

Emergence and extinction of Dipterocarpaceae in western India with reference to climate change: Fossil wood evidences

ANUMEHA SHUKLA*, R C MEHROTRA and J S GULERIA

Birbal Sahni Institute of Palaeobotany, 53 University road, Lucknow 226 007, India.

**Corresponding author. e-mail: anu_bsip@yahoo.co.in*

Climate has played a crucial role in assigning a different kind of topography to Rajasthan and Gujarat since the Cenozoic time. Evidently, three genera, namely, *Dipterocarpus* Gaert. f., *Hopea* Roxb. and *Shorea* Roxb. of the Dipterocarpaceae are described from the Neogene sediments of western India (Rajasthan and Gujarat). These taxa are marked by their complete absence in the region today. The presence of Dipterocarpaceae in western India has been noticed from the Early Eocene up to the Plio-Pleistocene in deep time. The family is usually a dominant component of the humid tropical and subtropical flora of the Indo-Malayan region and its discovery, along with earlier described fossils from western India indicates existence of ancient tropical rain forests in western India. A change in the climate affected warm and humid conditions occurring there during the Cenozoic resulting in arid to semi-arid climate at present which is responsible for the ultimate extinction of Dipterocarpaceae in the region. In addition, the palaeobiogeography of Dipterocarpaceae is reviewed.

1. Introduction

Dipterocarpaceae, a well known family of the Asian rain forests (Ashton 1982, 1988), has been variously assigned to Malvales and Theales and consists of the following three subfamilies with an intercontinental disjunct distribution: (1) Dipterocarpoideae in the Asian tropics and Seychelles, (2) Pakaraimoideae in Guyana and Venezuela of South America and (3) Monotoideae in African tropics, Madagascar and southeast Colombia of South America (Maguire and Ashton 1977; Ashton 1982, 2003; Maury-Lechon and Curtet 1998). There are approximately 520 species belonging to 17 genera amongst which the Asian dipterocarps include 470 species alone. It constitutes prominent elements of the lowland rain forests (Aiba and Kitayama 1999) and is also well represented in the

understorey. In south Asia, the dipterocarps are mainly distributed in tropical peninsula from Karnataka coast to the tip of southern India and north-east India (figure 1). *Shorea robusta* Roth (locally known as sal), commercially the most important timber of India, is a large deciduous tree occurring widely in northern and central India. In the northern or sub-Himalayan region, it has western limit in east Punjab and then extends eastwards through Uttar Pradesh, Bihar, Nepal, West Bengal, Bangladesh and Assam (Ghosh 1958). Asian dipterocarps deeply imprint the forest ecology and economy of the places where they grow.

The family Dipterocarpaceae was reported from the Palaeogene and Neogene sediments of India (Guleria 1992b; Srivastava and Mehrotra 2010), including the westernmost part (Lakhanpal *et al.* 1984; Dutta *et al.* 2009, 2011a, b; Rust *et al.* 2010;

Keywords. Origin; western India; *Dipterocarpus*; *Shorea*; *Hopea*; palaeoclimate; phytogeography.

