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ORIGINAL ARTICLE

Dipterocarpus (Dipterocarpaceae) leaves from the K-Pg of India: a Cretaceous Gondwana presence of the Dipterocarpaceae

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Abstract

Dipterocarpaceae, a tropical plant family that forms a major component of low-lying rainforests in Southeast Asia, is represented by a large number of fossils from the Cenozoic sedimentary successions of India, but the origin and antiquity of this family has been actively debated. The earliest reliable dipterocarp megafossils so far reported in India come from Eocene (34–23 Ma) sediments of the Cambay Basin of western India and in Southeast Asia from Eocene (34–23 Ma) sediments within China. More recently, pollen attributable to the family was recovered from Maastrichtian sediments in India, but because pollen is highly durable, can be transported over long distances and offers only low taxonomic resolution, more definitive evidence is required to demonstrate, unequivocally, that the Dipterocarpaceae were in India prior to its contact with Eurasia early in the Paleogene. The Late Cretaceous (Maastrichtian) leaf fossils documented here have an affinity with the extant genus *Dipterocarpus* (family Dipterocarpaceae) and come from the Mandla Lobe Deccan Intertrappean Beds of Central India. They provide compelling evidence that this tropical rain forest element was present in India during Chron 29R, which spans the K-Pg transition, and when the bulk of the subcontinent was still in the Southern Hemisphere. We suggest that only later did their dispersal to Southeast Asia occur, consistent with the "Out-of-India" hypothesis. These fossil leaves represent the earliest reliable fossil record of the Dipterocarpaceae and, in particular, *Dipterocarpus*.

Keywords Deccan intertrappean beds · Dipterocarpaceae · India · Late Cretaceous · Leaf fossils · Palaeophytogeography

Introduction

The Dipterocarpaceae, a well-known family of trees in today's Asian tropical lowland rain forests, has received considerable attention due to its economic and ecological significance (Aiba and Kitayama 1999). Currently, the dipterocarps dominate the international tropical timber market and therefore play an important role in the economy of many Southeast Asian countries (Poore 1989). All dipterocarps are arborescent, resinous, and are the main constituents of tropical rain forests of Asia (Ashton 1982, 1988; Aiba and Kitayama 1999). The Dipterocarpaceae comprise three subfamilies with an intercontinental disjunct distribution: subfamily Dipterocarpoideae is found in the Asian tropics and Seychelles; Pakaraimoideae are endemic in Guyana and Venezuela, South America; and Monotoideae occur in the African tropics, Madagascar and southeastern Colombia, South America (Maguire and Ashton 1977; Ashton 1982, 2003; Maury-Lechon and Curtet 1998).

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Based on molecular phylogenetic studies, the Dipterocarpaceae are considered a member of the order Malvales (Alverson et al. 1998; Dayanandan et al. 1999; APG IV 2016). The family consists of 16 genera and about 680 species distributed within tropical Asia, Africa and South America, but 92% of the species occur throughout the lowland equatorial rainforests of Asia (Mabberley 1997; Maury-Lechon and Curtet 1998). In south Asia, the dipterocarps grow mainly in tropical peninsula India from the Karnataka coast to the tip of southern India, and within northeastern India.

Dipterocarps are well known in Cenozoic fossil floras of India, Northeast and East Africa as well as South and Southeast Asia (Muller 1981; Bande and Prakash 1986; Lakhanpal et al. 1984; Guleria 1992; Dutta et al. 2009, 2011; Srivastava and Mehrotra 2010; Rust et al. 2010; Shukla et al. 2012, 2013; Feng et al. 2013; Khan et al. 2011, 2015, 2016). They are mostly represented by fossil woods (Bancroft 1935; Ramanujam and Rao 1967; Schweitzer 1958; Navale 1962; Edye 1963; Prakash 1965a, b; Lakhanpal 1970; Awasthi 1974; Lemoigne 1978; Roy and Ghosh 1981; Awasthi and Srivastava 1992; Prasad 1993; Prakash et al. 1994; Guleria 1996; Awasthi and Mehrotra 1997; Srivastava and Saxena 1998; Mehrotra et. al. 1999; Tiwari and Mehrotra 2000; Bera and Banerjee 2001; Prasad and Tripathi 2000; Mehrotra and Bhattacharyya 2002; Shar et al. 2007; Gregory et al. 2009; Wang et al. 2006; Rust et al. 2010) and leaves (Lakhanpal and Guleria 1987; Bande and Srivastava 1990; Prasad 1990a, 1994; Antal and Awasthi 1993; Antal and Prasad 1996, 1997; Konomatsu and Awasthi 1999; Prasad et al. 1999; Prasad et al. 2004; Joshi and Mehrotra 2007; Prasad and Pandey 2008; Feng et al. 2013; Khan et al. 2015; Prasad et al. 2016, 2019) with fewer records of fruit wings (Grote 2007; Khan and Bera 2010; Shi and Li 2010; Shi et al. 2014; Shukla et al. 2012) and pollen (Muller 1981; Acharya 2000; Songtham et al. 2005; Rugmai et al. 2008; Dutta et al. 2011). In India, megafossil records of Dipterocarpaceae are found only from the early Eocene onwards up to the Plio-Pleistocene (Lakhanpal et al. 1984; Dutta et al. 2009, 2011; Khan et al. 2011, 2015, 2016; Shukla et al. 2012). No dipterocarp fossils older than the Eocene have been found in Southeast Asia (Feng et al. 2013; Shi et al. 2014; Wang et al. 2018).

Here we report and describe, for the first time, leaf fossils of *Dipterocarpus* C. F. Gaertn., of the family Dipterocarpaceae, from the latest Cretaceous (Maastrichtian) to earliest Danian (Chron 29R, 66–65 Ma) Deccan Intertrappean Beds of India, and prior to the most likely date of India-Asia land contact. This new find from India is the oldest megafossil example of the Dipterocarpaceae to be confirmed from the fossil record to-date, and one that provides the strongest evidence so far discovered for a Gondwanan presence of this important family of trees that today are a major characteristic component of tropical lowland forests in Asia.

Material and methods

Four fossil leaf specimens studied here were collected during fieldwork in 2018 from the latest Maastrichtian (Late Cretaceous) to earliest Danian (early Paleocene) sediments of the Mandla Lobe Deccan Intertrappean Beds of Umaria (ca. lat. 23° 5.451′ N, long. 80° 37.652′ E) in Dindori District, Madhya Pradesh, Central India (Fig. 1).

The Deccan traps were formed as a result of successive enormous outpourings of lava that spread over a vast area of western, central and southern India at a critical time in the development of modern angiosperm-dominated vegetation (Smith et al. 2015a, b). Much of the Mandla Lobe Intertrappean sediments represent lacustrine and fluviatile environments that formed during quiescent periods between volcanic episodes, while the Indian plate was still an isolated land mass moving towards Asia (Chatterjee et al. 2013) (Fig. 2). Current studies indicate, based on radiometric dating ($^{40}Ar/^{39}Ar$ dating), planktonic foraminifera and magnetostratigraphy, that the age of these Intertrappean sediments is latest Maastrichtian–earliest Danian (Venkatesan et al. 1993; Khosla 1999; Hofmann et al. 2000; Sheth et al. 2001; Keller et al. 2009; Chenet et al. 2009; Srivastava et al. 2014, 2015; Renne et al. 2015; Schoene et al. 2015; Smith et al. 2015a, b). The fossils described here come from the Mandla Lobe, a 900 m thick package of 29 flows dated as primarily belonging to Chron 29R (Pathak et al. 2016), lasting < 1 Ma and spanning the K-Pg transition. At the time of deposition, the fossil site would have been between 15 and 20°S (Molnar and Stock 2009; Chatterjee et al. 2013).

Macroscopic images of fossil and relevant extant specimens were photographed using a digital camera (Canon Power Shot A720IS) (Figs. 3, 4, 5, 6, 7). In order to isolate leaf cuticles, the conventional method of using Schulze's solution for maceration was employed (treatment with 48% hydrofluoric acid followed by oxidation with 50% nitric acid and repeated washing after treating with 2–5% potassium hydroxide) (Kerp and Krings 1999). Structural details, including epidermal features of fossil leaves and their nearest living relatives, were recorded using an incident light compound microscope (Stemi SV 11, Zeiss), and a transmitted light compound microscope with a photographic attachment (Zeiss Axioskop 40).

