

## 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).

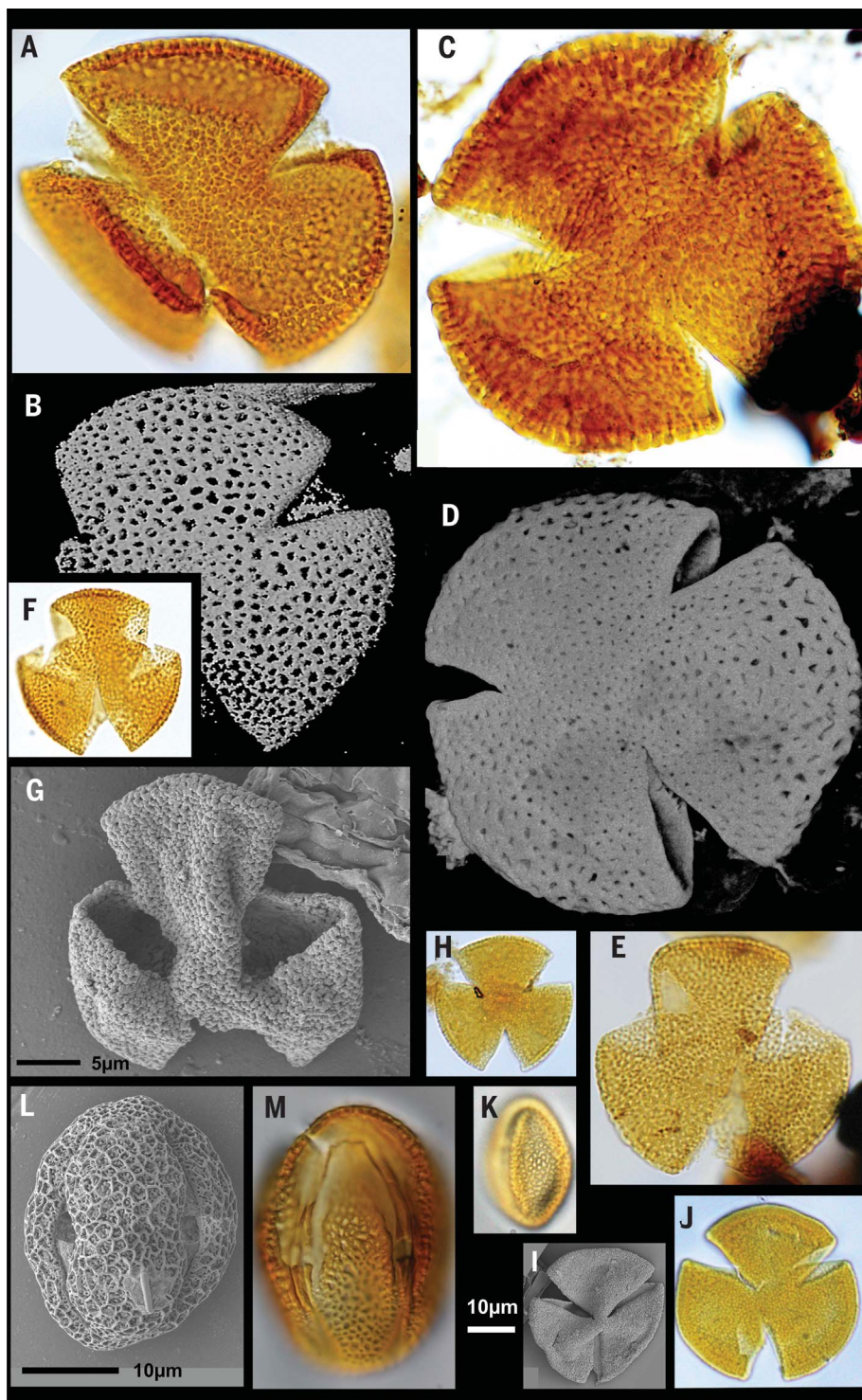
The discovery of fossil pollen with clear affinity to the subfamilies Dipterocarpoideae and Monotoideae from the Maastrichtian of Sudan and the Paleocene of India refutes