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Winged fruits of *Shorea* (Dipterocarpaceae) from the Miocene of Southeast China: Evidence for the northward extension of dipterocarps during the Mid-Miocene Climatic Optimum

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ABSTRACT

Dipterocarpaceae are a dominant tree family in pantropical rain forests. Molecular phylogenetic studies suggest that it had an ancient Gondwanan origin. However, the family has a poor fossil record, making hypotheses concerning its origin and dispersal difficult to evaluate. Here we describe a new species of *Shorea*, *Shorea fujianensis* sp. nov., which inhabited southeastern China ca. 14.8 million years ago and we evaluate its ecology. The fossils were collected from the middle Miocene Fotan Group of Zhangpu County, southeastern Fujian Province, southeastern China. Morphological comparison with extant taxa demonstrates that the fossil fruits are most similar to the living *Shorea hypochra*. The large size of the longer lobes of the fruit indicates that it was probably produced by a large, emergent tree. The discovery corroborates previous evidence for the existence of a dipterocarp forest in southeastern China during the Mid-Miocene Climatic Optimum. Northward dispersal of the dipterocarps in the middle Miocene possibly correlates with the warm global climate and a weak winter monsoon in East Asia during that time. We hypothesize that *S. fujianensis* may have migrated northwards to Zhangpu from mainland Southeast Asia along the coastal regions, rather than via the inland region of southern China.

1. Introduction

Dipterocarpaceae are considered a key family for understanding the ecology of Asian tropical rain forests. Its trees dominate the emergent canopy of most lowland rain forests in the Southeast Asian tropics to the West of Wallace's Line (Ashton, 1982, 1988, 2003; Ashton and Gunatilleke, 1987). They are also the region's most important commercial timber species and dominant in the international tropical hardwood markets (Appanah and Turnbull, 1998). The family comprises 17 genera and about 500 species in three subfamilies: Dipterocarpoideae in the Asian tropics and Seychelles; Pakaraimoideae restricted to Guyana and Venezuela of tropical South America, and Monotoideae in tropical Africa, Madagascar, and Southeast Colombia (Ashton, 1982, 2003; Maury-Lechon and Curtet, 1998). These transoceanic disjunct distributions indicated that the family had an ancient Gondwanan origin and arrived in Asia after the establishment of the land connection between the Indian and Asian plates during the middle Eocene (Ashton, 1982; Maury-Lechon and Curtet, 1998; Dayanandan et al., 1999; Dutta et al., 2011).

However, the origin and phytogeographic evolution of the Dipterocarpaceae are far from being settled, mainly because of incomplete knowledge of the fossil records of the family. In stark contrast to its high species richness and wide geographical distribution today, substantiated fossil records of the Dipterocarpaceae currently are sparse. The fossils of the family so far reported are represented primarily by wood and leaves (Bancroft, 1935; Schweitzer, 1958; Prakash, 1965; Lakhanpal, 1970; Lakhanpal and Guleria, 1987; Prasad and Prakash, 1987; Awasthi and Mehrotra, 1993; Prasad, 1993; Prakash et al., 1994; Guleria et al., 2000), sometimes by resin and by dispersed pollen (Dutta et al., 2009, 2011; Prasad et al., 2009; Rust et al., 2010). Most of these fossil occurrences are from the Indian subcontinent. In contrast to other organs of the plant, the fruits of Dipterocarpaceae, characterized by their persistent enlarged to greatly enlarged calyx lobes, are easily identifiable and critical in the generic classification of this family (Ashton, 1982). However they are very rarely preserved as fossils, with only seven species reported so far (Heer, 1874; Prasad, 2006; Grote, 2007; Khan and Bera, 2010; Shi and Li, 2010; Shukla et al., 2012; Feng et al., 2013). In a previous paper, Shi and Li (2010) described a fruit wing of the genus *Dipterocarpus* Gaertner, *Dipterocarpus zhengae* Shi et Li, from the middle Miocene Fotan Group of southeastern Fujian Province and at that time no other plant macrofossils were known from the Fotan Group and suggested a tropical paleoclimate and tropical rainforest for this region. In contrast, Ghazoul (2011) pointed out that the presence of *Dipterocarpus* in southeastern Fujian might as well be taken as evidence for a highly seasonal subtropical and relatively cool and dry climate similar to the present one. In order to learn more

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about the coeval vegetation that occurred with *D. zhengae*, we carried out further field work in the Fotan Group of southeastern Fujian, resulting in a collection of numerous well preserved plant fossils. Of great interest are several winged fruits of Dipterocarpaceae affinity including the new species described here. A preliminary study suggests that these winged fruits including the previously reported *D. zhengae* may altogether belong to four species from different genera of the family. In this paper, we describe a new species of *Shorea, Shorea fujianensis* sp. nov., on the basis of a well-preserved winged fruit and a detached fruit wing still bearing cuticle. This provides further evidence for the northward movement of Dipterocarpaceae during the Mid-Miocene Climatic Optimum. In addition, the paleoecology and paleoenvironment of *S. fujianensis* are reconstructed on the basis of uniformitarian comparison with the physiological and ecological characteristics of comparable extant species. Hypotheses concerning the origin and phytogeographic history of Dipterocarpaceae are briefly reviewed. In conclusion, we propose that *S. fujianensis* most likely migrated northwards to Zhangpu along the coastal regions from the mainland Southeast Asia.

2. Material and methods

The two fossil specimens studied in this paper were collected in 2011 from the Fotan Group at Lindai village (24°12′N, 117°53′E), Zhangpu County, southeastern Fujian Province (Shi and Li, 2010; Fig. 1). The Fotan Group is mainly distributed in the coastal areas of southeastern Fujian, and in Mingxi and Ninghua Counties of western Fujian (Zheng, 1984, 1987). It comprises three layers of sedimentary rocks alternating with three layers of intrusive basaltic rocks resulting from several episodes of volcanic activity during the Neogene (Zheng and Wang, 1994). The outcrop in Lindai village is in the secondary unit of sedimentary rocks according to the division of Zheng and Wang (1994). It is apparently a continuous succession and can be subdivided into an upper layer of light-brown diatomite and a lower layer of blue-gray mudstone. Both layers yield abundant plant fossils, dominated by leaves, many of which are with excellently preserved venation and in some cases with cuticle. The families so far recognized include Clusiaceae Lindley, Dipterocarpaceae Blume, Fabaceae Lindley, Fagaceae Dumortier, Hamamelidaceae R. Brown, Lauraceae Jussieu and Moraceae Gaudichaud-Beaupré. Fossil fruits are relatively rare and most of the identifiable ones belong to Dipterocarpaceae. Of the two specimens attributed to *Shorea* described here, the winged fruit impression is from the diatomite layer and the detached fruit wing compression with cuticle preserved is from the mudstone layer.

The Fotan flora is assigned to the Langhian Stage (middle Miocene) of 14.8 ± 0.6 Ma according to ^{40}Ar/^{39}Ar radiometric dating of the basaltic rocks in Zhangpu underlying the fossiliferous layer (Ho et al., 2003). Palynostratigraphic investigation of the Fotan Group supports this age assignment (Zheng and Wang, 1994).