Taxonomic determination required extensive literature and herbarium searches to compare the Deccan leaf specimens with other previously identified fossil and extant taxa that share similar morphological features. Extant *Dipterocarpus* specimens were examined and photographed in the collections of the Central National Herbarium (CAL), Sibpur, Howrah. Terms used to describe the leaves are in conformity with the standard terminology for architectural

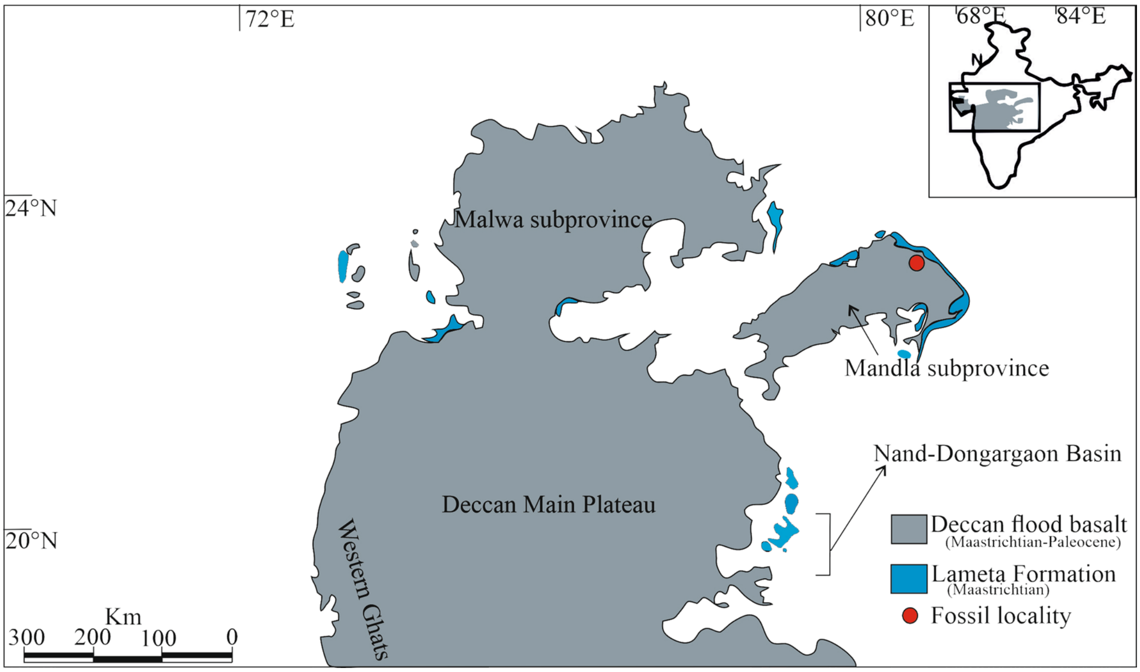

Fig. 1 Map showing Deccan Volcanic Province (DVP), red star showing fossil locality (modified after Smith et al. 2015a, b)

Fig. 2 Palaeogeographic reconstruction for the end Cretaceous (Chron 29R, ~ 65 Ma) simplified from Chatterjee et al. (2013), showing the position of the fossil site (red filled circle), the Kohistan-Ladakh Island Arc and the open south Atlantic

description of dicotyledonous leaves (Hickey 1973; Leaf Architecture Working Group 1999). Author citation of plant fossil species is mainly after Punt (1994). Both the fossil (specimen numbers SKBUH/PPL/D/L/1; SKBUH/PPL/D/L/7, SKBUH/PPL/D/L/18; SKBUH/PPL/D/L/28) and modern specimens and slides are deposited in the Museum of the Department of Botany, Sidho-Kanho-Birsha University (SKBU).

Results

One recovered fossil leaf from the Late Maastrichtian-Danian sediments of the Deccan Intertrappean Beds of Central India is identified as a new species: *Dipterocarpus dindoriensis* Khan, R.A.Spicer & Bera, sp. nov., having an affinity with the extant *Dipterocarpus alatus* Roxb. & G. Don (Fig. 3). Three other leaf impressions recovered from the same locality are identified only as *Dipterocarpus* and display an affinity with the modern genus (Fig. 4), but due to specimen incompleteness it is difficult to assign the remains at species level. The distinctive macromorphological characteristic features of the fossil leaves are mesophyll size, coriaceous texture, the obtuse to rounded base, pinnate craspedodromous venation, narrow to moderate acute angle of divergence of secondary veins, and abruptly curved secondary veins near the margin and percurrent tertiary veins. We also examined the cuticular characters of both fossil and modern leaves of *Dipterocarpus* (Fig. 3) to confirm the identification of the fossil specimens. Based on the combination of both macromorphology (venation pattern) and micromorphological epidermal features (pentagonal to hexagonal epidermal cells; curved anticlinal cell walls,