frequent references to the unreliability in determination of fossil dipterocarp pollen (16). The previous skepticism largely stems 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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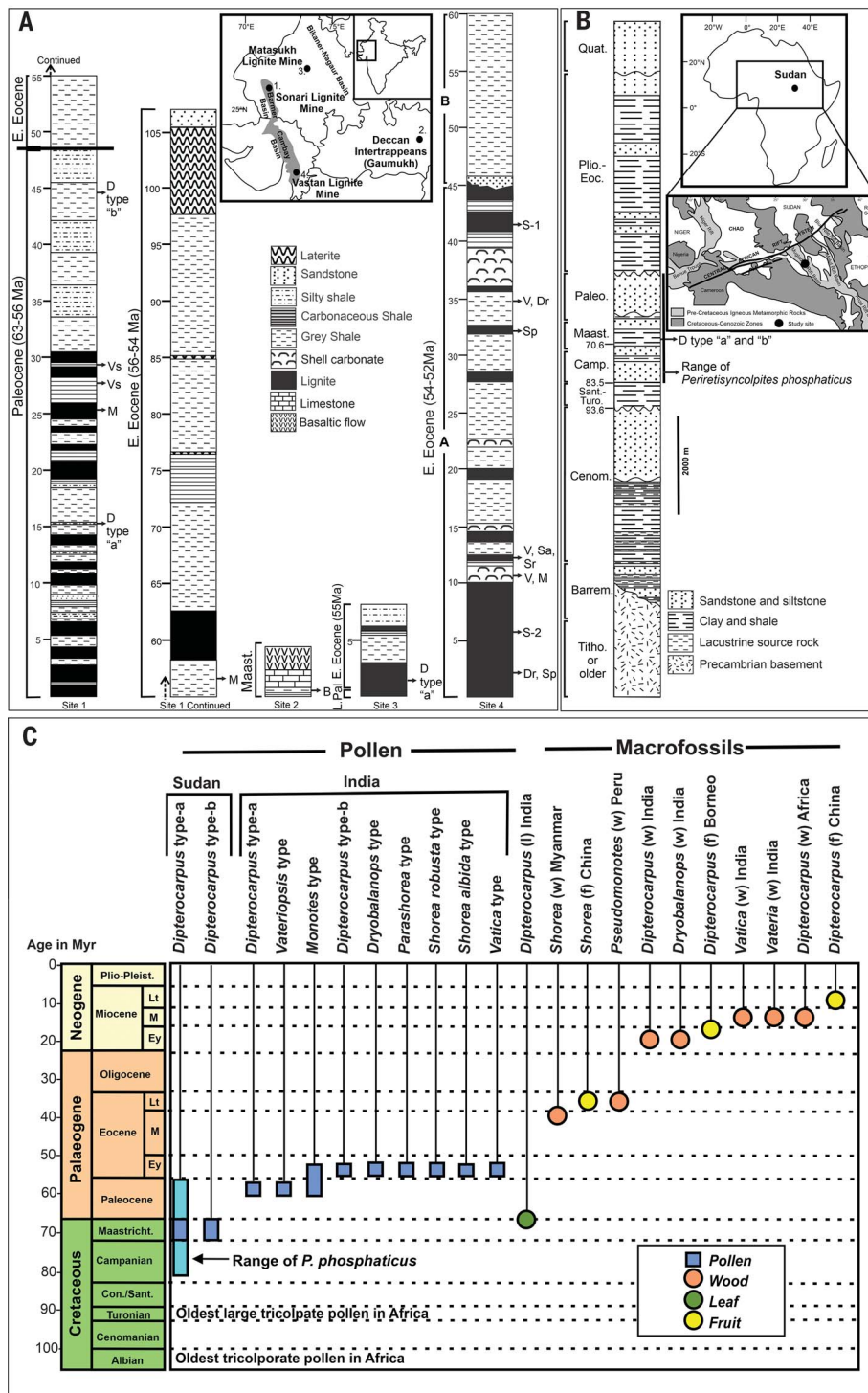