The *Shorea* fruit fossils were examined under a dissecting microscope and photographed using a Nikon D90 digital camera with a 60 mm Micro-Nikkor lens. The fruit wing films were cleaned with 10% hydrochloric acid for 10 min, and then with 40% hydrofluoric acid overnight. Cuticles were prepared by maceration using Schulze's solution followed by dilute Ammonia and stained with Safranin T (detailed method see Shi et al., 2010). They were mounted on thin slides with phenol–glycerin jelly, sealed with nail polish, and examined and photographed on a Zeiss Axioscope A1 microscope using differential interference contrast (DIC). The cleaned, unmacerated fruit wing fragments were mounted on stubs, dried in air, and observed and photographed using a Leo 1530VP instrument at 8 kV and with a working distance of 6 mm.

The figured fossils including cuticle slides and SEM stubs are deposited in the Nanjing Institute of Geology and Palaeontology, CAS, see below for repository address. Letter suffixes (a, b) indicate part and counterpart.

Winged fruits of extant Dipterocarpaceae were examined for comparison from the Bangkok Forest Herbarium (BKF) and the Herbarium of Singapore Botanical Garden (SING). Cuticles of selected comparable extant species were also examined, prepared by maceration in 20% chromium trioxide. The fruit wing fragment for SEM examination was mounted on the stub without treatment.

2.1. Terminology

The winged fruits of Dipterocarpaceae have five persistent calyx lobes (Ashton, 1982, 2003). In mature fruits, these lobes are either free down to the base and are imbricately or valvately arranged; or else they are fused at the base to form a cup or tube more or less enclosing the fruit (Ashton, 1982, 2003). In the latter arrangement the

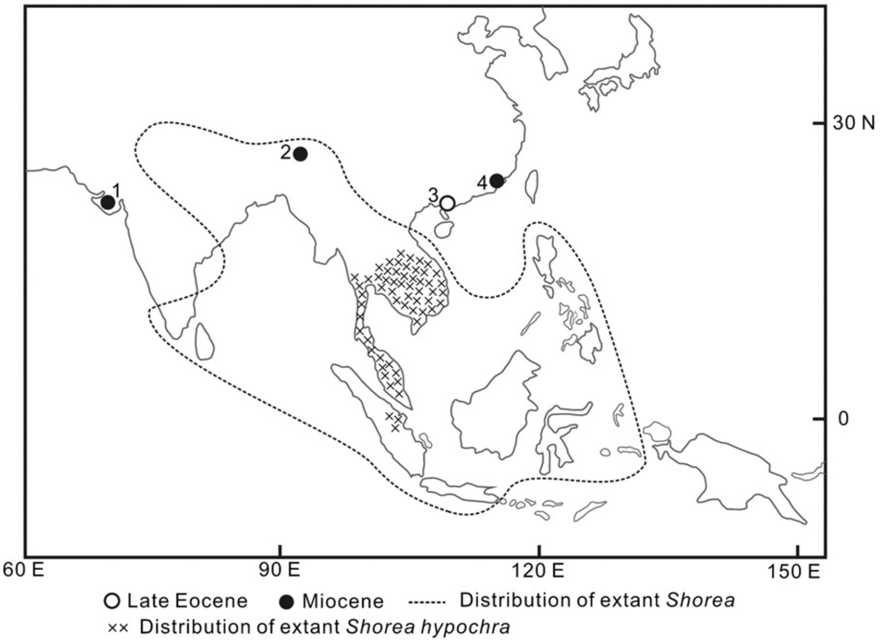


Fig. 1. Map showing the distribution of modern *Shorea*, the localities of *Shorea* fossil winged fruits, as well as the distribution of extant *S. hypochra*, the nearest living relative of *S. fujianensis* sp. nov.. 1. Kachchh, Gujarat, India. 2. Pinjoli area in West Kameng district, India. 3. Maoming, Guangdong Province, China. 4. Zhangpu, Fujian Province, China.

fruits are either free or are adnate to the calyx cup or tube (Ashton, 1982, 2003). In all forms, usually two or three, or sometimes all five of the calyx lobes are greatly extended to be wing-like. The number of such 'longer lobes' (sensu Ashton, 1982, 2003) is usually constant in one species. Ashton terms the non-enlarged or only relatively slightly enlarged ones 'shorter lobes'. We follow this terminology. Otherwise the terms used here to describe the gross morphology and venation of the fruit calyx lobes are generally based on the standard terminology for describing leaf architecture (Ellis et al., 2009).

3. Systematic paleobotany

Order: Malvales Jussieu ex Berchtold et Presl
Family: Dipterocarpaceae Blume
Subfamily: Dipterocarpoideae Burnett
Tribe: Shoreae Ashton
Genus: *Shorea* Roxburgh ex Gaertner. f.
Species: *Shorea fujianensis* Shi, Jacques et Li sp. nov. (Plates I–III and Plate IV, 1–7).