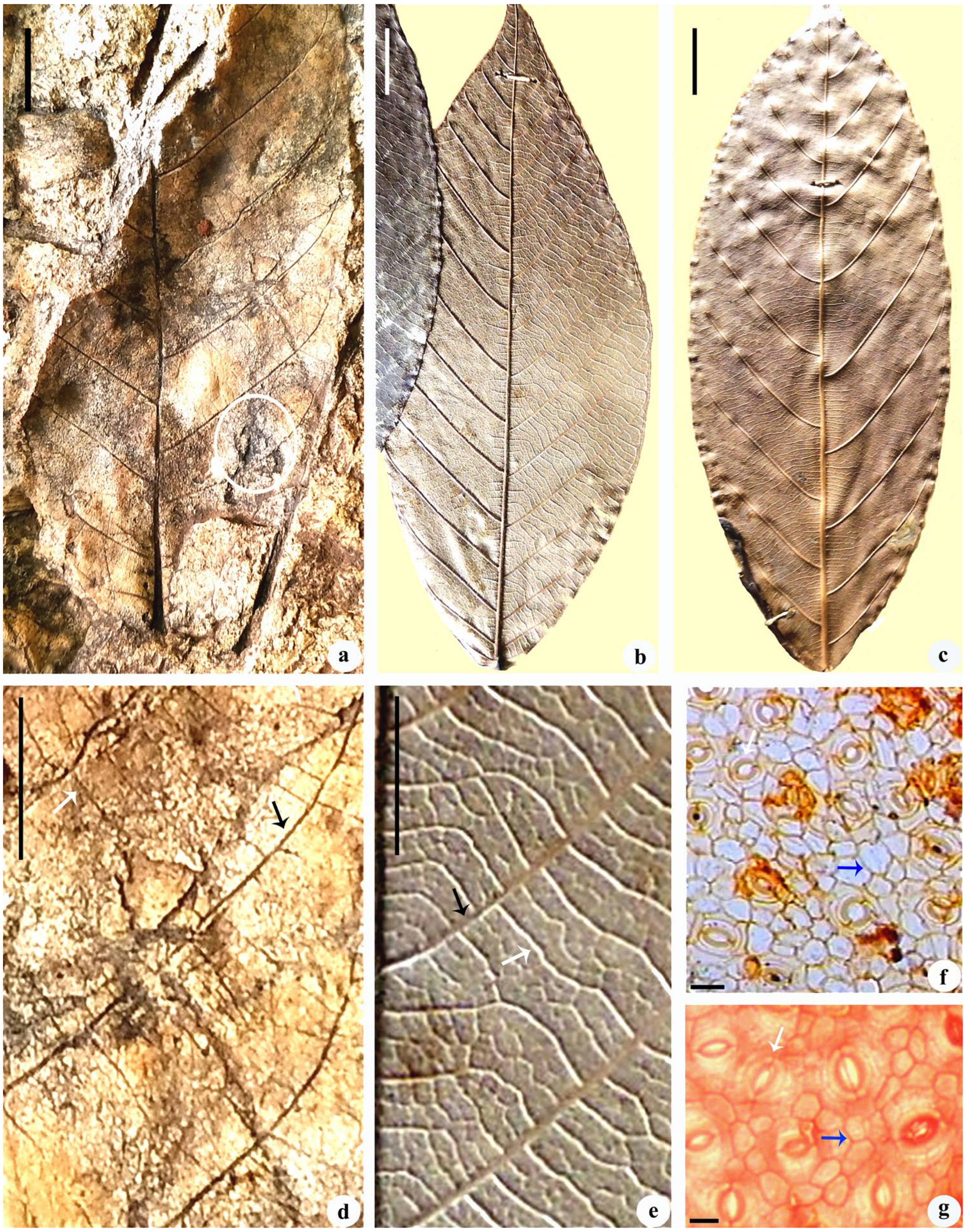

Fig. 3 *Dipterocarpus* leaves. **a** Fossil leaf of *Dipterocarpus dindoriensis* Khan, R.A.Spicer & Bera, sp. nov. showing size, shape and venation pattern; **b**, **c** modern leaf of *D. alatus* showing similar size, shape and venation pattern; **d** enlarged portion of the fossil leaf showing secondary veins (black arrow) and tertiary veins (white arrow); **e** enlarged portion of the modern leaf of *D. alatus* showing similar secondary veins (yellow arrow) and tertiary veins (blue arrow) (scale bar = 1 cm); **f** *D. dindoriensis* - Abaxial cuticle with anticlinal wall (blue arrow) and paracytic type stomata (white arrow) (scale Bar = 10 µm); **g** *D. alatus* - Abaxial cuticle with same type of anticlinal wall (blue arrow) and paracytic type stomata (white arrow) (scale bar = 10 µm)

paracytic type stomata, stomata size, shape, orientation as well as stomatal distribution) one leaf specimen is assigned to the genus *Dipterocarpus* and *D. alatus* is regarded as the closest possible modern related form. The detailed systematic description refers only to the newly discovered fossil leaf specimen named here as *D. dindoriensis* Khan, R.A.Spicer & Bera, sp. nov., having an affinity with the extant *D. alatus*.

Discussion

Information on dipterocarp fossils, particularly the more convincing megafossils, not only can provide important information regarding the origin of the Dipterocarpaceae, but also contributes to our knowledge of the phylogenetic history of this important family. Various scenarios have been proposed for the dipterocarp origin, and to contextualize the new finds described here we review those scenarios based on current evidence.

Much of the interpretation of the fossil record in terms of dipterocarp history depends upon the timing of land contact between India and Asia, despite the fact that India was not entirely biotically isolated before that contact was made. Even Late Cretaceous deposits of the sub-continent contain a mixture of Laurasian (Jaeger et al. 1989; Sahni and Bajpai 1991; Prasad and Sahni 1999; Samant et al. 2013), and Gondwanan (Krause et al. 1997; Prasad and Sahni 1999, 2009; Sahni and Prasad 2008) taxa, as

Fig. 4 *Dipterocarpus* leaves. **a**, **b** Fossil leaves of *Dipterocarpus* showing characteristic secondary veins; *c* part of modern leaf of *D. kerrii* showing similar nature of secondary veins; **d** fossil leaf of *Dipterocarpus*; **e** another fossil leaf of *Dipterocarpus* (scale bar = 1 cm)

well as endemics (Whatley and Bajpai 2006), and Morley (2018, p. 213) argues for a "rich and rapidly diversifying megathermal angiosperm flora rooted in Africa" before land contact was made.

In the context of dipterocarps, land contact is essential because the seeds of Dipterocarpaceae can be dispersed only over land, not by sea, because of their salt intolerance and lack of dormancy (Ashton 1982; Shi and Li 2010). Such a land contact between India and east Africa has been postulated by Chatterjee and Scotese (2010), but in a subsequent paper Chatterjee et al. (2013, p. 238) state that "Soon after the Deccan eruption, India drifted northward as an island continent by rapid motion carrying Gondwana biota". The same authors suggest that India, once separated from Madagascar at ~ 90 Ma, collided with the Kohistan-Ladakh Island Arc (KLIA) at ~ 85 Ma, and it was not until ~ 52 Ma that the collision with Asia was initiated. If this scenario is correct, it suggests that in the latest Cretaceous the India-KLIA amalgam was an island system separated from both Africa and Asia.

Bearing this latest Cretaceous island continent scenario in mind, two divergent hypotheses have been advanced to explain the origin and phytogeographical history of the Dipterocarpaceae. The first hypothesis favors a South East Asia origin for the family, while the other advocates a Gondwanan origin. The former gets strong support from the megafossils recorded from Paleogene sediments (Bande and Prakash 1986; Feng et al. 2013) and the remarkable species richness of the family in South East Asia today (Mabberley 1997). In this view, it is hypothesized that the dipterocarps migrated into India from South East Asia once the land connection between the Indian and Asian plates was established (Lakhanpal 1970; Awasthi 1996; Sasaki 2006). Although some Paleogene fossils of this family in

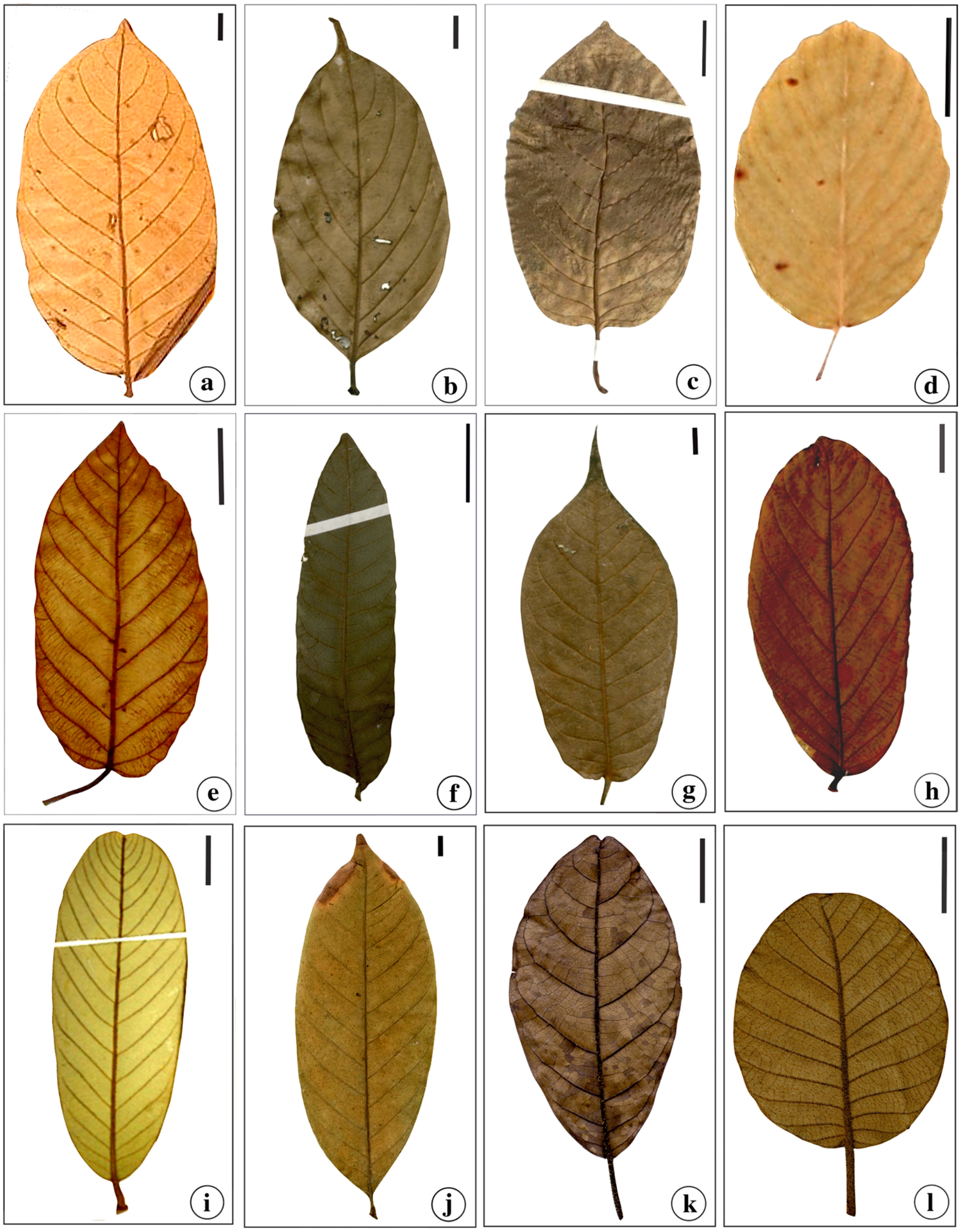

Fig. 5 Extant leaves of comparable dicot genera. **a** *Aglaia*; **b** *Hopea*; **c** *Mitragyna*; **d** *Berchemia*; **e** *Shorea*; **f** *Rhus*; **g** *Uvaria*; **h** *Bridelia*; **i** *Fissistigma*; **j** *Lansium*; **k** *Eremolaena*; **l** *Pentachlaena* (scale bar = 1 cm)