**Fig. 1. Pollen of Dipterocarpaceae from India and Sudan.** (A and B) *Dipterocarpus* type-a light microscopy (LM) image (A) and confocal laser scanning microscopy (CLSM) image (B) from the Matasukh Lignite Mine. (C and D) *Dipterocarpus* type-a LM image (C) and CLSM image (D) from the Baraka Formation, Sudan. (E) *Dipterocarpus* type-b LM image from the Sonari Lignite Mine. (F and G) *Dryobalanops* type LM image (F) and SEM image (G) from the Vastan Lignite Mine. (H) *Shorea* type LM image from the Vastan Lignite Mine. (I) *Vatica* type LM image from the Vastan Lignite Mine. (J and K) *Vateriaopsis* type LM image (J) and SEM image (K) from the Sonari Lignite Mine. (L and M) *Monotes* type LM image (L) and SEM image (M) from the Sonari Lignite Mine. All images are scaled to the 10- $\mu$ m bar at base of the plate except for (G) and (L), which are scaled as indicated.

Eocene of northwest India testifies to a much wider geographical range of Monotoideae during the early Paleogene. The Monotoideae, which also extends to the Neotropics, is estimated to have a stem molecular age of  $\sim$ 102 million years (Myr) (Fig. 3B and table S3), and it is likely that its distribution from Africa to South America was established at a very early age, as has been suggested by Moyersoen (18). Our results suggest the evolution of Dipterocarpaceae during the mid-Cretaceous [ $\sim$ 102.9 million years ago (Ma); 93.5 to 112.2 Ma] and its diversification across tropical Africa as the climate changed from semi-arid to wet seasonal and perhumid during the Late Cretaceous (Fig. 3B, fig. S9, and table S3). Thus, the estimated mid-Cretaceous molecular age of origin and fossil records dating back to the late Cretaceous to the early Eocene (table S3) from Africa and India indicate a longer evolutionary history of Dipterocarpaceae than that suggested previously (6, 15) and ranks the family as one of the first obligate megathermal eudicot clades to originate in the mid-Cretaceous of Africa.

The family diverged into two main lineages, Monotoideae with an approximate crown age of 72.1 Myr (63 to 84.5 Myr) and Dipterocarpoideae at  $\sim$ 94.6 Ma (85 to 104.3 Ma), and their adaptation to tropical dry seasonal and wet seasonal habitats, respectively, could be attributable to phylogenetic niche conservatism of habitat specialization in the family. We further suggest a subsequent climatic adaptation of Dipterocarpoideae to wet seasonal settings for the genus *Dipterocarpus* (clade I) and to perhumid settings for the divergence of the near-basal genera *Stemonoporus*, *Vateriopsis*, and *Cotylelobium* (clade IV). Subsequent divergences followed the same pattern, with *Dipterocarpus* (clade I) (wet seasonal) diverging into *Dryobalanops* (clade II) (perhumid) and *Shorea* diverging into perhumid (IIIA) and seasonal (IIIB) clades (Fig. 3B and table S3). As noted above, diversification in Dipterocarpoideae corresponded with the development of more wet seasonal and perhumid climates across tropical Africa since the Santonian-Coniacian, and they may have contributed to the first multistoried rainforests (1) (Fig. 4). In India too, the diversification pattern of dipterocarps follows the same trend, with the association of *Dipterocarpus*-type pollen (clade I) with pollen floras of seasonally wet climates during the Paleocene (19) and of pollen of clade IV (*Vatica*- and *Vateriopsis*-type pollen) with a perhumid climate during the late Paleocene–early Eocene (Fig. 4). The presence of *Shorea* fossil pollen (20) and possible wood in the Vastan lignites (21) and Myanmar red-beds (22), respectively, suggests the association of *Shorea* with perhumid and seasonal climates during the Eocene.