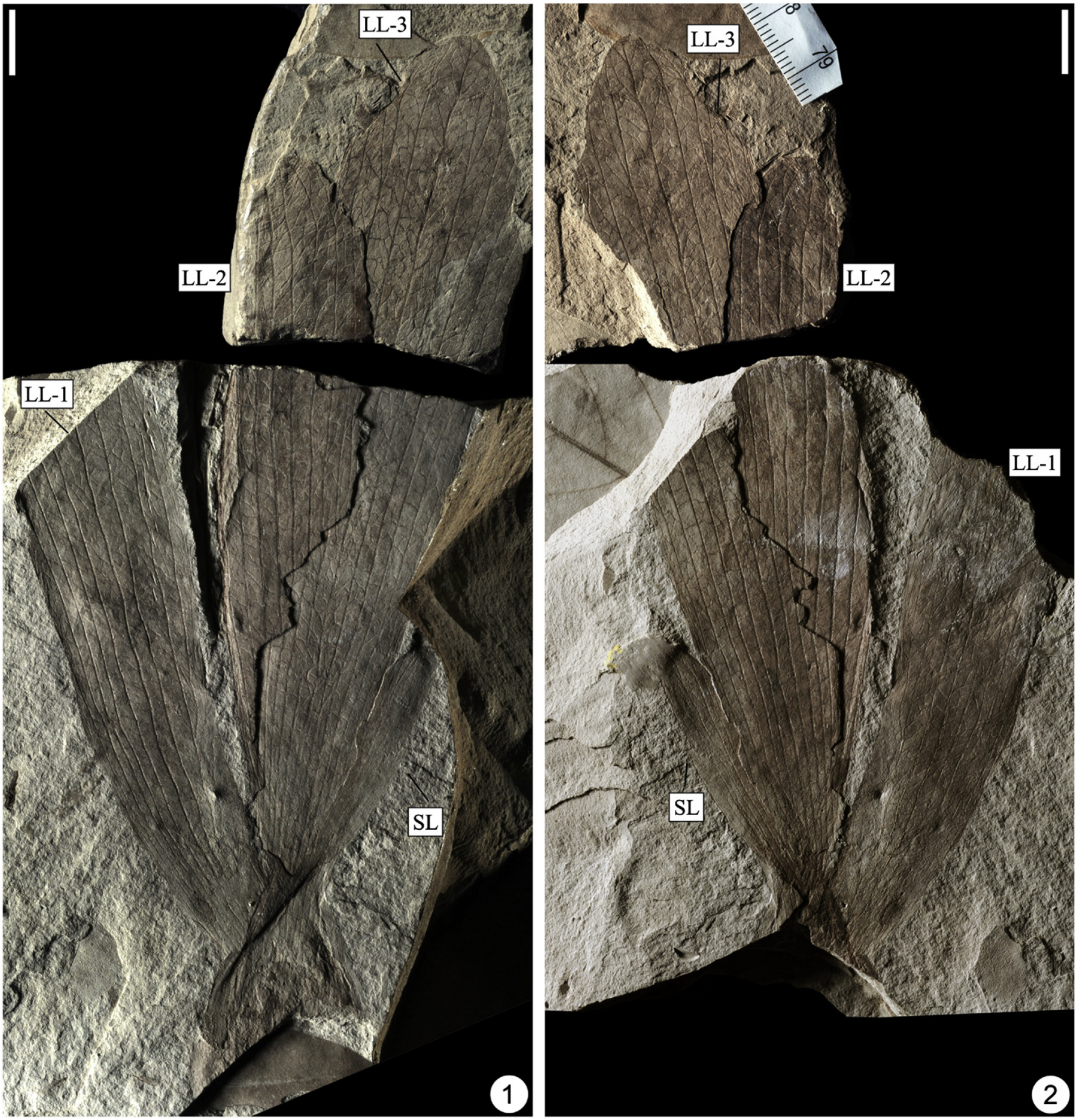


Plate I. *Shorea fujianensis* Shi, Jacques et Li. Holotype. Scale bar = 1 cm.

1. A winged fruit with three longer lobes (LL-1, 2, 3) and one visible shorter lobe (SL). Part of the holotype. PB21515-a.
2. Counterpart of the specimen in 1. PB21515-b. LL-1, 2, 3 indicate the longer calyx lobes and SL indicates the shorter lobe.

Holotype: PB21515a, b (Plate I, 1, 2; designated here; part and counterpart).
Paratype: PB21516a, b (Plate III, 4, 5; part and counterpart).
Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.
Type locality: Lindai village, Zhangpu County, Fujian Province, China.
Stratigraphy: Fotan Group, middle Miocene.
Etymology: The specific epithet is derived from Fujian, the Province in which the type locality is located.

3.1. Specific diagnosis

Winged fruit with three persistent, greatly enlarged calyx lobes (longer lobes); longer lobes oblanceolate with entire margin and parallelodromous-like venation; 11–13 longitudinal parallel primary veins arising from base, often branching in distal region; secondary veins and tertiary veins mostly opposite percurrent; shorter lobes lanceolate, with entire margin and parallelodromous-like venation.

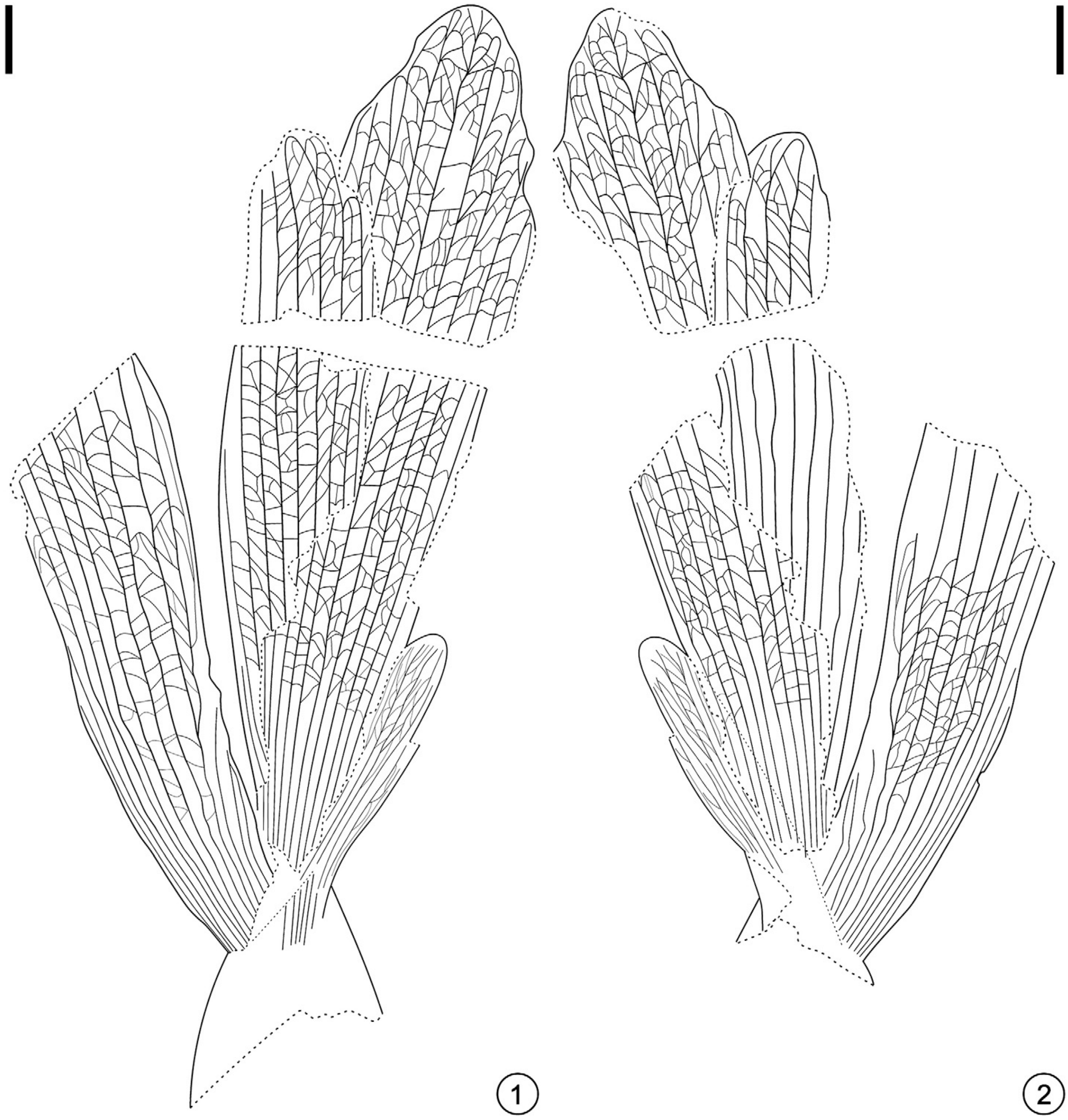


Plate II. *Shorea fujianensis* Shi, Jacques et Li. Scale bar = 1 cm.

1. Drawing of the part of the holotype in Plate I, 1.
2. Drawing of the counterpart of the holotype in Plate I, 2.

Longer lobe amphistomatic; adaxial and abaxial cuticles generally similar in structure, both with dense trichome bases and sparse stomata; trichome bases solitary, rounded; stomatal complexes irregular in distribution, random in orientation, anomocytic to incompletely cyclocytic; guard cell pairs sub-circular to oval, outlined by well-defined anticlinal walls.