the form of pollen and wood have been reported from India (Rust et al. 2010; Dutta et al. 2011), their identification is questionable (Shukla et al. 2013). Further, both pollen and wood fragments can be transported long distances prior to their final deposition and preservation. So, the abundance of authentic leaf and fruit megafossil records, which are far less durable and are usually preserved proximal to their growth site, are critical for locating unambiguous dipterocarp presence. Such fossils occur in Paleogene sediments of Southeast Asia (Bande and Prakash 1986; Feng et al. 2013), but only in Neogene sediments of India (Khan et al. 2010, 2011, 2015, 2016; Shukla et al. 2012, 2013), which could indicate that the family arrived in India after land contact was established between India and Eurasia (Srivastava and Mehrotra 2010). However, this hypothesis cannot explain the present-day distribution of this family in other Gondwanan components such as South America, Africa, Madagascar and the Seychelles, because these areas were never connected with South East Asia (Metcalfe 1996; Ali and Aitchison 2008).

The second hypothesis is referred to as the "Out-of-India" hypothesis and holds that some Asian biotic elements have an ancient Gondwanan origin and arrived in Asia by rafting on the Indian plate (McKenna 1973). The dramatic latitudinal and climatic changes that affected India during the Late Cretaceous and early Cenozoic, as the plate travelled

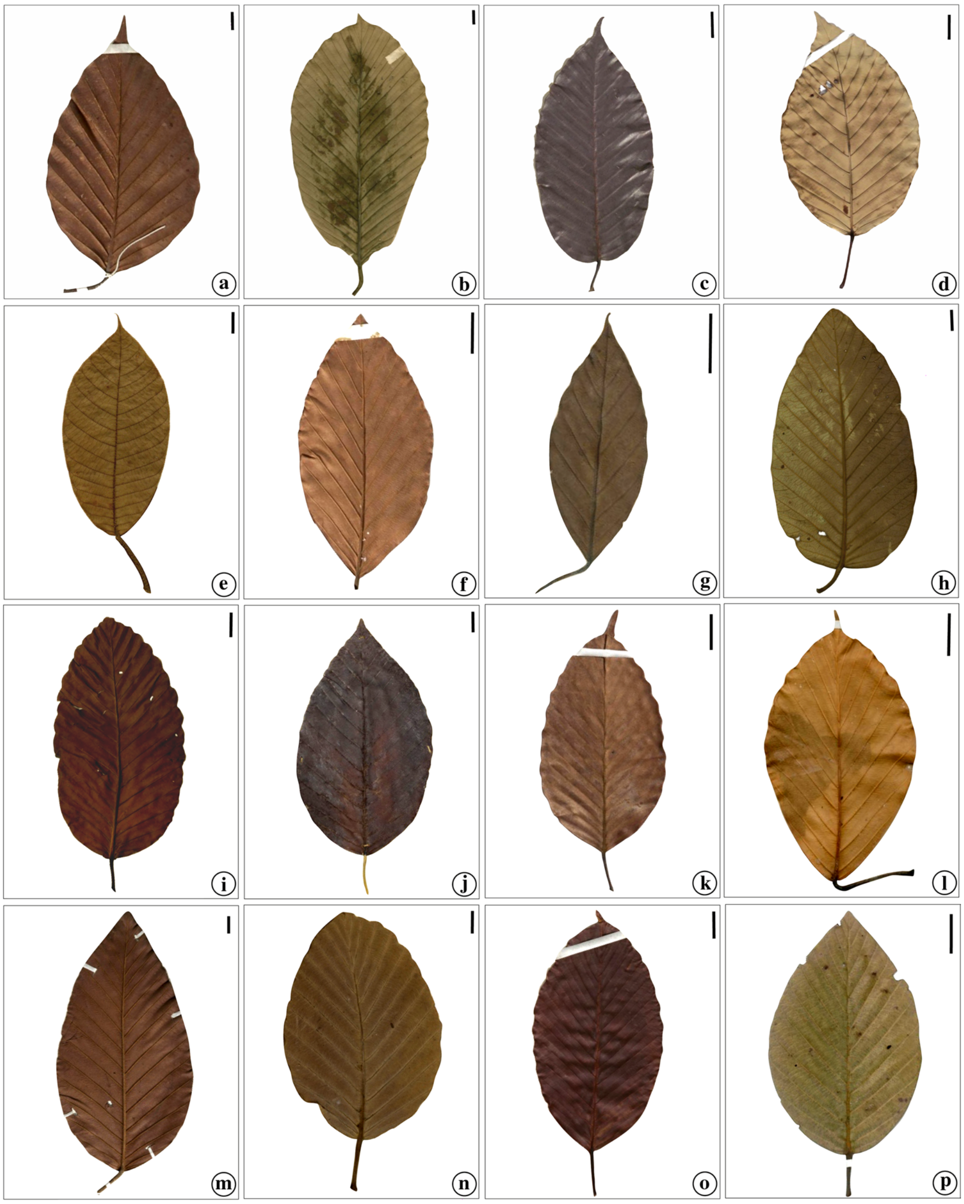

Fig. 6 Extant *Dipterocarpus* leaves. **a** *Dipterocarpus acutangulus*; **b** *D. cornatus*; **c** *D. turbinatus;* **d** *D. grandiflorus*; **e** *D. critinus*; **f** *D. gracilis*; **g** *D. fagineus*; **h** *D. intricatus*; **i** *D. hasseltii*; **j** *D. indicus*; **k** *D. costatus*; **l** *D. kerrii*; **m** *D. rigidus*; **n** *D. oblongifolius*; **o** *D. costatus*; **p** *D. nudus* (scale bar = 1 cm)

from Gondwana across the equator before colliding with Asia, caused numerous extinctions among the rafted biota, making it difficult to find evidence for out-of-India dispersal (Raven and Axelrod 1974). Historically fossils provided only limited support for angiosperm (Bande and Prakash 1986; Bande 1992; Klause et al. 2016; Morley, 2018) and vertebrate (Krause and Maas 1990) dispersal from India into Asia, and range shifts of dated phylogenies show that after 65 Ma the maximal number of dispersal events from India to Asia accelerated, but was consistently less than that from Asia to India (Klause et al. 2016). By the middle Miocene, when the rate of dispersal events both ways began to decline, the rate of India to Asia dispersal events was only half of that from Asia to India. In dipterocarps, current distribution patterns, microfossils and fossil resin chemistry suggest an out-of-India dispersal, but authentic fossil documentation has so far not been available. The megafossils reported here help fill that gap in our knowledge, but uncertainties remain as to where and when in Gondwana the first dipterocarps appeared.