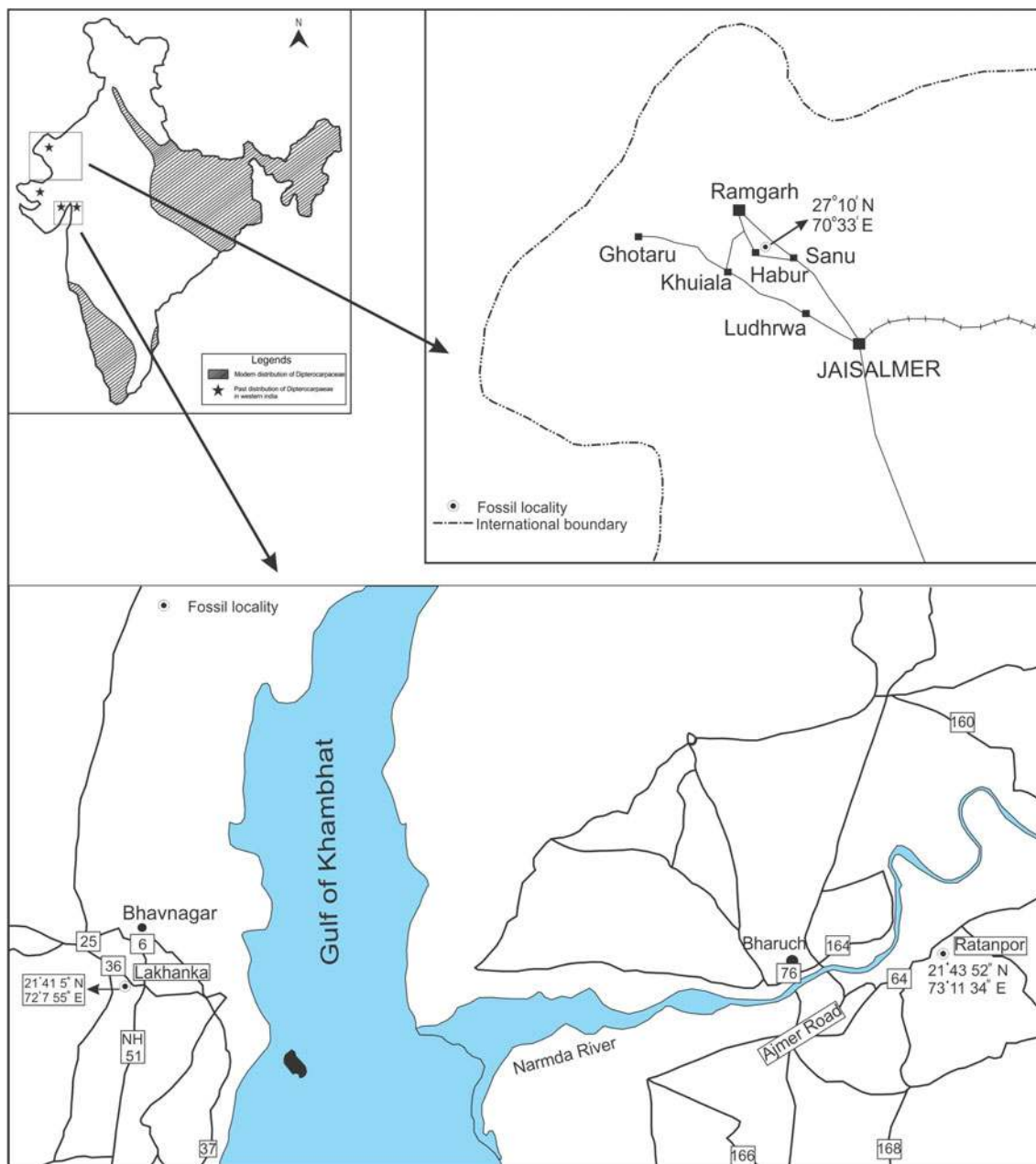


Figure 1. Map showing fossiliferous localities of Rajasthan and Gujarat. (Inset: map of India showing present (shaded area) and past (marked by stars) distribution of Dipterocarpaceae.)

Shukla *et al.* 2012). Apart from India, dipterocarpaceous remains were also reported from the Cenozoic of northeast and east Africa as well as south and southeast Asia. The fossil records are mainly represented by woods (Bancroft 1935; Ramanujam 1956; Schweitzer 1958; Navale 1962; Prakash 1965a, b; Lakhanpal 1970; Lemoigne 1978; Awasthi and Mehrotra 1993; Prasad 1993; Prakash *et al.* 1994; Guleria 1996; Tiwari and Mehrotra 2000; Mehrotra and Bhattacharyya 2002; Wang *et al.* 2006; Rust *et al.* 2010), leaves

(Lakhanpal and Guleria 1987; Prasad 1990, 1994; Antal and Prasad 1996), pollen grains (Muller 1981; Songtham *et al.* 2005; Rugmai *et al.* 2008; Dutta *et al.* 2011a, b) and fruit wings (Khan and Bera 2010; Shi and Li 2010; Shukla *et al.* 2012). The earliest confirmed fossil dipterocarp so far reported from SE Asia was from the Oligocene (34–23 Ma) sediments of Borneo (Muller 1981) which is also a centre of diversity of extant dipterocarps with more than 280 species (Ashton 1982, 1988). In the last decade, dipterocarpaceous pollen grains

have been recorded from the Early Eocene sediments of western India (Acharya 2000; Dutta *et al.* 2011a, b).

The presence of Dipterocarpaceae in the Early Eocene to Plio-Pleistocene sediments of western India and its complete absence today in the region is a sign of drastic change in the climate which might be responsible for the complete extinction of the family from the region. The family may perhaps hold the distinction of being the most well known trees in the tropics and consequently the origin and antiquity of it is always a matter of concern.

1.1 Regional geology

The fossils collected for the present study from Rajasthan belong to the Shumar Formation of the Jaisalmer Basin. The formation is best exposed

in Shumarwali Talai area and has a thickness of about 9.5 m in the type section (Narayanan *et al.* 1961). The surface and sub-surface geology indicates that the Shumar Formation comprises a sequence of alternating variegated clays, sandstone and glauconitic clay at the base followed by sandstone and variegated clays, limestone and calcareous sandstone and loose sandstone at the top (Guleria and Shukla 2011). In the outcrop, the formation is mainly composed of conglomerate with streaks of sandstone and silty clays (Dasgupta 1975). Singh (1982) opined that the sediments of this formation are not typical Sub-recent or Recent type such as alluvium, terraces, calcrete boulder beds, etc., and therefore, it may be logical to tentatively assign Pleistocene to Sub-recent age to this formation (Singh 2007, p. 152). The plant assemblage being described here is almost similar to the one recovered from the Mar Formation

Stratigraphy			Cambay Basin		Saurashtra Basin		
Era	Period	Age	Formation	Lithology	Formation	Lithology	
C E N O Z I C T E R T I A R Y	QUATERNARY	HOLOCENE	Gujarat alluvium	Sand, silt, clays with gravel beds	—	Alluvium, soils, coastal deposits	
		PLEISTACENE	Narmada Formation		Chaya Formation	Shelly beach rocks	
	TERTIARY	PLEISTACENE		Jambusar Fm. (not exposed)	Coarse sand, clays, calcrete	Lakhanka Fm. Miliolite	Agate conglomerate, sandstone coastal & inland miliolites
			PLIOCENE	Broach Fm (not exposed)	Claystone, sandstone	Dwarka Fm.	Silty clays, marls, sandy limestone, grit, sandy clays, sst, fossil conglomerate
		Jhagadia Formation		Conglomerate, sandstone			
		MIOCENE	*Kand Formation	Conglomerate fossils, limestone, clac. sst	Piram Beds	Gaj Fm. Kuda Sandstone Member *Bhumbli Conglomerate Member Ratanpur Clay Member	Fossil, gypseous, clays limestone, grit
			Babaguru Formation	Conglomerate, sandstone			
		OLIGOCENE	?	? ?			
		EOCENE	Dinod Formation	Fossil limestone marl			
			Vagadkhol Formation	Conglomerate grit, sandstone clay siltstone			
	PALAEOCENE	Laterite		Bauxite, bentonite	Laterite	Bauxite, bentonite	
		Deccan Trap			Deccan Trap		

Figure 2. Generalized stratigraphic chart of the Cenozoic basins of Gujarat (after Merh 1995) (fossiliferous horizons marked by stars).