3.2. Description

The holotype specimen (PB21515a, b) is a winged fruit preserved as the part and counterpart of an imprint lacking carbonaceous material but showing the form and venation very clearly (Plate I, 1, 2). The fruit consists of a fruit body with three persistent longer calyx lobes and

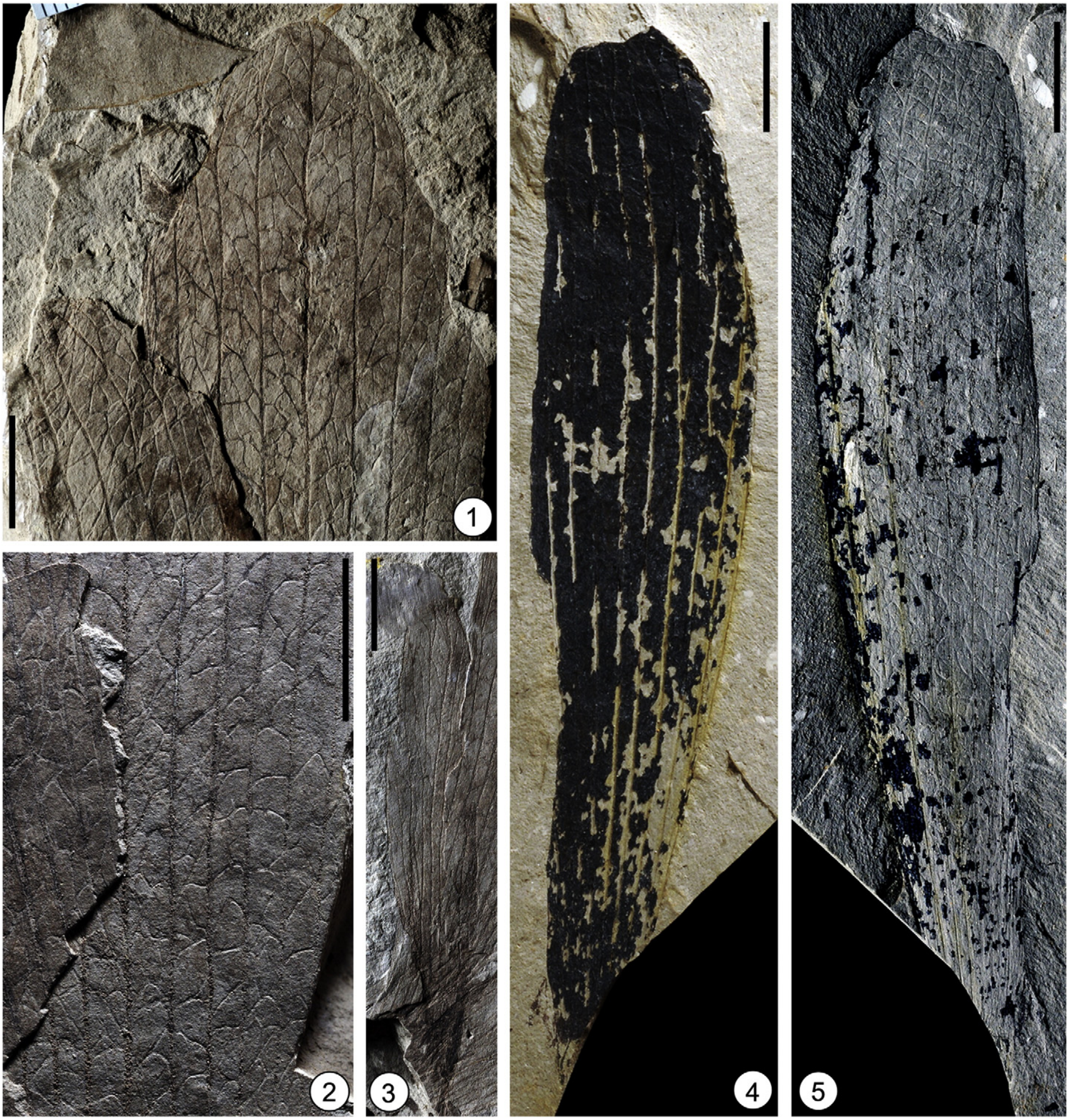


Plate III. *Shorea fujianensis* Shi, Jacques et Li. Scale bar = 1 cm.

1. Apex of a longer lobe, enlarged from Plate I, 1, showing details of venation in the apical region. Note the variously branching veins. PB21515-a.
2. Middle region of a longer lobe, also enlarged from Plate I, 1, showing the usually oppositely percurrent secondary veins. PB21515-a.
3. A shorter calyx lobe from the holotype, enlarged from Plate I, 2 at left, showing details of venation. PB21515-b.
4. The detached longer calyx lobe, compression with cuticle preserved. Part of the Paratype. PB21516-a.
5. Counterpart of the specimen in 4. PB21516-b.

one preserved shorter lobe (Plates I, 1, 2 and II, 1, 2). The fruit body is incomplete, with the basal region missing when it was recovered (Plate I, 1, 2). It is symmetrical in the apical region, 3 cm wide in the widest part and is ovoid in shape (Plate I, 1, 2). Two of the three longer lobes are relatively completely preserved (Plate I, 1, 2). They are slightly unequal in size, almost symmetrical, oblanceolate in shape, 14 cm and 11.7 cm long respectively (measured from the apex of the fruit body), 3.1 cm and 2.6 cm wide respectively, with a length to width ratio ca. 4.5, the widest part of the longer lobe occurring at the base of the distal one-third of the lobe. The longer lobe with much of the distal region missing is 2.6 cm × 9 cm and was clearly much longer originally (Plate I, 1, 2). The apices of the two more or less complete longer lobes are rounded and their margins are entire with some localized sinuosity probably resulting from insect damage (Plate III, 1).

The venation of the longer lobes is parallelodromous-like, with 11–13 parallel primary veins arising collaterally from the base (Plates I, 1, 2 and II, 1, 2). The primary veins are mostly straight, sometimes slightly curved. The middle 7–9 primary veins are almost equal in size, nearly evenly or only slightly unevenly spaced, ca. 0.3–0.5 mm apart in the widest part of the lobes (Plate III, 2). The lateral 4–6 primaries are slightly thinner and a little more closely spaced than the middle ones, usually tapering and disappearing in the lower or middle region (Plate I, 1, 2). In the distal region of the lobe the primaries are not convergent as in parallelodromous venation, but are connected with adjacent primaries by their branches or secondary veins (Plate III, 1). The branching veins often connect back to the primary vein from which they originated, or else to the superjacent branches to form a loop (Plate III, 1). The primary vein often branches in the distal region (Plate III, 1). One exceptional lateral primary vein branches once in the proximal region of the wing, and this branch is similar to the primaries in thickness, running in parallel with them (Plate I, 1). The secondary veins which connect neighboring primaries with each other and that connect neighboring primary veins with their branch veins, are often opposite percurrent (Plate III, 2). They are straight, convex, sinuous or forming a chevron, perpendicular or at an obtuse or acute angle to the long axis of the lobe (Plate III, 2). In the apical region they are occasionally looped to the primary veins (Plate III, 1). The tertiary veins are usually opposite percurrent, or occasionally alternate percurrent, straight, convex, sinuous or forming a chevron, parallel or at an obtuse or acute angle to the long axis of the lobe (Plate III, 2).

The shorter lobe (seen only in the holotype) is lanceolate, 1 cm wide and 6 cm long from the apex of the fruit body (Plate III, 3). Its venation is also parallelodromous-like as in the longer lobes (Plate III, 3). The shorter lobe is preserved partly under one longer lobe and only 6 primary veins are visible (Plate III, 3). We estimate that there were 8–9 primaries in the shorter lobe, assuming the venation was symmetrical. The primary veins often branch dichotomously in either the proximal or distal region of the lobe (Plate III, 3). The branches are slightly thinner than the primaries, running parallel to them. The secondary veins are often opposite percurrent (Plate III, 3). They are usually at a fairly oblique angle to the primaries. Sometimes the secondary veins are arched to form small loops with primaries (Plate III, 3).