A “Gondwana Origin” for dipterocarps (Ashton 1982; Ducousso et al. 2004; Dutta et al. 2011) does not necessarily mean that they first arose in India. If the dipterocarps originated in western Gondwana, it would easily explain their current distribution in Africa and South America, but to also occur in India this must have happened before East Gondwana (India, Antarctica and Australia) broke away from West Gondwana (Africa and South America) at

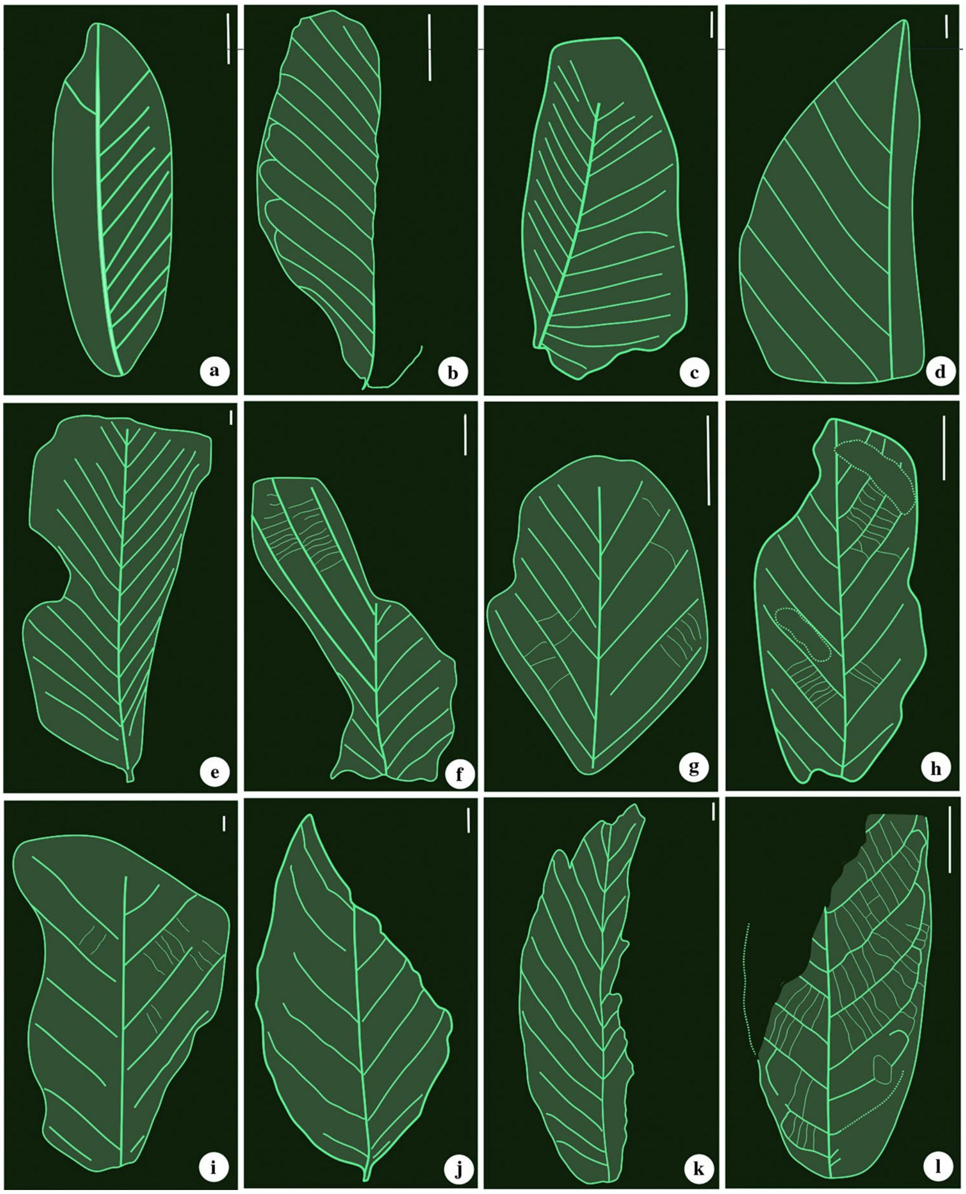

Fig. 7 Fossil *Dipterocarpus* leaves. **a** *Dipterocarpus siwalicus* Antal & Prasad 1996; **b** *D. suraikholaensis* Prasad & Pandey 2008; **c** *D. siwalicus* Awasthi & Prasad 1990; **d** *D. siwalicus* Prasad & Pradhan 1998; **e** *D. koilabasensis* Prasad et al. 1999; **f** *Dipterocarpus* sp. Srivastava et al. 2017; **g** *D. siwalicus* Prasad & Tripathi 2000; **h** *D. siwalicus* Khan et al. 2011; **i** *D. koilabasensis* Khan et al. 2015; **j** *D. koilabasensis* Prasad et al. 2019; **k** *D. palaeoindicus* Prasad et al. 2019; **l** *D. dindoriensis* Khan, R.A.Spicer & Bera, sp. nov. (scale bar = 1 cm)

170 Ma. This would place the origins of the dipterocarps remarkably early in angiosperm evolution and at high, cool, southern latitudes. This seems highly unlikely given the lack of a relevant fossil record and their exclusively tropical distribution today. It is possible that dipterocarp origins were in West Gondwana after 170 Ma, but that would have prevented them being in India while it remained an island continent before contact with Asia, and we would expect widespread Cretaceous fossil records in Africa and South America, but not India. Known fossil records do not support this.

The consistent ectomycorrhizal (ECM) status in the three subfamilies of Dipterocarpaceae and Sarcolaenaceae Caruel, a tree family endemic to Madagascar, has been used to argue that they were likely all derived from a single common ancestor present in Gondwana during the Cretaceous before separation of the South American and India-Madagascar-Seychelles blocks (Ducousso et al. 2004; Beimforde et al. 2011). According to Chatterjee et al. (2013), India, attached to Madagascar, maintained contact with Somalia until ~ 120 Ma and then Madagascar separated from India at ~ 90 Ma as India was approaching the southern sub-tropical latitudes. This would again suggest that the dipterocarps arose quite early in the angiosperm radiation and were extra-tropical in origin, although warm Late Cretaceous global temperatures (e.g. Frakes 1979; Skelton 2003) would have meant that they need not have been cold-adapted.

Alternatively, the origin of the dipterocarps may have been on the KLIA, which was at low latitudes throughout the

Late Cretaceous, or in Africa which was close to the KLIA. If the dipterocarp origins were on the KLIA or in Africa in the late Early Cretaceous, before the formation of the southern Atlantic at ~ 100 Ma, it would easily explain their current distribution, but this would need fossil confirmation from remnants of the KLIA in today's western Himalaya and/or in Africa. More importantly, it would again require a very early origin for the family. Morley (2000) suggested that the family underwent widespread expansion during the warm climates of the Paleogene into the rain forests of Africa or South America before their separation, but because the Atlantic formed in mid Cretaceous time and an arid rift valley must have existed before separation, this scenario is also not without its problems. Nevertheless, this hypothesis is generally accepted currently as it readily explains these transoceanic disjunct distributions (Dayanandan et al. 1999; Ashton 2003). In this scenario, India inherited the dipterocarps during, or after, collision with the KLIA ~ 95 Ma and would still have been the dipterocarp delivery route to Asia. A Cretaceous migration of this moisture-loving group out of Africa eastwards along the southern margin of Asia would have been frustrated by the arid landscape that prevailed across southern Eurasia at that time, and this aridity persisted into the Paleocene (Farnsworth et al. 2019 and references therein). It is also worth noting that what Late Cretaceous and Paleocene fossils there are in South East Asia suggest a depauperate flora lacking families, such as the dipterocarps, that are so characteristic of the region today (Morley 2018). On balance our fossil discovery suggests that even if the dipterocarps did not originate in India while it was an island continent, it was India that delivered them to South East Asia.

A few microfossils (dipterocarpaceous pollen) and chemical analysis of amber (Dutta et al. 2009, 2011) from the early Eocene sediments of western India have been used to support the "Out-of-India" hypothesis for this family in which dispersal into South East Asia was envisioned to have taken place only from the Indian plate. Dipterocarps produce characteristic resin that can be preserved in the fossil record, and such resin has been found in late Oligocene sediments of the Lunpola Basin, central Tibet, probably reworked from Eocene sediments (Wang et al. 2018). If these fossil resins are sourced from Eocene deposits, and definitively represent dipterocarps, they challenge inferences derived from Eocene pollen and amber in India that Gondwana was the ancestral home of this important group to forest taxa. To re-assert a Gondwanan origin requires a discovery of pre-Eocene dipterocarp remains in India.