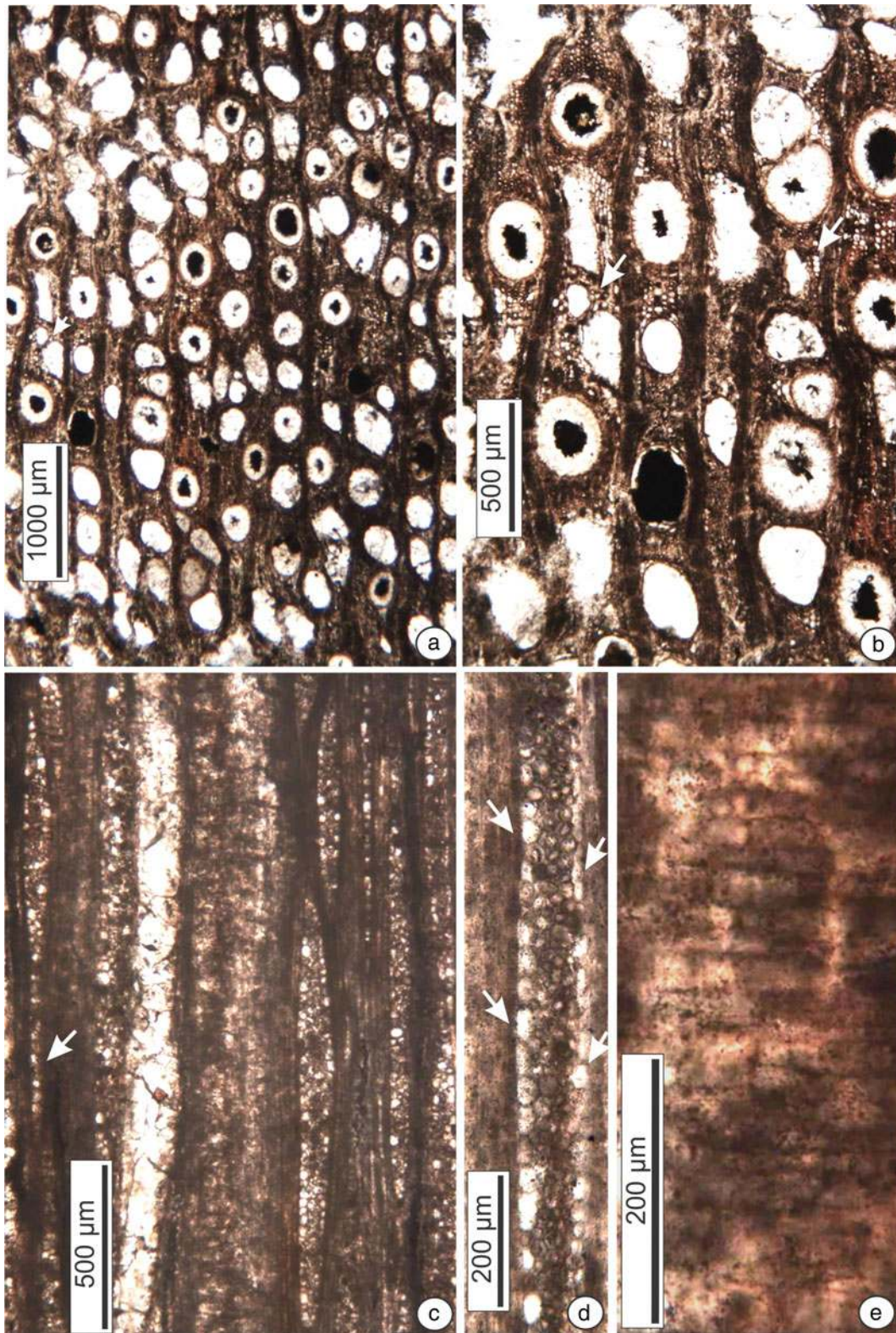


Figure 3. *Dipterocarpoxyylon jammuense* Guleria and Srivastava (a), (b) transverse sections (T.S.) of the fossil showing exclusively solitary vessels and scattered gum canals (marked by arrow), (c) tangential longitudinal section (T.L.S.) of the fossil showing multiseriate rays with long tails (marked by arrow), (d) T.L.S. showing sheath cells on the flanks of a multiseriate ray (marked by arrows) and (e) radial longitudinal section (R.L.S.) showing heterogeneous ray tissue.

of Bikanar and Kankawati Series (Pliocene) of Kachchh (Guleria 1983, 1984a, b, 1990, 1992a, 1996). As the age of Kankawati Series is considered to be Pliocene (Biswas 1965, 1971; Biswas and Deshpande 1970), the age of this formation could be equivalent to the Kankawati Series. Sedimentological and palaeontological studies are needed for more precise correlation and dating of this formation.

From Gujarat, the fossil woods were collected from two different horizons of Bharuch and Bhavnagar districts. From Bharuch, they were collected from Kand Formation which overlies the Babaguru Formation with an unconformity (figure 2) and constituted by calcareous sandstone with occasional conglomerate, clays, marl and thin fossiliferous limestone bands. A Lower Miocene (Burdigalian) age has been assigned to this formation (Merh 1995). A few fossil woods were also collected from Bhumbli Conglomerate of Gaj Formation in Bhavnagar, Gujarat. This formation is unconformably overlying the Deccan Traps and Lateritic rocks of the basin. The highly fossiliferous rocks of the Gaj Formation (Early to Middle Miocene) have been found exposed all along the coastal tracts from Bhavnagar to Okha Rann (Pandey *et al.* 2008). Fedden (1884) mapped these as 'Gaj Beds' and assigned an Upper Miocene age. The Gaj rocks have a characteristic earthy yellow appearance, contrasting with red and brown coloured landscape, wherever they overlie the lateritic rocks. Srivastava (1963) divided the Gaj Formation into three members – the lower Ratanpur Clay Member, the Bhumbli Conglomerate and the topmost Kuda Sandstone Member (figure 2). The Bhumbli Conglomerate Member is made up of fossiliferous conglomerate, grit and argillaceous sandstone with minor content of clay layers. Some plant fossils were recorded from this formation (Merh 1995). On the basis of microfossils and foraminifers, a Miocene age has been assigned to this formation (Merh 1995).