The detached longer lobe compression is oblanceolate, 2.1 cm wide with a length of 9.7 cm preserved (Plate III, 4, 5). The margin is entire although feeding or injury traces are often seen in the apical and marginal regions (Plate III, 4, 5). This longer lobe has 11 primary veins arising collaterally from the base, and its venation is generally similar to that of the longer lobes attached to the winged fruit described above (Plate III, 4, 5).

The longer lobe is amphistomatic, and in general the structure of the adaxial and abaxial cuticles is similar, both being comprised mainly of ordinary epidermal cells, dense trichome bases and sparse stomatal complexes (Plate IV, 1, 2). As only intercostal fragments of cuticle appear to have been obtained, epidermal cells over the veins are not evident. In the intercostal areas the ordinary epidermal cells are usually irregularly arranged (Plate IV, 3), although those surrounding the trichome bases are more or less radially arranged and tend to be wedge shaped (Plate IV, 2). They are isodiametric or elongated, often quadrangular, to sometimes pentagonal, 6.5–11 μm × 8.5–17 μm in dimension, with length to width ratios 1–2.6 (Plate IV, 3). The anticlinal walls of the ordinary epidermal cells are straight or slightly curved, unbuttressed; the periclinal walls are smooth (Plate IV, 6). The solitary celled trichome bases are evenly distributed (Plate IV, 2). They are rounded, 8–9 μm in diameter, surrounded by 6–8 radial epidermal cells as described above, and slightly thickened (Plate IV, 2, 6). The stomatal complexes are irregularly distributed, randomly oriented, anomocytic to incompletely cyclocytic, with 5–9 subsidiary cells (Plate IV, 1, 4, 5). Guard cell pairs are subcircular to oval, outlined by well-defined anticlinal walls, 12–16 μm × 16–17 μm (Plate IV, 4, 5). The outer stomatal ledges are fusiform to elliptic in outline, 5–6.5 μm × 9–16 μm, with length to width ratios 1.4–2.8 (Plate IV, 7). The stomatal apertures are slit-like (Plate IV, 7).

4. Comparisons

4.1. Family determination

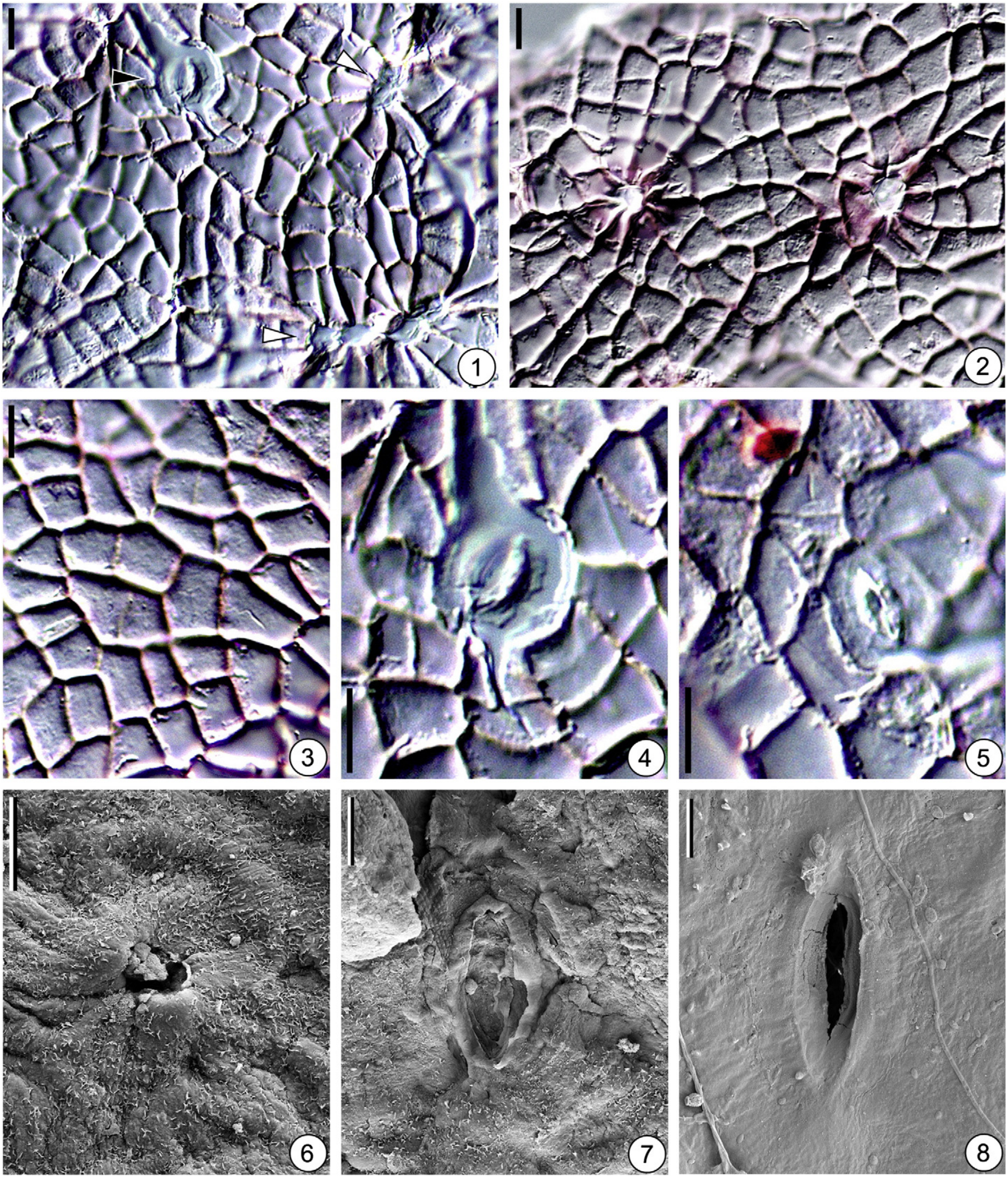
The studied winged fruit with three characteristic greatly enlarged calyx lobes represent a member of the Dipterocarpaceae. Although winged fruits are commonly found in angiosperms, those with such large wings are very rare and nearly all occur in Dipterocarpaceae. *Parishia insignis* Hooker f. (Anacardiaceae) is amongst the few other species in which the fruit wings are similar in size (Hou, 1978). However, in *P. insignis* the fruits have four wing-like calyx lobes with a flabellate venation (Hou, 1978) and thus are clearly different from our material. The enlarged calyx lobes of fruits of *Tridynamia sinensis* (Hemsley) Staples (Convolvulaceae) have a parallelodromous-like venation and can attain a length of 7.8 cm (Fang and Staples, 1995). They differ however from our fossil in having two longer lobes with 7–9 parallel longitudinal veins (Fang and Staples, 1995). In addition, the cotyledons of the Welwitschiaceae Markgraf (Gnetales) appear to be a little comparable to the present fruit wings in venation (Rodin, 1953; Dilcher et al., 2005). However, the seedlings in the cotyledonary stage of Welwitschiaceae only have a pair of cotyledons and the secondary veins of the cotyledons are irregularly fused to be inverted Y shaped (Rodin, 1953; Rydin et al., 2003; Dilcher et al., 2005). As mentioned above, fruits of Dipterocarpaceae typically have five persistent calyx lobes. They may seem different from our fossil in which only four lobes are visible. However, the five lobes of extant Dipterocarpaceae fruits are rarely all visible when the fruit is viewed from only one side, with at least one shorter lobe generally concealed behind the longer lobes. This corresponds with the appearance of the present fossil fruit.