Prasad et al. (2009) attempted to track the affinities of some fossil palynomorphs recovered from late Paleocene-early Eocene (~ 55 to 50 Ma) sedimentary deposits of western and northeastern India and compared them with the pollen of dipterocarps, but identification remains uncertain. More recently, pollen attributable to the family has been recovered from Maastrichtian sediments in India, but because pollen can be transported over long distances more definitive evidence of the Dipterocarpaceae in India before 55 ± 10 Ma, the likely range of dates when India contacted Asia (Wang et al. 2014), is required to demonstrate without doubt their presence on the subcontinent before a land bridge was established. Megafossils, particularly if both macromorphological and micromorphological details are preserved, offer much more reliable identification than pollen because the limited character suite of pollen grains often only afford low taxonomic resolution (Mander and Punyasena 2014).

As far as megafossil records in India are concerned, unambiguous dipterocarp remains have been reported from the Neogene (mainly from the Early Miocene onwards) (Lakhanpal et al. 1976; Guleria 1992; Khan et al. 2011, 2015, 2016; Shukla et al. 2012, 2013) with just a single record of dipterocarpaceous wood from the Paleogene (early Eocene) sediments of western India (Rust et al. 2010). However, identification of the wood as dipterocarpaceous is doubted by Shukla et al. (2013). The reported wood needs re-investigation as it exhibits many important features of the family Lauraceae. These include thin and low parenchyma ray cells and oil cells among the fibres, which were misinterpreted by the primary authors as gum canals in cross-section. Given these identification uncertainties, the occurrence of leaf remains bearing cuticular epidermal features of *Dipterocarpus* from the latest Cretaceous to the earliest Paleocene sediments of Central India (Fig. 2) is highly significant, and with the support of the pollen evidence demonstrates that dipterocarps were present in India in the Cretaceous. This early presence in India strengthens the argument that dipterocarps dispersed from India into Asia once the land connection between the Indian and Asian plate became established (Fig. 8). Exactly when that occurred remains a topic of intense debate (Spicer et al. 2020).

Conclusions

Evidence from fossils, palaeogeography, and current distribution patterns argue for an ancient Gondwanan presence of the Dipterocarpaceae in the Late Cretaceous, and here we show that they were present on the rafting Indian plate at the start of the Cenozoic before the most likely time of land contact with Asia. Despite massive volcanism and rapid latitudinal changes, this ancient Gondwanan element thrived on the Indian plate, even while still in the Southern Hemisphere. The dipterocarps were not alone and numerous other taxa must have arrived on the Indian raft (Klause et al. 2016), particularly if Morley's contention that "the south-east Asian area was a backwater of angiosperm evolution until the collision of the Indian plate with Asia during the early Cenozoic" (Morley 2018, p. 209) has any merit. The presence of dipterocarps in India at the very beginning of the Cenozoic shows they were likely an important immigrant that went on to become a characteristic component of modern South East Asian forests.

Taxonomic treatment

Dipterocarpus dindoriensis Khan, R.A.Spicer & Bera, **sp. nov.**—HOLOTYPE: SKBU/PPL/D/L/1, Madhya Pradesh, the surface exposure of Deccan Intertrappean Beds of Umaria in Dindori District, 23° 5.451′ N, 80° 37.652′ E, 26 Dec 2018 (Fig. 3).

Etymology: The specific epithet "*dindoriensis*" recognizes Dindori district, the locality where fossil leaf specimen was collected.

Description: Leaf simple; preserved lamina almost complete, mesophyll, symmetrical, wide elliptic; maximum length about 8.2 cm and maximum width about 4.1 cm; apex missing; base obtuse to rounded; petiole not preserved; margin entire; texture coriaceous; venation pinnate, simple, craspedodromous; primary vein thickness 0.13 cm, single, prominent, moderately stout, straight, thick in the basal half and gradually thinning upward, terminating at the apex; secondary veins alternate to sub-opposite, fine in thickness and unbranched, 7 pairs visible, 0.7–1.1 cm apart, angle of divergence narrow to moderate acute (30°–55°), the secondary veins start almost straight, then gradually and uniformly curved up, and connected to the adjacent secondaries by tertiary cross veins, forming secondary characteristic marginal loops; inter-secondary and intra-marginal veins not seen; tertiary veins very faint, simple, forked percurrent and recurved, oblique in relation to midvein, predominantly alternate and close; quaternary veins percurrent, predominantly quadrangular, further details not clearly preserved.

Epidermal anatomy: Hypostomatic leaf; epidermal cells mostly pentagonal to hexagonal, sometimes triangular, arranged irregularly, 11–15 μm long and 10–22 μm wide; anticlinal walls mostly curved, sometimes straight, 1.8 μm wide; periclinal walls smooth, unspecialised; stomata almost circular, irregularly distributed and oriented, 15–19 μm long and 10–13 μm wide; stomatal apparati paracytic, with one lateral specialised neighbouring cell or subsidiary cell per guard cell; guard cells superficial, elongated, 10–11 μm long and 3–4 μm wide; subsidiary cells 13–15 μm long and 4–5 μm wide.

Diagnosis: Leaf lamina mesophyllous, wide elliptic; entire margin; texture coriaceous, base obtuse to rounded; venation pinnate craspedodromous; secondary veins mostly alternate, narrow to moderate acute angle of divergence, straight and

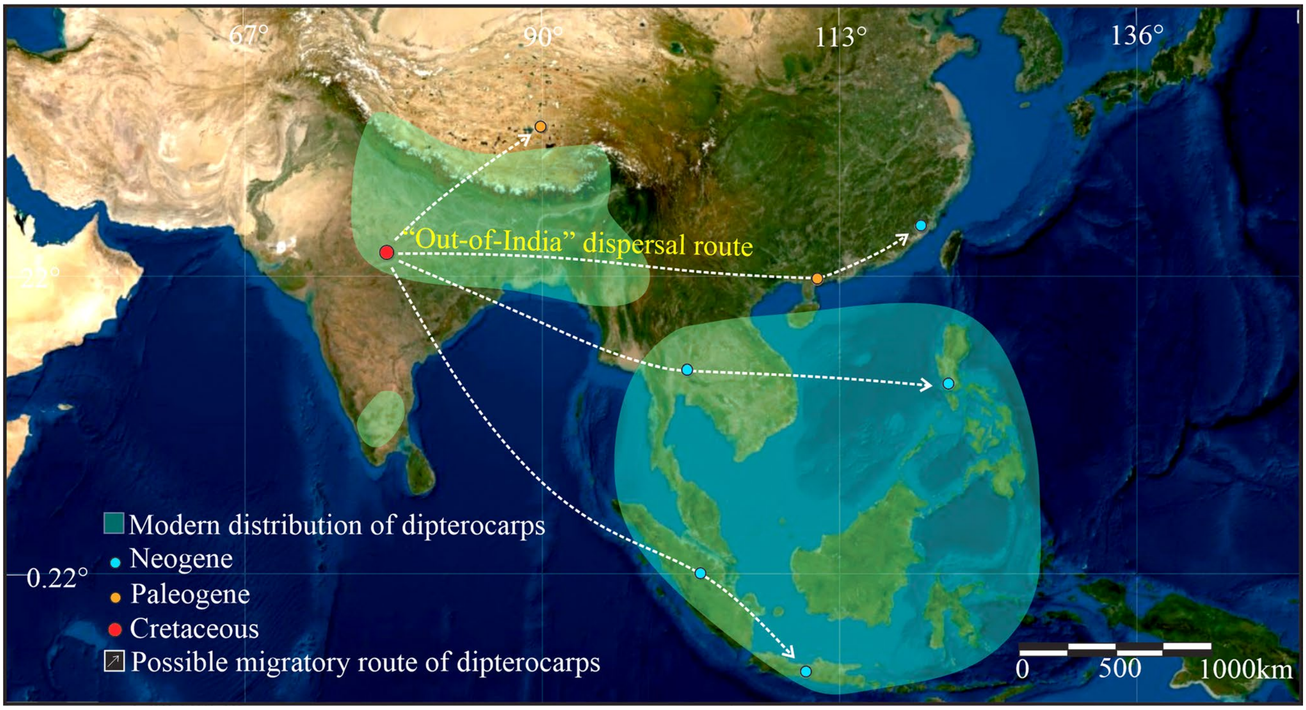

Fig. 8 Map showing modern distribution and possible migratory path of dipterocarps to Southeast Asia

Table 1 Comparative morphological chart of the available extant leaf remains among genera in different angiosperm families