2. Materials and methods

Materials for the study came from the Neogene sediments of western India, including Rajasthan and Gujarat. From Rajasthan, a large number of silicified woods were collected from the Khuiala Limestone ridge situated 3–5 km west of the Habur Village (lat. 27°10'N, long. 70°33'E), which is about 57 km north of Jaisalmer (figure 1). From Gujarat, a few fossil woods were collected from Lakhanka (21°41'5"N: 72°7'55"E) to Mithi–Virī road, about 1–2 km before Mithi–Virī (figure 1). These woods were found embedded in soft sandstone layers. A few fossil woods were also

collected from Ratanpurni River bed, Ratanpor (21°43'52"N: 73°11'34"E) lying between Rajpardi and Jhagadia villages of the Bharuch District (figure 1).

For the study of xylotomical characters, thin-sections of the fossil woods were prepared by standard lapidary techniques. Sections were cut in three planes, i.e., transverse, tangential longitudinal and radial longitudinal. Each face was polished and mounted onto a glass slide and surfaces were ground and polished with carborundum powder to a thickness of 30–40 µm. These sections were studied using high-power microscope and photographed with an attached DFC 290 digital camera. Identifications were made by comparing the anatomical characters with modern wood slides available at the Birbal Sahni Institute of Palaeobotany (BSIP), Lucknow and the Forest Research Institute, Dehradun. Descriptions follow the terminology of the IAWA Committee (1989). The type slides are housed in the museum of the Birbal Sahni Institute of Palaeobotany, Lucknow.

3. Systematic description

Family: Dipterocarpaceae

Genus: *Dipterocarpoxylo* Holden emend. Den Berger (1927)

Dipterocarpoxylo jammuense Guleria and Srivastava (2001)

Description: Wood diffuse-porous. Growth rings not seen. Vessels almost solitary, rarely in pairs, medium to large (figure 3a, b), evenly distributed 3–7 per mm², circular to oval in shape, filled with tyloses or black colour content (figure 3b), t.d. 147–270 µm and r.d. 215–349 µm, vessel elements 140–600 µm long with truncate or oblique end walls; perforations simple; intervessel pits poorly preserved, alternate. Vasicentric tracheids present intermingled with parenchymatous cells forming thin sheath around the vessels. Axial parenchyma apotracheal and paratracheal, paratracheal parenchyma vasicentric, 1–3 cells wide (figure 3b), rarely short extensions joining adjacent vessels, apotracheal parenchyma scanty, only few diffuse cells present, occasionally in short tangential bands enclosing vertical gum canals (figure 3b); cells thin walled, 56–105 µm long and 19–22 µm wide. Rays 1–7 (mostly 3–6) seriate (figure 3c, d), homocellular to heterocellular (figure 3e), uniseriate rays 2–11 cells or 180–750 µm high, made up of upright cells only or both upright and procumbent cells, multiseriate rays made up of procumbent cells in the centre with uniseriate extensions of 2–10 upright cells at one or both the ends (figure 4c), 6–95 cells or 160–2163 µm