Plate IV 1–7. *Shorea fujianensis* Shi, Jacques et Li. Illustrations of longer lobe cuticle, all taken from Paratype PB21516-a. Scale bars all = 10 μm. 1–5 viewed by differential interference contrast (DIC) light microscopy; 6–7 by scanning electron microscopy (SEM).

1. Cuticle of a longer lobe, showing the stomatal complex (black arrowhead) and solitary trichome bases (white arrowheads). PB21516-a1.
2. Cuticle of a longer lobe, showing the trichome bases surrounded by more or less radial and wedge shaped epidermal cells. PB21516-a1.
3. Cuticle of a longer lobe, showing morphology and arrangement of the ordinary epidermal cells. PB21516-a1.
4. Details of an incompletely cyclocytic stomatal complex, with 9 subsidiary cells. PB21516-a1.
5. Details of an anomocytic stomatal complex, with 6 subsidiary cells. PB21516-1.
6. Outer view of a trichome base. PB21516-as.
7. Outer view of a stomatal complex. PB21516-as.
8. *Shorea hypochra* Hance. Extant. SEM photograph of outer view of a stomatal complex of a longer calyx lobe. Scale bar = 10 μm.

It is likely that the other short lobe of the fossil fruit is in fact preserved and concealed beneath the visible ones.

In the present study, the detached fruit wing compression (Plate III, 4, 5) is believed to belong to the same species as the winged fruit because they share close similarities in both shape and venation of the longer lobe. The slight difference in dimension between the detached longer lobe (9.7 cm × 2.1 cm) and the attached longer lobes of the holotype (14 cm × 3.1 cm; 11.7 cm × 2.6 cm) can be due to intraspecific variation. According to our observation on winged fruits of living dipterocarps trees as well as on herbarium materials, such a range of variation commonly occurs amongst winged fruits of a single species and even amongst those of an individual tree.



4.2. Generic determination

Within living Dipterocarpaceae, the winged fruit described in this study can be referred securely to the Asian subfamily Dipterocarpoideae because it has unequally enlarged calyx lobes. The other two subfamilies, Pakaraimoideae and Monotoideae, both have fruits with five equal or subequal aliform short calyx lobes (Ashton, 1982, 2003).

Amongst extant genera of Dipterocarpoideae, our fossil most closely resembles fruits of *Shorea* in having three longer lobes, in the significant discrepancy in size between the longer and shorter lobes, and in the longer lobes having 11–13 longitudinal primary veins. Shi and Li (2010) summarized the numbers of longer and shorter fruit calyx lobes in all 13 extant genera of Dipterocarpoideae. Within this subfamily only the two genera *Shorea* and *Parashorea* Kurz have fruits with three longer lobes and two shorter ones, similar to our fossil fruit (Ashton, 1982, 2003; Shi and Li, 2010).

As their names indicate, *Shorea* and *Parashorea* are two closely related genera (Smitinand et al., 1980; Ashton, 1982, 2003). They have been placed in the tribe Shoreae along with *Dryobalanops* Gaertner, *Hopea* Roxburgh and *Neobalanocarpus* Ashton (Ashton, 1982; Maury-Lechon and Curtet, 1998). Recent molecular phylogenetic work has revealed *Parashorea* as sister to a group of most *Shorea* species (Tsumura et al., 1996; Kajita et al., 1998; Kamiya et al., 2005), and it has even been suggested that *Parashorea* should be included within *Shorea* (Yulita et al., 2005).

Generally, in *Parashorea*, the calyx lobes are narrowly imbricately arranged, frequently subequal in dimensions with three slightly larger than the other two, or equally shorter than the nuts; the nuts are globose and the leaves have subpersistent plicate folding (Ashton, 1982, 2003). In *Shorea*, the calyx lobes are prominently imbricately arranged, mostly unequal in dimensions with the outer three usually considerably longer than the inner two, or occasionally subequal; the nuts are ovoid and the leaves don't have plicate folding (Ashton, 1982, 2003). In addition, Shi and Li (2010) noticed that the number of primary veins in the longer lobes of *Parashorea* (5–7) is often less than in *Shorea* (5–14) based on limited illustrations in relevant publications. After checking actual herbarium material, we have found that this character, although useful, is not always applicable to distinguishing these two genera since some extant *Parashorea* species with large fruit wings (e.g. *Parashorea malaanonan* (Blanco) Merriam, *Parashorea tomentella* (Symington) Meijer) have longer lobes with up to 11 primary veins.

Although the preservation of our fossil winged fruit does not allow a detailed examination of the arrangement of calyx lobes and the fruit shape, it can nonetheless be distinguished with high confidence from *Parashorea* in its calyx lobes of greatly unequal length. Its longer lobes (14 cm, 11.7 cm) are more or less twice as long as the shorter lobes (6 cm). In addition, the number of primary veins of the longer lobes also appears to be in favor of *Shorea* rather than the *Parashorea* affinity of the fossil winged fruit.

Most living species of *Shorea* differ from *Shorea fujianensis* in having smaller longer lobes. *Shorea farinosa* Fischer, *Shorea polita* Vidal, *Shorea cordata* Ashton, and a few other species appear to be comparable with *S. fujianensis* in the morphology of their calyx lobes but differ in having much smaller nuts (1–1.5 cm wide). Of the extant *Shorea* species, *Shorea hypochra* Hance (Plate IV, 8 and Plate V, 1–3) is most similar to *S. fujianensis*. The similarities they share include: the shape and size of the longer and shorter calyx lobes and nuts; the longer lobe venation including the number of primary veins; longer lobe amphistomatic; longer lobe cuticle with dense trichome bases and sparse, irregularly distributed stomata; and anomocytic to incompletely cyclocytic stomatal complexes (Plate IV, 4, 5 and V, 3). It should be mentioned that the length of the longer and shorter lobes of *S. hypochra* recorded in Ashton (1982) is 17 cm and 12 cm respectively. However, the lobes of *S. fujianensis* fit well within the size ranges of *S. hypochra* in specimens that we have observed and measured from the SING and BKF herbaria. *S. fujianensis* is however attributed to a new species because its other organs are not yet known. *S. hypochra* belongs to the section *Anthoshorea* Heim of *Shorea* and therefore *S. fujianensis* is likely to be closely related, or even represented an ancient member of this section as its nearest living relative.