Modern genera	Apex	Base	Margin	Shape	Balance	Venation pattern	Angle of divergence of secondary veins	Inter-secondary veins	Tertiary veins
Aglaia Lour.	Acute to acuminate	Oblique	Entire	Elliptic	Symmetrical	Craspedodromous-brochidodromous	Moderate to wide acute	Present	Predominantly orthogonal
Hopea Roxb.	Acuminate	Acute	Entire	Elliptic	Symmetrical-asymmetrical	Eucamptodromous-craspedodromous	Moderate acute	Generally absent	Horizontally percurrent
Mitragyna Korth.	Obtuse	Mostly round	Entire	Oblong	Symmetrical	Eucamptodromous	Narrow acute	Generally absent	Percurrent
Berchemia Neck. ex DC.	Acute to round	Round	Slightly undulate	Oblong	Symmetrical	Eucamptodromous	Narrow acute	Present	Generally percurrent
Shorea Roxb. ex C.F.Gaertn.	Acute to obtuse	Obtuse to cordate	Entire	Oblong-elliptic	Symmetrical	Eucamptodromous	Moderate to wide acute	Present	Percurrent
Rhus L.	Acuminate	Cuneate	Sinous	Elliptic	Symmetrical	Brochidodromous	Moderate acute	Present	Weakly percurrent
Uvaria L.	Acuminate	Generally sub-cunate to acute	Entire	Lanceolate	Symmetrical-Asymmetrical	Brochidodromous	Moderate acute	Present	Alternate percurrent
Bridelia Willd.	Obtuse to retuse	Round	Entire	Elliptic	Symmetrical	Craspedodroumous	Acute	Generally present	Straight percurrent
Fissistigma Griff.	Generally obtuse	Round	Entire	Elliptic	Symmetrical	Scalariform-eucamptodromous	Moderate acute	Generally absent	Weakly percurrent
Lansium Correia.	Acute to Acuminate	Sub-cuneate to acute	Entire	Elliptic	Symmetrical-asymmetrical	Generally brochidodromous	Moderate Acute	Present	Percurrent
Eremolaena Baill.	Emarginate	Subcordate to attenuate	Entire	Ovate-obovate	Symmetrical	Brochidodromous	Moderate acute	Absent	Percurrent to reticulate
Pentachlaena H. Perrier	Retuse to emarginate	Subcordate to rounded	Entire	Ovate-oblong	Symmetrical	Generally Craspedodromous	Narrow acute	Absent	Percurrent
Dipterocarpus C. F. Gaertn.	Acute	Obtuse-round	Entire	Elliptic	Symmetrical	Eucamptodromous	Narrow acute	Absent	Percurrent

abruptly turned up near the margin joining superadjacent secondary veins with tertiary veins; intersecondary veins absent; tertiary veins percurrent; hypostomatic leaf; curved anticlinal walls; stomatal apparati paracytic.

Comparison: The morphological features of the recovered Cretaceous fossil leaf resemble the leaves of some modern dicot genera such as *Dipterocarpus* C.F.Gaertn., *Shorea* Roxb. ex C.F.Gaertn., *Hopea* Roxb. of the family Dipterocarpaceae, *Aglaia* Lour., *Lansium* Correia. (Meliaceae), *Mitragyna* Korth. (Rubiaceae), *Berchemia* Neck. ex Dc. (Rhamnaceae), *Rhus* L. (Anacardiaceae), *Uvaria* L., *Fissistigma* Griff. (Annonaceae) and *Bridelia* Willd. (Phyllanthaceae) (Table 1; Fig. 5a–j). In *Aglaia*, *Lansium*, *Rhus* and *Uvaria*, the secondary venation pattern is somewhat brochidodromous, in contrast to the craspedodromous venation pattern of the Cretaceous leaf. Our Cretaceous specimen differs from *Mitragyna* in having an obtuse to rounded base. In *Bridelia* curvature of the secondaries is dissimilar. *Berchemia* differs in having a small size and a slightly undulate lamina margin. However, our specimen differs from *Fissistigma*, *Shorea* and *Hopea* in the angle of divergence of

Table 2 Earlier records of leaf remains of *Dipterocarpus* from Cenozoic sediments of India and abroad

Fossil species	NLR (Nearest Living Relative)	Locality and age	References
Dipterocarpus siwalicus	*D. tuberculatus* Roxb.	Himachal Pradesh (Miocene)	Prasad (1990a, b)
D. siwalicus	*Dipterocarpus* sp.	Uttarakhand (Miocene)	Prasad (1994) and Prasad et al. (2017)
D. siwalicus	*D. tuberculatus* Roxb.	Darjeeling (Mio-Pliocene)	Antal and Prasad (1996)
D. siwalicus	*D. turbinatus* Gaertn.	Himachal Pradesh (Miocene)	Lakhanpal and Guleria (1987) and Konomalsu and Awasthi (1996)
D. siwalicus	*Dipterocarpus* sp.	Arunachal Pradesh (late Pliocene-early Pleistocene)	Khan et al. (2011)
D. siwalicus	*Dipterocarpus* sp.	Himachal Pradesh (Miocene)	Guleria et al. (2000)
D. siwalicus	*Dipterocarpus* sp.	Bhutan (Mio-Pliocene)	Prasad and Tripathi (2000)
D. suraikholaensis	*Dipterocarpus* sp.	Western Nepal (Miocene)	Prasad and Pandey (2008)
D. palaeoindicus	*D. indicus* Bedd.	Western Nepal (Miocene)	Prasad et al. (2019)
D. koilabasensis	*D. turbinatus* Gaertn.	Western Nepal (Miocene); Arunachal Pradesh (late Pliocene-early Pleistocene)	Prasad et al. (1999, 2019) and Khan et al. (2015)
Dipterocarpus sp.	*Dipterocarpus* sp.	Eastern Nepal (middle Miocene)	Srivastava et al. (2017)
D. siwalicus	*D. tuberculatus* Roxb. *D. turbinatus* Gaertn.	Western Nepal (Miocene)	Awasthi and Prasad (1990)
D. siwalicus	*D. tuberculatus* Roxb.	Eastern Nepal (middle Miocene)	Prasad and Pradhan (1998)
D. antiquus	?*Dipterocarpus*	Sumatra (Tertiary)	Heer (1883)
D. atavinus	?*Dipterocarpus*	Sumatra (Tertiary)	Heer (1883)
D. labuanus	?*Dipterocarpus*	Labuan (Tertiary)	Geyler (1887)
D. nordenski'oldi	?*Dipterocarpus*	Labuan (Tertiary)	Geyler (1887)
Dipterocarpus sp.	?*Dipterocarpus*	Labuan (Tertiary)	Geyler (1887)
Phyllites dipterocarpoides	?*Dipterocarpus*	Java (Pliocene)	Crié (1888)
Dipterocarpaceophyllum sumatrense	Dipterocarpaceae	Sumatra (?Pliocene)	Kräusel (1929)
Dipterocarpophyllum gregoryi	Dipterocarpaceae	Myanmar (Tertiary)	Edwards (1923)
D. dindoriensis Khan, R.A.Spicer & Bera, sp. nov	*D. alatus* Roxb. & G.Don	Madhya Pradesh, India [Latest Maastrichtian (Late Cretaceous) to earliest Danian (early Paleocene)]	Present study

the secondary veins. In *Fissistigma*, *Shorea* and *Hopea*, the angle of divergence of the secondary veins is relatively less acute than in the fossil specimen. So, based on the remarkable features such as the wide elliptical shape, mesophyll size, obtuse to rounded base, thick texture, secondaries coming off straight from the midrib and curving up near the margin, the angle of divergence of the secondaries decreasing from base towards the apex, and percurrent tertiaries, our Cretaceous leaf certainly belongs to *Dipterocarpus* of the family Dipterocarpaceae. As the family Sarcolaenaceae is a sister taxon to the Dipterocarpaceae based on molecular phylogenetic studies (Ducousso et al. 2004), we also compare our fossil specimen with its modern representatives (Table 1; Fig. 5k, l). Sarcolaenaceae is a relect tree family retricted to littoral forest ecosystems of Madagascar and consists of ten genera (APG IV 2016). The herbarium specimens of all the available genera of this family have been studied, and it is found that genera viz., *Sarcolaena* Thours, *Schizolaena* Thours, *Eremolaena* Baill., *Pentachlaena* H. Perrier, *Perrierodendron* Cavaco and *Leptolaena* Thouars come close to the fossil specimen. Both *Sarcolaena* and *Schizolaena* differ from our Deccan specimen in having a lanceolate shape. In *Leptolaena*, *Perrierodendron* and *Eremolaena* secondary venation is brochidodromous, whereas in the fossil specimen it is craspedodromous. *Perrierodendron* and *Eremolaena* also differ by having ovate to obovate shaped lamina. In *Pentachlaena* the leaf base is subcordate in contrast to the obtuse to rounded base in the current specimen. In addition, we also studied the cuticular characters of both fossil *D. dindoriensis* sp. nov. and extant leaves of Sarcolaenaceae. Our fossil specimen differs in having paracytic type of stomata. However, stomata are more or less anomocytic in the leaves of modern members of Sarcolaenaceae (Watson and Dallwitz 1992).