The dispersal of Dipterocarpaceae from Africa to India is most likely to have taken place when



**Fig. 2. Stratigraphy, location, and distribution of Dipterocarpaceae pollen in Sudan and India.**

(A) Location and stratigraphy of Indian localities: the Sonari Lignite Mine (site 1), the Gaumukh section (site 2), the Matusukh Lignite Mine (site 3), and the Vastan Lignite Mine (site 4). (B) Location and stratigraphy of the Baraka Formation in Sudan. (C) Stratigraphic distribution of Dipterocarpaceae pollen in Sudan and India and the oldest records of dipterocarp macrofossils from Africa, South America, and tropical Asia (6, 16, 24, 35–37). E. Eocene, early Eocene; Maast., Maastrichtian; L. Pal, late Paleocene; Quat., Quaternary; Plio.-Eoc., Pliocene-Eocene; Paleo., Paleocene; Camp., Campanian; Sant.-Turo., Santonian-Turonian; Cenom., Cenomanian; Barrem., Barremian; Titho., Tithonian; Myr, million years; B, geochemical biomarker; Vs, *Vateriopsis* type; M, *Monotes* type; D, *Dipterocarpus* type-a and *Dipterocarpus* type-b; V, *Vatica* type; Dr, *Dryobalanops* type; Sp, *Parashorea* type; Sa, *Shorea albida* type; Sr, *Shorea robusta* type.

the same climatic conditions prevailed on adjacent landmasses (23). For the seasonal *Dipterocarpus* and *Monotes*, appropriate habitats may have been available in Africa from ~75 Ma onward, but for the perhumid *Dryobalanops* and clade IV genera, habitats were unlikely to have been in place until the Late Maastrichtian (Fig. 4A). At this time, the African and Indian plates were separated by a wide ocean, which would have hampered the dispersal of large-seeded taxa, such as dipterocarps. The presence of Dipterocarpaceae in the geologically very young islands of Sulawesi (24) and New Guinea (25) testifies to their ability to disperse across substantial water bodies within the same climatic zone. The taxa present on these islands are all winged, which raises the possibility of their dispersal by wind, suggesting that a similar mechanism may have enabled the dispersal of dipterocarps from Africa to India. The wingless configuration seen in *Stemonoporus* and *Vateriopsis* may appear to conflict with this suggestion, but these genera may have lost wings after their arrival on their respective islands, as reflected by their fruit wing evolution patterns (fig. S10). This finding is congruent with a well-established pattern of loss of dispersal mechanism in plants arriving on islands (26, 27).

At the time of dispersal of dipterocarps from Africa to India, the Indian Plate was in collision with a series of Tethyan island arcs termed the Kohistan-Ladakh Island Arc (KLIA) (28), which was aligned with the Burma Plate (29) and the Horn of Africa, all within the equatorial zone. It has been suggested that this island arc could have provided stepping-stones between Africa and the Indian Plate along which both fauna (30) and flora (6, 23) were able to disperse. This series of islands may have been sufficiently closely spaced to permit the land or airborne dispersal of dipterocarps into India from Africa.

The early Maastrichtian Indian sediments are characterized by gymnosperm-dominated pollen floras (31), with the widespread occurrence of calcrete lithologies suggesting a strongly water-deficient climate (32) unsuitable for the tropical angiosperm flora to flourish. We suggest that the presence of a surprising diversity of modern tropical plant families' fossils in the form of woods, leaves, fruits, and pollen in the Late Maastrichtian Intertrappean sediments may reflect their dispersal from Africa via the KLIA along with members of Dipterocarpaceae. The establishment of a dispersal corridor from Africa to India along an island arc in a setting of changing climatic conditions from semi-arid to seasonal tropical may explain this sudden diversification of tropical elements on the Indian subcontinent. This filter corridor is here referred to as the Africa-India floristic interchange (AIFI).