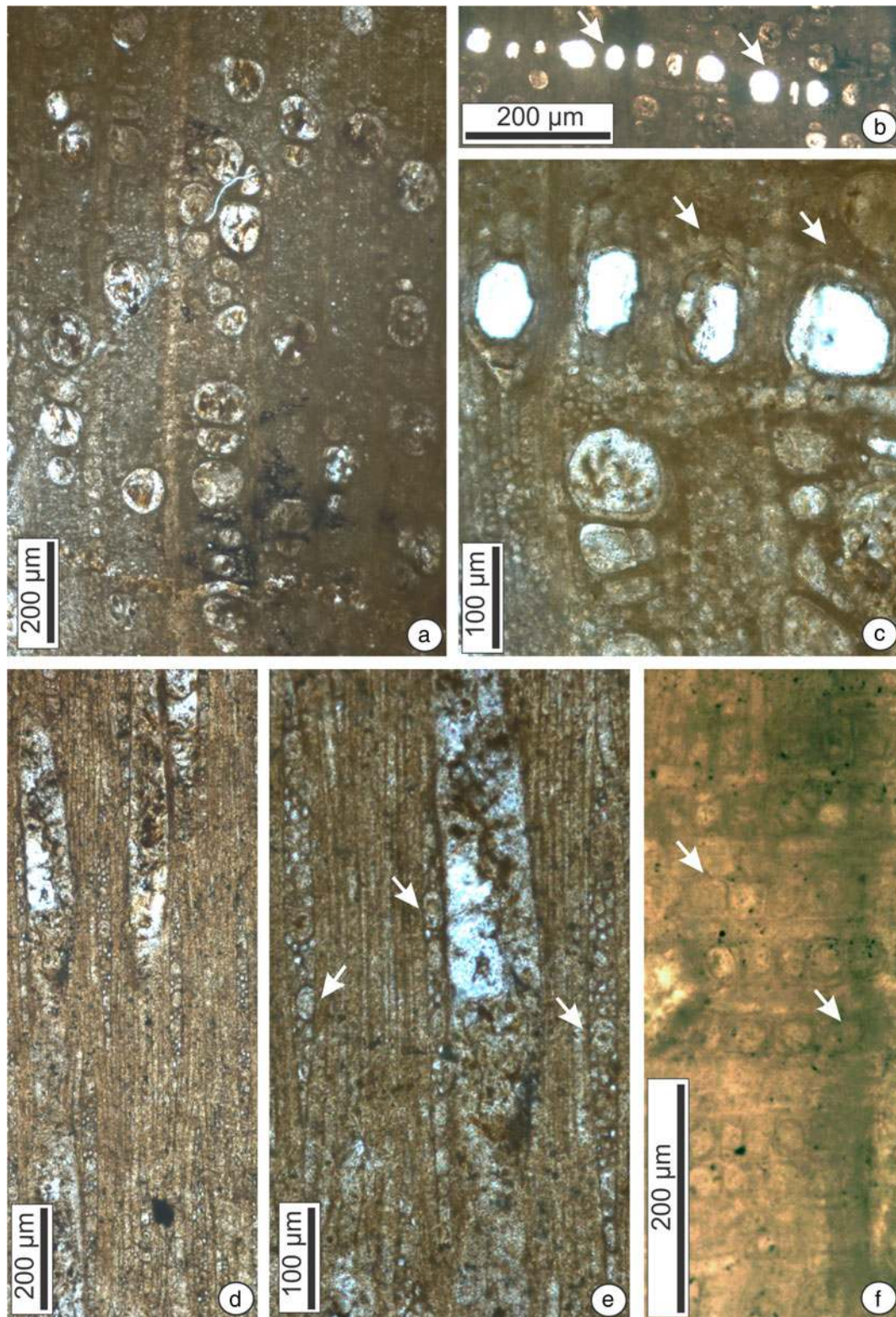


Figure 4. *Hopenium pondicherriense* Awasthi (a) T.S. of the fossil showing solitary as well as grouping of vessels, (b) T.S. showing tangentially arranged gum canals (marked by arrows), (c) T.S. showing gum canals enclosed in parenchyma bands (marked by arrows), (d), (e) T.L.S. of the fossil showing 3-4 seriate rays with crystalliferous upright cells interspersed among the procumbent cells (marked by arrows), and (f) R.L.S. of the fossil showing heterogeneous ray tissues with crystalliferous upright cells (marked by arrows).

high and 22–100 μm wide, sheath cells present on the flanks of multiseriate rays (figure 3d); diameter of procumbent and upright cells 13–15 μm and 20–45 μm , respectively. Fibres thick walled, non-septate, semi-libriform, 36–48 μm wide. Gum canals vertical, normal, solitary or in tangential groups of 2–4, smaller than vessels, t.d. 65–80 μm and r.d. 35–65 μm (figure 3b).

Figured specimen: Specimen no. BSIP 40065.

Horizon: Shumar Formation.

Locality: Near Habur Village, Jaisalmer District, Rajasthan.

Age: ?Plio-Pleistocene.

Affinities: The characteristic features of the fossil such as almost solitary medium to large vessels, vasicentric tracheids, broad rays with uniseriate tails of upright cells, sheath cells, non-septate fibres and diffuse gum canals indicate its close proximity to the dipterocarpaceous woods (Pearson and Brown 1932; Metcalfe and Chalk 1950; Kribs 1959; Miles 1978; Ilic 1991). The genera of the family have been categorized into two groups on the basis of the arrangement of gum canals (Ghosh 1958); (i) gum canals always in concentric rings (e.g., *Shorea* Roxb., *Doona* Thwaites, *Hopea* Roxb., *Parashorea* Kurz., *Pantacme* A. DC., *Balanocarpus* Bedd. and *Dryobalanops* C.F. Gaertn.) and (ii) gum canals diffuse, solitary and in short tangential rows (e.g., *Anisoptera* Korth., *Dipterocarpus* Gaert f., *Vatica* L., *Vateria* L. and *Cotylelobium* Pierre). The present fossil in possessing diffuse gum canals falls into the second category. Among the genera of this category, the fossil best resembles to the *Dipterocarpus* particularly with *D. indicus* Bedd. (BSIP wood slide no. 308) and *D. lowii* Hook. f. (BSIP wood slide no. 2106). However, the former can be separated from the fossil by having greater frequency of gum canals.

Den Berger (1927) instituted the organ genus *Dipterocarpoxyton* Holden emend. Den Berger for the fossil woods resembling to *Dipterocarpus*. So far, a number of fossil woods have been described from various Tertiary exposures (Prakash 1973; Awasthi 1974, 1980; Mehrotra *et al.* 2006). Prasad and Khare (1994) have described their fossil wood directly under the modern genus *Dipterocarprus*. The present fossil wood was compared with the known fossil species and found similar to *Dipterocarparoxyton jammuense* (Guleria *et al.* 2002) described from the upper Tertiary sediments of Jammu region. This species has also been recorded from the Siwalik sediments of Dehradun, Uttaranchal (Guleria *et al.* 2005). Since our fossil wood is identical to *D. jammuense*, it has been placed under the same species.

The genus *Dipterocarpus* Gaertn. f. includes about 69 species and is mainly confined to the Indo-Malaysian region with maximum development in Borneo, Malaysian Peninsula and Sumatra (Mabberley 1997). The genus ranges in its distribution from India in the west to Philippines in the east. In India it is found in Assam, Andamans and Western Ghats (Ghosh 1958). *Dipterocarpus lowii* Hook. f., the modern counterpart of the fossil is mainly found in the Malaysian region.

Genus: *Hopenium* Awasthi (1980)

Hopenium pondicherriense Awasthi (1980)

Description: Wood diffuse porous. Growth rings indistinct. Vessels small to medium, rarely very small, solitary to radial multiples of 2–5 (mostly 2–3) or forming clusters (figure 4a), circular to oval in shape, evenly distributed, t.d. 42–107 μm , r.d. 59–127 μm , heavily tylosed (figure 4a, c); vessel elements 140–550 μm long; perforations simple; intervessel pits poorly preserved, alternate. Vasicentric tracheids present, not easily recognizable from parenchyma. Axial parenchyma paratracheal and apotracheal, paratracheal parenchyma intermingled with vasicentric tracheids, forming thin sheath around the vessels or vessel groups (figure 4c), sometimes appearing aliform or confluent when vessels are closely spaced; apotracheal parenchyma in the form of tangential bands enclosing gum canals (figure 4c); cells thin walled. Rays 1–4 (mostly 3–4) seriate (figure 4d), 10–50 cells or 595–800 μm high and 20–28 μm wide; ray tissue heterogeneous (figure 4f); rays heterocellular consisting of 1–5 marginal rows of upright to square cells and procumbent cells through the median portion; crystalliferous upright cells interspersed among the procumbent cells (figure 4e), diameter of procumbent cells 12–18 μm and upright cells 28–39 μm . Fibres thick walled, 16–28 μm wide, non-septate. Gum canals normal, vertical, aligned in tangential rows forming concentric rings (figure 4b), circular to oval, 93–124 μm in diameter.

Figured specimen: Specimen no. BSIP 40066.

Horizon: Bhumbli Conglomerate.

Locality: Lakhanka-Mithi-Viri (east coast of Bhavnagar), Bhavnagar District, Gujarat.