Table 3 Fossil species of *Dipterocarpus* (from Cenozoic sediments of India, Nepal and Bhutan) with their main morphological characters

Fossil species of *Dipterocarpus*	Size	Shape	Apex	Base	Venation pattern	Nature of 2° veins
Dipterocarpus siwalicus Antal & Prasad 1996	14.2×6 cm	Elliptic	Apex slightly broken, seemingly acute	Base acute to seemingly obtuse	Eucamptodromous	16 pairs, mostly alternate, angle of divergence narrow to moderate (40°–55°)
D. siwalicus Prasad & Tripathi 2000	5–5.5×4 cm	Elliptic	Broken	Broken	Eucampodromous	8 pairs, alternate, angle of divergence narrow acute (less than 45°)
D. siwalicus Khan et al. 2011	9×5 cm	Elliptic	Acute	Broken	Eucampodromous	8 pairs, alternate, angle of divergence narrow to moderate (40°–55°)
D. suraikholaensis Prasad & Pandey 2008	12.0×9.0 cm	Elliptic	Broken	Obtuse	Eucampodromous	9–11 pairs, alternate, angle of divergence narrow to moderate acute (40°–65°)
D. koilabasensis Prasad et al. 1999	21.0×11.0 cm	Elliptic	Broken	Obtuse	Craspedodromous-eucampodromous	16 pairs, alternate to opposite, angle of divergence acute (55°)
D. koilabasensis Khan et al. 2015	5.8–6×4.4–4.8 cm	Elliptic	Broken	Broken	Craspedodromous-eucampodromous	5–7 pairs, alternate, angle of divergence acute (40°–55°)
D. koilabasensis Prasad et al. 2019	7.2×4.0 cm	Widely elliptical	Broken	Obtuse	Craspedodromous-eucampodromous	6 pairs, alternate to opposite, angle of divergence moderately acute (50°)
Dipterocarpus sp. Srivastava et al. 2017	7.6–13.8×5.5–14.4 cm	Elliptic	Broken	Broken	Eucampodromous	8 pairs, alternate to sub-opposite, angle of divergence narrow to moderate acute (23°–63°)
D. siwalicus Awasthi & Prasad 1990	13×8 cm	Ovate to elliptic	Missing	More or less round to cordate	Eucampodromous	16 pairs, sub-opposite to alternate, angle of divergence acute (45°–70°)
D. siwalicus Prasad & Pradhan 1998	6.5×4.5 cm	Seemingly elliptical	Acute, slightly curved	Missing	Eucamptodromous	9–10 pairs, sub-opposite to alternate, angle of divergence acute to moderate (50°–60°), upper more acute than lower
D. palaeoindicus Prasad et al. 2019	15.7×4.8 cm	Elliptic	Missing	Missing	Craspedodromous-eucampodromous	11 pairs, opposite to alternate, angle of divergence narrowly acute (55°), lower secondaries almost straight but shallowly curved near the margin

Table 3 (continued)

Fossil species of *Diptero-carpus*	Size	Shape	Apex	Base	Venation pattern	Nature of 2° veins
D. dindoriensis Khan, R. A. Spicer & Bera, sp. nov.	8.2×4.1 cm	Elliptic	Broken	Obtuse to rounded	Craspedodromous	7 pairs, alternate to sub-opposite, angle of divergence narrow to moderate acute (30°–55°), the secondary veins start almost straight, then gradually and uniformly curved up towards the apex

Herbarium specimens of all the available species of the genus *Dipterocarpus*, namely *D. acutangulus* Vesque., *D. cornatus* Dyer., *D. turbinatus* C.F.Gaertn., *D. grandiflorus* Blanco., *D. critinus* Dyer., *D. gracilis* Blume; *D. fagineus* Vesque; *D. intricatus* Dyer; *D. hasseltii* Blume; *D. indicus* Bedd., *D. costatus* C.F. Gaertn., *D. kerrii* King; *D. rigidus* Ridl., *D. oblongifolius* Blume; *D. costatus* C.F.Gaertn., and *D. nudus* Vesque. (Fig. 6a–p), were examined critically in order to determine the nearest specific affinity. A detailed comparison revealed that most of the species could not be differentiated from each other easily on the basis of leaf size, shape and venation pattern. However, on the basis of leaf morphology (size, shape, nature of base, texture and venation pattern) *D. alatus* (C. N. Herbarium Sheet No. 50597) shows the closest resemblance to the Cretaceous leaf specimen (Fig. 3b, c, e).

Dipterocarpus fossil leaves have been reported from the Cenozoic sediments of India and abroad (Table 2). Heer (1883) reported *Dipterocarpus antiques* and *D. atavinus* from the Tertiary sediments of Sumatra, while Geyler (1887) reported *D. tabuanus, Dipterocarpus* sp. *D. nordenskioldi* from the Tertiary sediments of Labuan. Crié (1888) described *Phyllites dipterocarpoides* from the Pliocene sediments of Java. However, these authors attempted to track the affinities of aforesaid fossil leaves by comparing them with the modern leaves of *Dipterocarpus*, but their identification is dubious. Edwards (1923) reported a fossil leaf *Dipterocarpophyllum gregoryi* having affinity with extant Dipterocarpaceae leaf from the Tertiary sediments of Myanmar. Later, Kräusel (1929) also described a fossil dipterocarpaceous leaf fragment *Dipterocarpaceophyllum sumatrense* from the Pliocene (?) sediments of Sumatra. In addition, several fossil leaves having similarity with *Dipterocarpus* have been described from the Siwalik sedimentary units of India, Nepal and Bhutan (Lakhanpal and Guleria 1987; Awasthi and Prasad 1990; Prasad 1990b, 1994; Antal and Prasad 1996; Konomalsu and Awasthi 1996; Prasad and Pradhan 1998; Prasad et al. 1999, 2017, 2019; Guleria et al. 2000; Prasad and Tripathi 2000; Prasad and Pandey 2008; Khan et al. 2011, 2015). By comparing the present specimen with the previously published fossil species of *Dipterocarpus* reported so far, we observe that our Cretaceous specimen differs from them in size, shape, and venation patterns (Table 3, Fig. 7). Fossil species viz., *D. siwalicus*, *D. suraikholaensis* and *Dipterocarpus* sp. differ from our specimen in having eucampodromous secondary veins. However, the present fossil specimen possesses craspedodromous secondary veins. On the other hand, *D. palaeoindicus* and *D. koilabasensis* differ in having a craspedodromous-eucampodromous pattern of secondary veins. Therefore, on the basis of distinctive differences between the current specimen and the earlier known species of *Dipterocarpus*, here, we propose a new species *D. dindoriensis* Khan, R.A.Spicer & Bera, sp. nov. We also examined the cuticular characters of both fossil *D. dindoriensis* sp. nov. and extant leaves of *D. alatus*. Cuticle obtained from the fossil specimen shows similar features to those found in modern *D. alatus* (Fig. 3f, g). The cuticular epidermal cell structure, curved anticlinal cell walls, the presence of paracytic stomata, their arrangement and orientation suggest the fossils described here resemble closely leaves of the extant species *D. alatus*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no any conflict of interest.

Ethical statement No specific permits were required for the described field studies. The sampling sites are not protected in any way, and the field studies did not involve endangered or protected species.

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