The isolation of *Vateriopsis* on the Seychelles also alludes to its dispersal during the Maastrichtian. The Seychelles separated from

India between 75 and 68 Ma, and the crown age of *Vateriopsis* is 68 Myr (Fig. 3B), which suggests that it originated on the Seychelles or the Seychelles-India block.

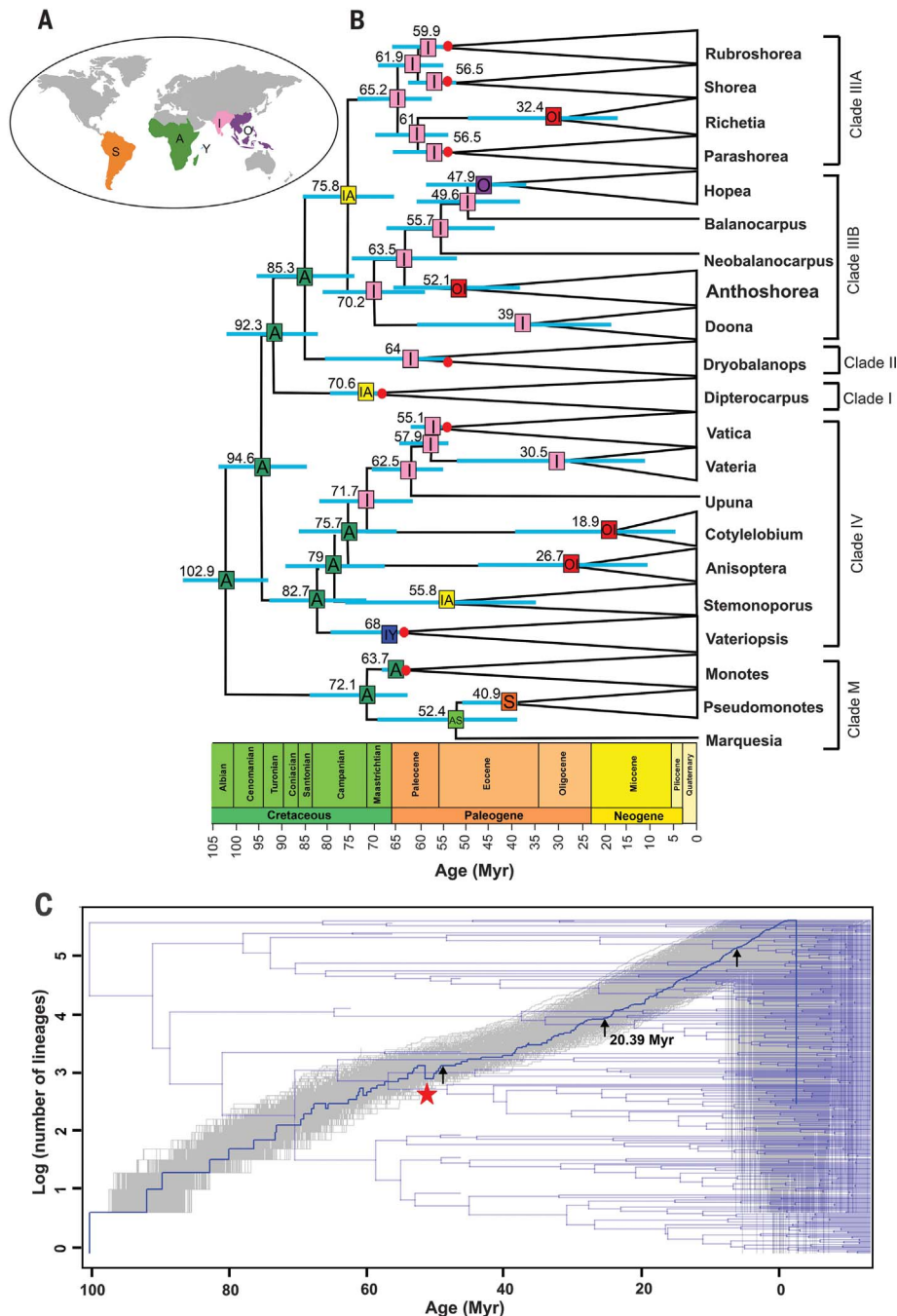
Two distinct *Vatica*-type pollen fossils are recorded in the early Eocene of the Vastan Lignite Mine. The stem and crown ages of