Age: Miocene.

Affinities: The characteristic features of the fossil such as small to medium tylosed vessels forming clusters, vasicentric tracheids, concentric rings of vertical gum canals, heterocellular rays, crystalliferous upright to square cells interspersed among procumbent cells in the median portion indicate its affinity to the family Dipterocarpaceae. The categorization of the genera of Dipterocarpaceae on the

basis of gum canals has been discussed in the earlier pages and since the present fossil possesses gum canals in concentric rings, it falls in the Ist category. Among the genera of Ist category, the fossil shows best resemblance to the genus *Hopea* Roxb. (including a *Balanocarpus* species, i.e., *B. heimii* King). However, *Balanocarpus heimii* also differs from the present fossil wood in having storied rays. A detailed comparison of the fossil was made with a large number of woods of the modern species of *Hopea* from their thin sections as well as published anatomical descriptions and photographs and the fossil was found to have resemblance with *Hopea helferi* Brandis and *H. glabra* Wight and Arn.

A number of fossil woods of *Hopea* described from various Tertiary sediments of India under the organ genus *Hopenium* (Awasthi 1980) are: *Hopenium pondicherriense* from the Cuddalore Series of south India and from the Siwalik sediments of Kalagarh (Awasthi 1980; Prasad 1993), *H. neyveliense* from the Neyveli Lignite Mine (Awasthi 1984), *H. kalagarhensis* and *H. prenutasoides* from the Siwalik beds of Kalagarh (Prasad and Prakash 1988), *H. payangadiensis* from the Neogene sediments of Payangadi, Cannanore district, Kerala (Awasthi and Srivastava 1990) and *Hopenium* sp. cf. *Hopea odorata* (Prakash et al. 1994). Among these, the present wood is identical to *Hopenium pondicherriense* (Awasthi 1980). *H. neyveliense* could be differentiated by having bigger gum canals and closely spaced parenchyma bands, whereas in *H. prenutasoides*, gum canals are smaller than the present fossil and parenchyma bands are broader. *H. kalagarhensis* and *H. payangadiensis* also differ by having bigger gum canals, whereas *Hopenium* sp. cf. *Hopea odorata* can be distinguished by having mostly 4–5 seriate rays.

Hopea glabra is a medium-sized tree found only in south India in the evergreen forest of South Kanara, Travancore and Tinnevely up to 1200 m altitude and often grows along the river banks, whereas *H. helferi* is a large tree found in semi-evergreen and evergreen forests of Cambodia, India (Andaman), Malaysia, Myanmar and Thailand.

Genus: *Shoreoxylon* Den Berger (1923)
Shoreoxylon burmense Prakash (1965a, b)

Description: Wood diffuse-porous. Growth rings not seen. Vessels medium to large, mostly solitary, rarely in pairs (figure 5a, b), t.d. 130–240 μm , r.d. 224–350 μm , evenly distributed, 5–6 per mm^2 , round to oval in shape; tyloses or gummy deposits present; vessel elements 400–650 μm long with truncate ends; perforations simple; intervessel pits small, alternate, bordered with liner to lenticular apertures (figure 5f). Vasicentric tracheids intermingled with paratracheal parenchyma. Axial

parenchyma paratracheal and apotracheal, paratracheal parenchyma vasicentric, 4–5 celled sheath around the vessels, rarely short extensions present (figure 5b); apotracheal parenchyma diffuse, occurring as solitary cells or in tangential bands associated with the gum canals (figure 5a); cells thin walled. Rays 1–4 (mostly 2–3) seriate (figure 5c, d), homocellular or weakly heterocellular, ray tissue weakly heterogeneous (figure 5e), rays 4–37 cells or 95–760 μm high and 12–75 μm wide, made up of mostly procumbent cells and sometimes upright cells present at the margins (figure 5e); diameter of procumbent cells 20–32 μm . Fibres libriform, thick walled, non-septate and polygonal as seen in cross section. Gum canals vertical, arranged in tangential rows, embedded in parenchymatous tissue, round to oval, 45–150 μm in diameter (figure 5a).

Figured specimen: Specimen no. BSIP 40067.

Horizon: Kand Formation.

Locality: Ratanpurni river bed, Ratanpor, Bharuch District, Gujarat.

Age: Lower Miocene.

Affinities: The important anatomical features of the fossil are: medium to large vessels, vasicentric tracheids, vasicentric and diffuse apotracheal parenchyma, mostly 2–3 seriate rays, weakly heterogeneous tissue, non-septate fibres and tangentially rowed gum canals embedded in parenchyma bands. All these anatomical features of the wood show its close affinity with the modern woods of the Dipterocarpaceae, particularly with the group of first category proposed by Ghosh (1958) who categorized the woods of the family into two groups on the basis of the arrangement of gum canals. In the present fossil, gum canals are tangentially arranged and hence, fall into the first group of Ghosh. Among the genera of this group, the fossil shows similarity with *Shorea*. For further identification the fossil was compared with the published literature (Ghosh 1958; Hayashi et al. 1973) and available thin sections of the modern woods of *Shorea* Roxb. and found similar to *Shorea ovalis* (Korth.) Bl. (BSIP wood slide no. 2129).