4.3. Fossil fruits of *Shorea*

Fruit fossils are believed to be much more reliable in identification than leaves or wood in the family Dipterocarpaceae. So far, however, only three fossil species of *Shorea* have been reported on the basis of fruits (Fig. 1; Khan and Bera, 2010; Shukla et al., 2012; Feng et al., 2013). All of them are different from *Shorea fujianensis*. *Shorea maomingensis* Feng, Kodrul et Jin from the late Eocene Huangniuling Formation of Guangdong, South China is the only record of the genus represented by winged fruits (Feng et al., 2013). Its longer lobes (5.2–6 cm × 0.7–1.5 cm) and fruit bodies (1.7 cm × 0.9–1.4 cm) are significantly smaller than *S. fujianensis*. *Shorea mioassamica* Khan et Bera from the middle to late Miocene Dafla Formation of the northeastern region of the Indian subcontinent is represented by a fruit wing fragment with only the lower part of the longer calyx lobe preserved (Khan and Bera, 2010). Despite its fragmentary preservation, it clearly differs from *S. fujianensis* in having fewer primary veins (7) (Khan and Bera, 2010). *Shorea kachchhensis* Shukla, Guleria et Mehrotra from the early Miocene Khari Nadi Formation of Gujarat, India, is a single fruit wing having 10–11 primary veins (Shukla et al., 2012). It is only 5.83 cm long and 1.48 cm wide (Shukla et al., 2012), much smaller than the longer lobes of *S. fujianensis*.

5. Discussions

5.1. Paleoecology and paleoenvironment

Suzuki and Ashton (1996) analyzed the size of the longer calyx lobes and nuts of Dipterocarpaceae species from Malaysia and Sri Lanka. Their results demonstrated that in *Shorea* the length of longer lobes and nuts correlates with the position of the mature trees in the forest canopy (Suzuki and Ashton, 1996). Specifically, most emergent trees and main canopy trees with a large tree size have gyration-dispersed fruits with a greater longer lobe length to nut length ratio. On the other hand, the fruits of most understory trees are not dispersed by gyration and have a smaller longer lobe length to nut length ratio (Suzuki and Ashton, 1996). Despite the incomplete preservation of its nut, the longer lobe length of *Shorea fujianensis* appears therefore to indicate that it was a giant, emergent tree in the middle Miocene forest in Zhangpu. Interestingly, trees of *Shorea hypochra* are very large, sometimes exceeding 350 cm in girth (Smitinand et al., 1980). In the mainland of Southeast Asia, where the modern forests are more comparable to the Miocene Fotan flora than the forests of the Malaysian peninsula and islands, most species of the section *Anthoshorea* of *Shorea*, which *S. fujianensis* most likely belongs to, occur in montane dipterocarp forest at 350–850 m, in the lowland dipterocarp forest (0–350 m), and in the coastal hills (Smitinand et al., 1980). *S. fujianensis* might inhabit a similar environment as its living relatives.

5.2. The origin and phytogeographic history of Dipterocarpaceae

Despite having its greatest species diversity in Malaysia and Borneo, the modern disjunct distributions of Dipterocarpaceae suggest that it had a Gondwanan origin and invaded Asia via the Indian fragment of Gondwana after its collision with Eurasia during the middle Eocene (Ashton, 1982; Ashton and Gunatilleke, 1987; Dayanandan et al., 1999; Dutta et al., 2011). This ‘out-of-India’ dispersal hypothesis has also been applied to some other Asian biotic elements, and is widely accepted (Morley, 2000). Phylogenetic analysis of Dipterocarpaceae and related taxa suggests that the Asian dipterocarps share a common ancestor with Sarcolaenaceae, a tree family endemic to Madagascar

(Ducousso et al., 2004). This may indicate that Asian dipterocarps drifted away from Madagascar together with the India–Seychelles landmass on their route to Asia (Ducousso et al., 2004).

A Gondwanan origin of Dipterocarpaceae however has not been well supported by its fossil record until recently (Rust et al., 2010; Dutta et al., 2011). Fossil wood and leaves of Dipterocarpaceae have been reported from Northeast Africa (Bancroft, 1935; Seward, 1935; Ashton, 1982). However, the chronostratigraphic study of these fossils was limited and the reliability of many African records is still uncertain (Kräusel, 1939; Ashton, 1982). Ashton (1982) reviewed the Northeast African fossil records of the family and pointed out that “it is clear that Dipterocarpoideae were present in East Africa at least in the upper Tertiary”. Therefore the African fossils cannot provide unequivocal evidence to substantiate the Gondwanan origin of Dipterocarpaceae. In India, macrofossils of Dipterocarpaceae had been found exclusively from the Miocene onwards (Shukla et al., 2012), which led to the proposal of a southeastern Asian origin for the family (Lakhanpal, 1970; Sasaki, 2006; Shukla et al., 2012). This hypothesis suggests that the

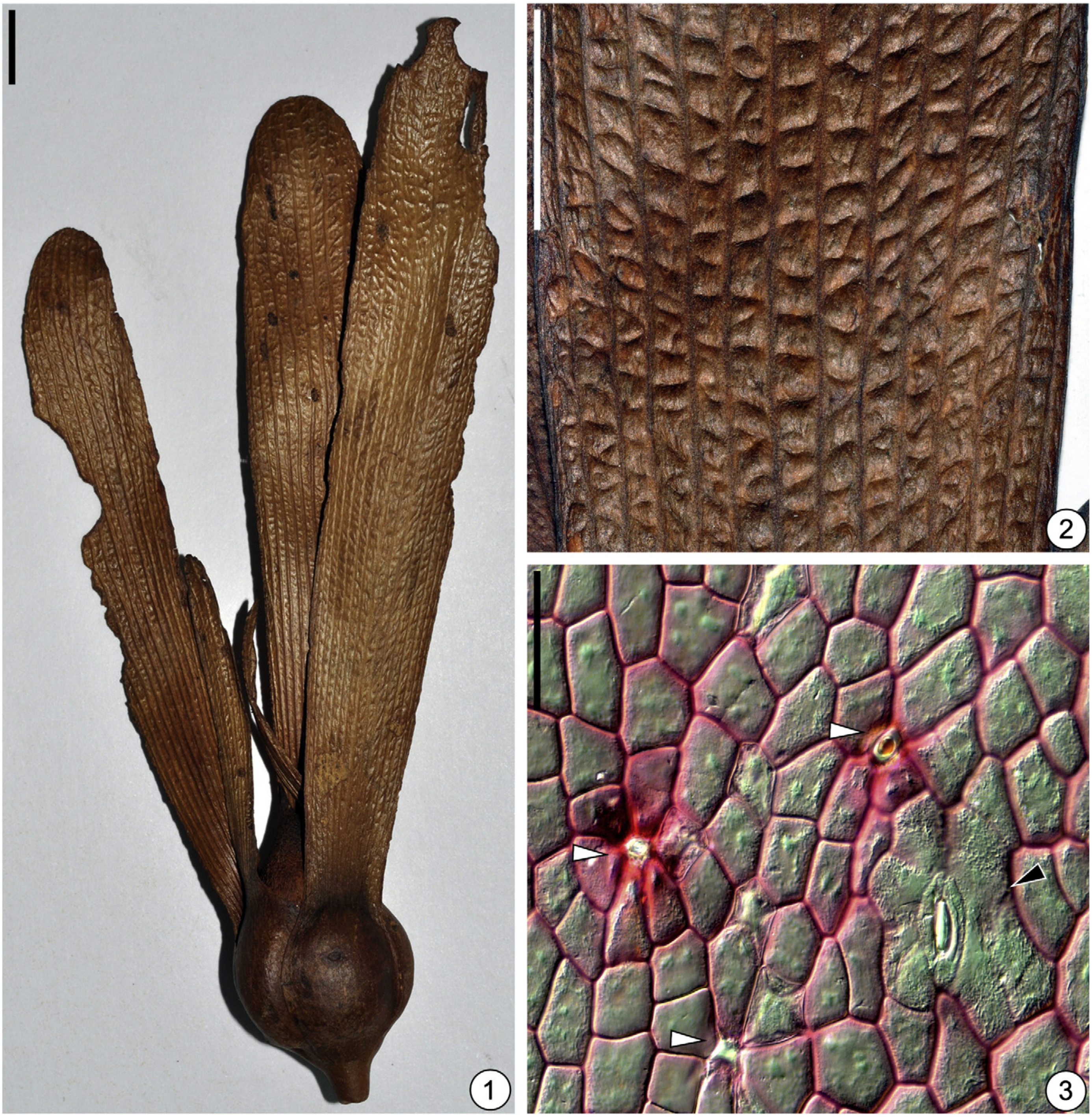


Plate V. *Shorea hypochra* Hance. Extant. Fruit morphology and cuticle of a longer lobe.