*Vatica* at 58 and 55 Ma, respectively, suggest its rapid evolution during the late Paleocene, either on the KLIA or on the Indian Plate within a perhumid climatic setting. *Shorea* clades exhibit an acceleration in divergence during the Late Maastrichtian and Paleocene—Doona at 70 Ma, Anthoshorea at 63 Ma,

Rubroshorea at 62 Ma, and Parashorea at 61 Ma. This divergence pattern is also supported by the presence of the fossil woods *Shoreoxylon panganense*, *Shoreoxylon burmense*, and *Shoreoxylon deomaliense* from the middle Eocene of the Burma Plate. These fossil woods occur in red-beds and are likely to have grown in an area of seasonally dry climate like that of *Shorea robusta* today, with which *S. panganense* has been compared (22). This suggests that ecological segregation of areas with perhumid and seasonally dry climates may have been a primary driver of *Shorea* diversification. The Dipterocarpoideae lineages are further suggested to have dispersed to Southeast Asia from India after the India-Asia collision during the middle to late Eocene (20). This implies that, despite rapid latitudinal changes, massive volcanism, and pronounced orogenic events, early dipterocarps managed to survive the Cretaceous-Paleogene (K-Pg) impact event and the Deccan Trap eruptions and eventually dispersed to Southeast Asia.

Despite the doubtful identification of an *Anisoptera* fossil from the London Clay Formation (33) as a dipterocarp, the expansion of the plant family Dipterocarpaceae into northern mid-latitudes via boreo-tropical dispersal routes (34) cannot be dismissed. The family might have dispersed from Africa or India to Eurasia during the Paleocene-Eocene hothouse periods of frost-free and humid climate in Eurasia. The validation of boreo-tropical migration of Dipterocarpaceae requires the recovery of authentically identified dipterocarps from the early Paleogene of the boreotropics.

Dipterocarpaceae maintains high endemism in Asian forests. Clades with a long evolutionary span are clearly paleoendemics, such as *Monotes*, *Upuna*, *Vateriopsis*, *Stemonoporos*, *Dipterocarpus*, and *Dryobalanops* (55.8 to 70.6 Myr) (table S3). The isolation of *Upuna* in Borneo, *Vateriopsis* in the Seychelles, *Stemonoporos* in Sri Lanka, and *Monotes* in Africa and Madagascar are extreme examples of such paleoendemism. However, most younger clades, such as *Anisoptera*, *Vateria*, and *Shorea* section Doona, with shorter evolutionary ages (18.9 to 39 Myr) are also paleoendemics because all show a clear range reduction since the Pliocene—mainly as a result of the expansion of seasonally dry climates across India (6, 23). Most neoendemism is therefore likely to be at the subclade level and is reflected in the increase in diversification after 20.4 Ma (Fig. 3C) and may account for the notable diversity of genera, such as *Shorea*, in areas like Borneo. The evolution of wingless and winged fruit in Dipterocarpaceae also explains some patterns of endemism in the family (fig. S10). The wingless species of the family are heavily represented as endemics in island habitats. Winglessness may restrict dispersal

