Johnson, K.R., Ellis, B., 2006. Decoupled plant and insect diversity after the end-Cretaceous extinction. Science 313, 1112–1115.

Wolfe, J.A., 1968. Paleogene Biostratigraphy of nonmarine rocks in King County, Washington. U. S. Geol. Surv. Prof. Pap. 571, 1–33.

Wolfe, J.A., 1972. An interpretation of Alaskan Tertiary floras. In: Graham, A. (Ed.), Floristics and Palaeofloristics of Asia and Eastern America. Elsevier, Amsterdam, The Netherlands, pp. 201–233.

Xia, K., Su, T., Liu, Y.S., Xing, Y.W., Jacques, F.M.B., Zhou, Z.K., 2009. Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 80–86.

Xing, Y.W., Utescher, T., Jacques, F.M.B., Su, T., Liu, Y.S., Huang, Y.J., Zhou, Z.K., 2012. Paleoclimatic estimation reveals a weak winter monsoon in southwestern China during the late Miocene: evidence from plant macrofossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 358–360, 19–26.

Yao, Y.F., Bruch, A.A., Mosbrugger, V., Li, C.S., 2011. Quantitative reconstruction of Miocene climate parameters and evolution in Southern China based on plant fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 291–307.

Yin, A., 2010. Cenozoic tectonic evolution of Asia: a preliminary synthesis. Tectonophysics 488, 293–295.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zheng, Y.H., 1984. *Marginipollis* (Lecythidaceae) from the upper Tertiary Fotan group in southern Fujian. Acta Palaeontol. Sin. 23, 764–767 (in Chinese with English abstract).

Zheng, Y.H., 2000. Pollen morphology of Dipterocarpaceae and fossil analogues in China. In: Song, Z.C. (Ed.), Palynofloras and Palynomorphs of China. Press of University of Science and Technology of China, Hefei, China, pp. 160–166.

Zheng, Y.H., Wang, W.X., 1994. Sequence of Miocene Fotan group in SE Fujian and its palyno-assemblages. Acta Palaeontol. Sin. 33, 200–216 (in Chinese with English abstract).

Zhu, H., 2006. Forest vegetation of Xishuangbanna, south China. For. Stud. China 8, 1–58.

Zhu, H., 2013. Geographical elements of seed plants suggest the boundary of the tropical zone in China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 16–22.