1. A winged fruit. Note the three longer lobes and two shorter lobes. SN152096 (BKF). Scale bar = 1 cm.
2. Details of venation of a longer lobe in middle region, showing the parallel primary veins and frequently oppositely percurrent secondary veins. SN132106 (BKF). Scale bar = 1 cm.
3. Cuticle of a longer lobe viewed by differential interference contrast microscopy. Note the incomplete cyclocytic stoma (black arrowhead) and the densely spaced trichome bases (white arrowheads). Cuticle was taken from SN145490 (BKF). Scale bar = 50 μm.

Asian dipterocarps migrated to India from southeastern Asia via Myanmar, after the connection of India to Asia in the middle Eocene (Lakhanpal, 1970; Sasaki, 2006). It appeared to be in agreement with the fossil record of Asian dipterocarps since pollen attributed to dipterocarps has been reported from the Oligocene of Borneo and been once considered to be the earliest fossil record of the family (Muller, 1981). Recent discoveries of fossil pollen of Dipterocarpaceae from the lower Paleogene of western and northeastern India (Prasad et al., 2009) and of fossil resin (amber) produced by dipterocarps from the lower Eocene of western India (Dutta et al., 2011), however support a Gondwanan rather than a southeastern Asian origin of the family (Rust et al., 2010; Dutta et al., 2011). Myanmar might be a midway through which Dipterocarpaceae migrated to Southeast Asia from India. The Myanmarese Tertiary fossils of the family (Holden, 1916; Edwards, 1923) can provide evidence for this hypothesis. Generally it is believed that Dipterocarpaceae have evolved from ancestors without enlarged fruit sepals because no family related to Dipterocarpaceae has such long and persistent sepals (Suzuki and Ashton, 1996). If true, this hypothesis may explain why typical Dipterocarpaceae fruits with enlarged calyx lobes are lacking from sediments of Paleogene and earlier age.

Wallace's Line is a major phytogeographic boundary for Dipterocarpaceae (Ashton, 1982). Borneo to the West of the Line is the center of the world's diversity for the family today (Ashton, 1982). In the regions to the East of the Line, which were derived from a series of micro-plates that broke off from Australia and moved northwards to form present day eastern Malaysia (van Welzen et al., 2011), the number of genera and species of Dipterocarpaceae greatly decreases (Ashton, 1982; Maury-Lechon and Curtet, 1998). Only one species is shared between Sulawesi to the East of Wallace's Line and Borneo. It is a riparian species with water-dispersed fruits (Ashton, 1988), and hence very easily dispersing. In Australia, neither living nor fossil Dipterocarpaceae have been found. Therefore, it is very likely that the ancient dipterocarps were absent in high-latitude regions of Gondwana and were exclusively distributed in the tropical regions as their living relatives today.

As indicated above, morphological comparisons indicate that *Shorea fujianensis* most likely represents a member of the section *Anthoshorea*. This suggests that the section had appeared at least as early as the middle Miocene. Some representatives of the section *Anthoshorea*, although having a wide distribution from India to east of Wallace's Line (Maury-Lechon and Curtet, 1998), were recognized as a monophyletic group occupying a basal position in the molecular phylogenetic tree of *Shorea* (Kamiya et al., 2005). Interestingly, the Indian late Miocene species *Shorea mioassamica* has a modern analogue (*Shorea assamica*) also belonging to the section *Anthoshorea*. The occurrences of fossil *Shorea* from the middle to upper Miocene of Southeast China and the Northeast Indian subcontinent appear to support the primitiveness of the section *Anthoshorea* within *Shorea* (Kamiya et al., 2005). This would be in agreement with the hypothesis of Maury-Lechon and Curtet (1998) that the section *Anthoshorea* provided the core from which new species of the genus arose by diversification.

Our fossils with huge and nearly completely preserved fruit wings indicate that they were not transported far before burial. This discovery therefore considerably expands the known biogeographic range of the dipterocarps. Today only one extant species of *Shorea*, *Shorea assamica* Dyer, is found in China (Li, 1990; Li et al., 2000, 2002). It is distributed in western Yunnan and southeastern Xizang of Southwest China. The fruits of *S. assamica* are morphologically different from those of *Shorea fujianensis* in having much smaller calyx lobes. In Southeast China, *Shorea* is unknown at present (Li, 1990; Li et al., 2000, 2002; Fig. 1). The existence of *S. fujianensis* in the middle Miocene of Zhangpu, which today has a subtropical monsoon climate and subtropical evergreen broadleaved forests (Wu, 1980), was possibly favored by global warming during the Mid-Miocene Climatic Optimum (Zachos et al., 2001), and probably also reflecting a weak winter monsoon in East Asia at that time (Sun and Wang, 2005). Today, the frost and cold wave caused by the winter monsoon in Southeast China may well form a climatic limit for the survival of dipterocarps there (Wu, 1980).

As mentioned earlier, we believe that *Shorea fujianensis* is more closely related to *S. hypochra* than to other extant dipterocarps. *S. hypochra* is now distributed in mainland Southeast Asia, the Malay Peninsula and Northeast Sumatra (Fig. 1). It is likely that *S. fujianensis* migrated northwards to Zhangpu from North mainland Southeast Asia during the middle Miocene along the coast of Southeast China. The reasons are as follows:

1) Fossil Dipterocarpaceae are unknown from the Neogene of inland regions of South and Southwest China including several fragmentary regions with dipterocarps forests today, even though potentially suitable fossil floras similar to that of the Fotan Group are known from these areas.
2) *Shorea hypochra* and some other species of the section *Anthoshorea* can inhabit both inland hills and hills near the coast (Smitinand et al., 1980).
3) The coastal regions have a warmer winter and stronger northward wind (such as typhoon) than more inland regions.
4) The fossil locality, Zhangpu, which is in the coastal area today, was not far from the paleo-coastline during the middle Miocene according to the paleogeographical reconstruction (Hall, 1998).

In closed forests dipterocarps fruits have limited abilities for dispersal. They are generally too heavy to disperse for more than 100 m (Ashton, 1982, 1988; Suzuki and Ashton, 1996). However, above the canopy and at forest borders storms and very strong winds at the beginning of the rainy season may transport them for several hundred meters and sometimes for about 1 km (Maury-Lechon and Curtet, 1998). Therefore typhoons might have played an important role in the northward dispersal of *Shorea fujianensis* in the middle Miocene.

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