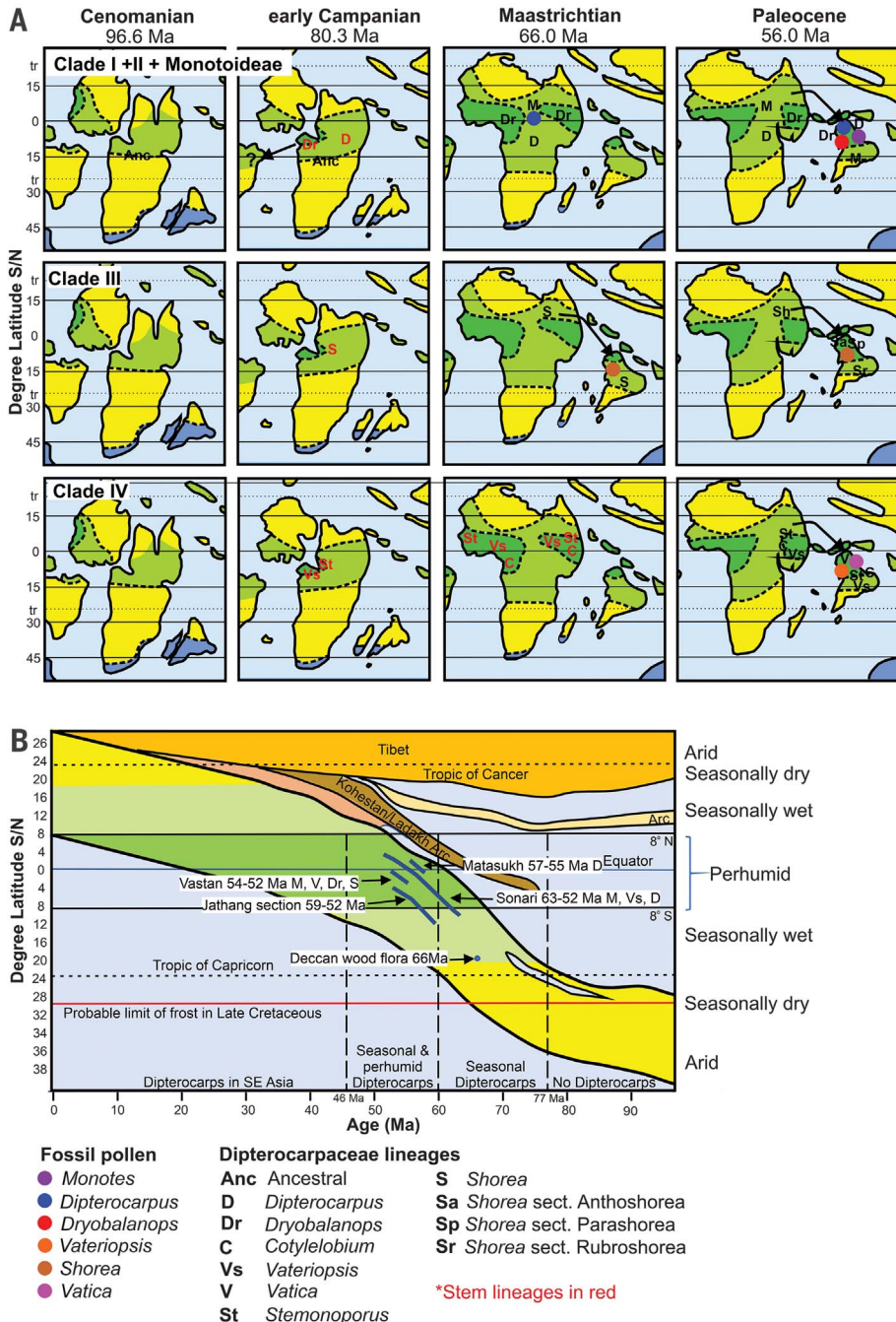


**Fig. 3. Divergence dating, biogeography, and diversification pattern of Dipterocarpaceae.** (A) Dipterocarpaceae geographic realms. S, South America; A, Africa; I, Peninsular India, including Bangladesh, Tibet, and Sri Lanka; Y, Seychelles; O, Southeast Asia, including Indonesia, Indochina, and China. (B) Dipterocarpaceae dated phylogram with 95% credibility intervals and ancestral area reconstruction. The clades are labeled following Heckenhauer *et al.* (14). Fossil occurrences are indicated by red dots, and reconstructed ancestral areas are shown for each internal node within rectangular boxes. (C) The LTT plot demonstrating Dipterocarpaceae diversification rates. The star symbol and arrows indicate diversification shifts over time.

distances, resulting in higher proportions of seed landing on preferred soil types, such as podsoils and humic ultisols. Such microhabitat adaptation might have led to paleo- and neo-endemism of some taxa on islands. Further, we found evidence for an increased speciation rate for the family after 20.4 Ma (Fig. 3C), coinciding with the expansion of perhumid climates across Southeast Asia (1, 23). Thus, we suggest

that after the India-Asia collision, Dipterocarpoideae species further adapted to wet climatic conditions, began to radiate and spread increasingly into the wet lowlands of the Sunda region, and became major components of Southeast Asian rainforests. By contrast, the Monotoideae went extinct from the Indian subcontinent during the mid-late Eocene and hence were unable to disperse to Southeast Asia.

The discovery of Dipterocarpoideae and Monotoideae fossils from the Maastrichtian of Sudan and the Maastrichtian, Paleocene, and early Eocene of India strengthens our understanding of tropical rainforest evolution across Asia in a deep time scale and substantially increases the recognized footprint of the AIFI in Asian tropical rainforests. However, our understanding of dispersals between Africa and India during the Late Cretaceous and the earliest Cenozoic is at a very early stage. Additional studies of fossil angiosperms from the African continent, India, and Southeast Asia will further clarify the manner in which megathermal plant taxa dispersed from Africa via India to the maritime continent of Southeast Asia, where they subsequently underwent explosive diversification within Malaysia's lowland rainforests.