About 30 fossil wood species of *Shorea* are known from India and abroad under the organ genus *Shoreoxylon* (Den Berger 1923; Prakash 1973; Awasthi 1974; Prasad and Prakash 1988; Bera and Banerjee 2001). Among these the following nine species were described from the Neogene of India: *Shoreoxylon arcotense* (Awasthi 1974), *S. cuddaloreense* (Gurusamy and Kumarasamy 2007) and *S. indicum* (Awasthi 1974) from south India, *S. robustoides* (Roy and Ghosh 1981) from West Bengal, *S. burmense* (Prakash et al. 1994), *S. deomaliense* (Prakash and Awasthi 1971),

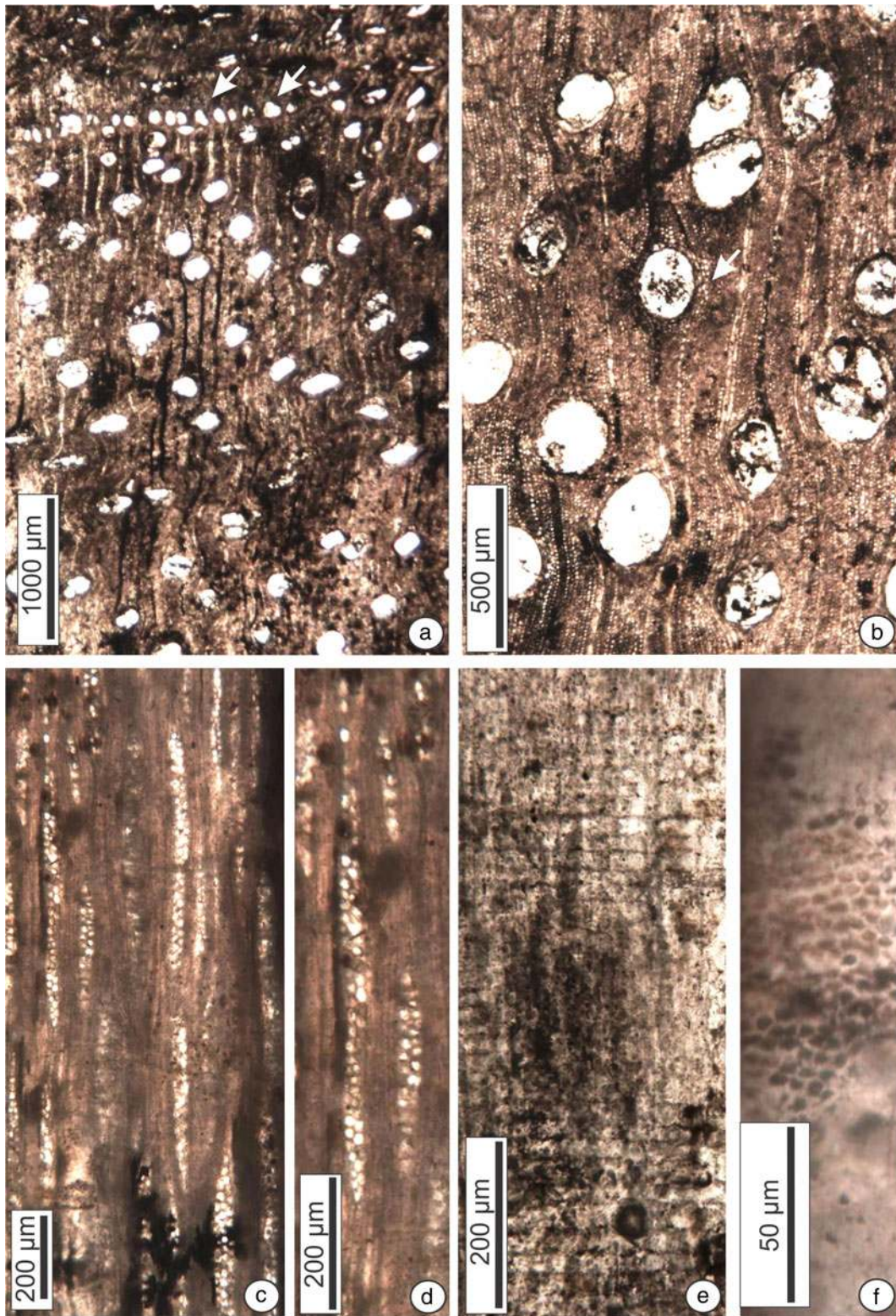


Figure 5. *Shoreoxylon burmense* Prakash (a) T.S. of the fossil showing predominantly solitary vessels and tangentially arranged gum canals (marked by arrows), (b) T.S. showing paratracheal parenchyma around the vessels (marked by arrow), (c), (d) T.L.S. of the fossil showing 2-3 seriate rays, (e) R.L.S. showing weakly heterogeneous ray tissue, and (f) R.L.S. showing alternate intervessel pits.

S. tipamense (Prakash and Awasthi 1970) from northeast India and *S. siwalicus* (Prasad and Prakash 1988) from Himachal Pradesh. After comparison, the fossil was found to resemble to *Shoreoxylon burmense*, reported from the Tertiary of Myanmar (Burma) and northeast India (Prakash 1965a, b; Prakash et al. 1994). The anatomical characters of the *S. burmense* are very similar to the present fossil except that the rays are slightly broader (4–5 seriate) in it. Considering it a minor variation, the present fossil has been assigned the same specific epithet.

Shorea is a genus of about 196 species of mainly rainforest trees and *S. ovalis*, the modern counterpart of the fossil, is a Malaysian species.

4. Discussion

The movement of the Indian plate from south to north *vis-à-vis* climate change has always been a matter of concern for the palaeobotanists. The Indian plate separated from the other Gondwanaland continents around 90 Ma and further moved from southern to northern hemisphere and collided with the Eurasian plate around the mid Cenozoic (Beck et al. 1995; Storey et al. 1995). This collision caused the uplift of the Himalaya and Tibetan plateau (~50 Ma) which constitutes a significant forcing factor on the intensity of the Asian monsoon (Kutzbach et al. 1989; Molnar et al. 1993; An et al. 2001; Zachos et al. 2001; Spicer et al. 2003). The northward movement from mid southern latitudes to the equatorial zone is evidenced by the tropical climate and thick vegetation cover, during the Cenozoic time, on the entire Indian subcontinent, including western India (Prasad et al. 2009) and is also envisaged by the presence of thick lignite deposits at the margins of western India. This indicates existence of well established equatorial rainforests, which are now restricted to the Western Ghats (Prasad et al. 2009), in the Indian subcontinent (including westernmost parts) during the early Palaeogene time. The best example of this is the presence of Dipterocarpaceae, usually a dominant component of the humid tropical and subtropical flora of the Indo-Malayan region with mean annual precipitation of ~1438–4172 mm, during the early Palaeogene time in western India. Here we have reported more dipterocarpaceous remains from the same region but from the Neogene sediments indicating the extension of the family into the Neogene time as well. Contrary to this, not a single taxon of Dipterocarpaceae is growing in the region today. Apart from western India, the family also suffered a gradual decline both numerically and phytogeographically (Awasthi 1994) on the entire Indian

subcontinent. The widespread distribution of the Dipterocarpaceae in the Indian subcontinent in deep time clearly indicates that the uniform tropical climate with higher amount of annual rainfall existed throughout the Indian peninsula during the early Eocene Pliocene (Awasthi 1994; Prasad et al. 2009; Shukla et al. 2012). The distribution of Dipterocarpaceae in the Indian subcontinent today is restricted to the evergreen forest of Assam, Western Ghats and Andamans (Ghosh 1958; Santapau and Henry 1973; Prasad et al. 2009).

