

PALEOBOTANY

Southeast Asian Dipterocarp origin and diversification driven by Africa-India floristic interchange

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The evolution and diversification of ancient megathermal angiosperm lineages with Africa-India origins in Asian tropical forests is poorly understood because of the lack of reliable fossils. Our palaeobiogeographical analysis of pollen fossils from Africa and India combined with molecular data and fossil amber records suggest a tropical-African origin of Dipterocarpaceae during the mid-Cretaceous and its dispersal to India during the Late Maastrichtian and Paleocene, leading to range expansion of aseasonal dipterocarps on the Indian Plate. The India-Asia collision further facilitated the dispersal of dipterocarps from India to similar climatic zones in Southeast Asia, which supports their out-of-India migration. The dispersal pathway suggested for Dipterocarpaceae may provide a framework for an alternative biogeographic hypothesis for several megathermal angiosperm families that are presently widely distributed in Southeast Asia.

Many of the megathermal angiosperm families that constitute major components of today's tropical rainforest, such as Annonaceae, Combretaceae, Ebenaceae, Myristicaceae, etc., show disjunct pantropical distributions. The colonization and diversification of megathermal angiosperms in Southeast Asian tropical forests is believed to be influenced by their ancient origin in Africa and out-of-India dispersal (1–4). However, the limited number of molecular studies and the sparse fossil record of megathermal angiosperms from the Cretaceous of Africa (1) and the Paleogene of India (4, 5) provide insufficient information to conclude their ancient African origin or that India aided their dispersal and diversification in Asian tropical forests. Here, we present fossil pollen data from the family Dipterocarpaceae that suggest their African origin during the mid-Cretaceous and subsequent dispersal to Southeast Asia.

Dipterocarpaceae are a pantropical, obligate megathermal angiosperm family comprising more than 500 species grouped into three

subfamilies with an intercontinental disjunct distribution: Monotoideae in Africa, Madagascar, and South America; Pakaraimaeoideae in South America; and Dipterocarpoideae in the Seychelles, India, and Southeast Asia (6). A specific combination of morphological and ecological characteristics determined the ecological success of Dipterocarpoideae and enabled them to out-shade the canopy of other tree families, which led to their dominance in the mature forests of Southeast Asia (6). These characteristics include ectotrophic mycorrhizal association, specific pollinators, mast fruiting overcoming seed predation, protective resin in multicellular secretory ducts, poorly nutritious and resinous unpalatable leaves for many herbivores, and plagiotropic followed by orthotropic branching patterns in trees. Dipterocarps have been the major source for timber extraction across Southeast Asia over the past 50 years, which has led to their overexploitation and has left many formerly superabundant species critically endangered.

We present eight fossil pollen types, extracted using the standard palynological techniques (7), referable to five living genera of the subfamily Dipterocarpoideae (*Dipterocarpus*, *Dryobalanops*, *Shorea*, *Vateriopsis*, and *Vatica*) and one genus of the subfamily Monotoideae (*Monotes*) (Fig. 1 and figs. S1 to S4) from the Maastrichtian of Sudan and the Paleocene and early Eocene of India (Fig. 2, appendix S1, and table S1). These are combined with the secobiscadinane biomarkers of dipterocarps retrieved from the Late Cretaceous sediments from central India (fig. S5), phylogenetic analysis (8–13) of pollen (fossil and extant) morphology, and DNA sequence data of 54% of the known Dipterocarpaceae species to do the following: (i) trace

the origin and evolution of the family; (ii) define the role of climate and dispersal pathways, including movement of the Indian Plate during the Late Cretaceous–early Paleogene in the diversification of the family; and (iii) resolve the paleobiogeographic history of lowland dipterocarp rainforests in Southeast Asia.

The pollen of the subfamily Dipterocarpoideae is distinctive in being tricolpate, with very long colpi reaching almost to the poles, and with exine consisting of a thin basal layer, except in *Vateriopsis* and allied genera, with a much thicker outer, sculptured layer. The columellae and frequently grooved or crenelated ridge-bearing tectum of the outer layer fuses into a tilioid structure, except in the tribe Shoreae (14). Pollen of most species of Dipterocarpoideae are smaller than 35 µm, whereas *Dipterocarpus* pollen ranges from ~50 to 100 µm. The diagnostic characteristics of *Dipterocarpus* pollen can mostly be seen in light microscopy (LM), whereas the identification of other genera also requires scanning electron microscopy (SEM) examination. No other plant family exhibits the combination of tricolpate configuration, absence or reduced endexine, and tilioid exine structure (table S2). By contrast, the subfamily Monotoideae pollen is tricolporate with the ectexine forming a fairly coarse tilioid structure (14). Phylogenetic analyses based on pollen morphological characters confirm the placement of seven of the eight fossil taxa within five extant genera of Dipterocarpoideae, namely *Vateriopsis*, *Dipterocarpus*, *Dryobalanops*, *Vatica*, and the three different *Shorea* sections—Anthoshorea, Parashorea, and Rubroshorea (figs. S6 to S8)—and the remaining one fossil taxon was placed within the genus *Monotes*, belonging to subfamily Monotoideae (figs. S6 to S8). The fossil pollen types represent five clades of Dipterocarpaceae based on our molecular phylogenetic analyses and previously published phylogenetic literature (15) (Fig. 3B, table S1, and appendix S2).

The discovery of fossil pollen with clear affinity to the subfamilies Dipterocarpoideae and Monotoideae from the Maastrichtian of Sudan and the Paleocene of India refutes frequent references to the unreliability in determination of fossil dipterocarp pollen (16). The previous skepticism largely stems from the fact that there are abundant records of Dipterocarpoideae leaves and woods from the Indian Neogene (17) but very few from the Late Cretaceous and Paleogene. This disparity most likely relates to many factors, including differences in the depositional setting. Other factors to bear in mind are (i) the possibility that the earliest phase of evolution of the family may have involved a long period of mosaic evolution and (ii) early macrofossils may not have borne anatomical features recognizable as Dipterocarpaceae.

The presence of pollen comparable to that of *Monotes* in the late Paleocene and early

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