**Fig. 4. Plate tectonic and paleoclimatic reconstruction and the position of the Africa and Indian plates over time.** (A) Plate tectonic and paleoclimatic reconstructions for Africa and India for the Cenomanian to the Paleocene, and suggested areas of clade differentiation along with their dispersal routes. (B) A diagrammatic representation exhibiting the position of the Indian plate through time, from the mid-Cretaceous to the present, showing paleolatitude shift in relation to paleoclimate zones over time.

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38. M. Bansal *et al.*, Southeast Asian Diptero carp origin, and diversification driven by Africa-India Floristic Interchange. *Figshare*, dataset (2021); <https://doi.org/10.6084/m9.figshare.16727071.v1>.

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M.B., S.K.N., and V.P. wrote the manuscript with inputs from all the authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All supporting data and analyses are available in the supplementary materials. The raw data (nexus files of phylogenetic trees, alignment files, and GenBank accession numbers) required to replicate the study are made publicly available on Figshare (38).

#### SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.abk2177](https://science.org/doi/10.1126/science.abk2177)

Materials and Methods

Appendices S1 to S8

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

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### The origin of the dipterocarps

The Dipterocarpaceae are a prominent family of mainly tropical trees, reaching particularly high diversity and dominance in present-day Southeast Asian rainforests, where several species regularly reach heights of 50 meters or more. Bansal *et al.* used fossil pollen, molecular data, and paleobiogeographic analysis to study the origin and dispersal of the family (see the Perspective by Hoon and Lim). The authors trace the origin of the dipterocarps to the mid-Cretaceous of tropical Africa, and postulate subsequent dispersal eastward across an Indian Ocean island arc to the then-isolated Indian subcontinent. The collision of the subcontinent with the Asian landmass then facilitated further dispersal toward Southeast Asia. —AMS

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