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Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

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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ARTICLE INFO

Article history: Received 19 May 2013 Received in revised form 24 August 2013 Accepted 11 September 2013 Available online 20 September 2013

Kevwords: Dipterocarpaceae Shorea winged fruit middle Miocene southeastern China wind dispersal

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.

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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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^{0034-6667/\$ -} see front matter © 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.revpalbo.2013.09.003

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 \pm 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.

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