The change in the vegetation type is directly related to the change in the climatic conditions. The uniform tropical conditions during the Cenozoic prevailing on the entire Indian subcontinent started deteriorating due to the initiation, evolution and strengthening of the monsoon during the Neogene. The continuous uplift of the Tibetan plateau, following the India-Asia collision, is considered as the primary cause of monsoon initiation and intensification (Ruddiman and Kutzbach 1989; An et al. 2001; Zheng et al. 2004). It was speculated that the monsoon intensified between 9 and 6 Ma, when the Tibetan plateau attained sufficient height to act as a heat source and to block northward air fluxes (Molnar et al. 1993). The winds rich in moisture are drawn towards Himalayas which act like a high wall, thus, forcing them to rise. With the gain in altitude of the clouds, the temperature drops and rains occur. Results of atmospheric circulation modelling suggest that the Himalayas acted as an orographic barrier (Boos and Kuang 2010), pushing the onset of monsoon intensification sometime into the mid-Miocene (Ramstein et al. 1997). The paleobotanical records of western India indeed agree with this view.

The age of initiation of the east and south Asian monsoons is controversial, but a variety of environmental factors suggest that the east Asian monsoon was established by the beginning of the Neogene (~24 Ma) (Clift et al. 2008). Recently, Srivastava et al. (2012) recorded a strong monsoon signal in the Late Oligocene (28–23 Ma) for the southeast Asia. There is a general consensus for a dramatic change in the monsoon system about 6–8 Ma ago, as marked by faunal evidences for increased upwelling in the Arabian Sea (Kroon et al. 1991), an increase in clay mineral fraction recovered from the Bengal fan (Derry and France-Lanord 1996) and ecological shift seen in northern Pakistan (Quade et al. 1989).

Zachos et al. (2001) on the basis of $\delta^{18}\text{O}$ isotopes showed episodes of global warming and cooling (Zachos et al. 2001). The most pronounced warming trend, as expressed by a 1.5% decrease in $\delta^{18}\text{O}$, occurred early in the Cenozoic from Paleocene (59 Ma) to Early Eocene (52 Ma) and

peaked with the Early Eocene Climatic Optimum (EECO; 52 Ma). This warming was followed by a 17-My-long trend towards cooler conditions and rapid expansion of Antarctica continental ice-sheets in the earliest Oligocene persisted until the later part of the Oligocene (26–27 Ma). A warming trend, late Middle Miocene Climatic Optimum (17 to 15 Ma), reduced the extent of Antarctic ice till the Middle Miocene (~15 Ma). The Middle Miocene climatic optimum has also been proposed as a period of enhanced weathering, erosion and organic carbon burial (Wan *et al.* 2009). This warm peak was followed by a gradual cooling and reestablishment of a major ice-sheet on Antarctica by 10 Ma. These warm phases are evidenced by the presence of typical wet tropical families like Dipterocarpaceae on the Indian subcontinent during both the Palaeogene and Neogene (Dutta *et al.* 2011a; Shukla *et al.* 2012). Similarly, by using eolian sediments from China and marine sediments from Indian and north Pacific Ocean, An *et al.* (2001) identified three stages in the evolution of Asian climates: (a) enhanced aridity in the Asian interior and onset of the India and east Asian monsoons (~9–8 Ma), (b) continental intensification of the east Asian summer and winter monsoons, together with increased dust transport to the north Pacific Ocean (~3.6–2.6 Ma) and (c) increased variability and possible weakening of the Indian and east Asian summer monsoons and continued strengthening of the east Asian winter monsoon since ~2.6 Ma. The above facts support the argument that the stages in evolution of Asian monsoons are linked to phases of Himalaya–Tibetan plateau and Northern Hemisphere glaciations. The other possible influences on Late Miocene–Pliocene climates are change in ocean gateways (Haug and Tiedemann 1998), decrease in atmospheric CO₂ concentration due to increased weathering or carbon burial (Raymo *et al.* 1988) and changes in land/ocean configuration (Ramstein *et al.* 1997).

All these factors are ultimately responsible for the establishment of drier climatic conditions in the westernmost part of the Indian subcontinent in the late Neogene (Prell *et al.* 1992; An *et al.* 2001) and extinction of the many tropical families, *viz.*, Dipterocarpaceae from the region. Stable isotope data on calcretes indicates initiation of a monsoonal climate in the Thar during the Neogene at around 0.8 Ma (Deotare *et al.* 2004).

A thorough review of the climatic shift during the Neogene which caused deterioration of ubiquitous tropical vegetation existed over entire Indian subcontinent led to a conclusion that the emergence as well as extinction of Dipterocarpaceae is directly related to the change in the climatic conditions. The family Dipterocarpaceae was widespread on the entire Indian subcontinent

from the Early Eocene onwards up to the Pliocene–Pleistocene (Lakhanpal *et al.* 1984; Dutta *et al.* 2009, 2011a, b; Shukla *et al.* 2012) (figure 1), along with the other known elements (Guleria 1983, 1984a, b, 1990, 1991, 1992a, 1994, 1996; Lakhanpal *et al.* 1984; Guleria *et al.* 2009; Shukla *et al.* 2012). This further indicates a more or less warm and humid climate supporting the luxuriant vegetation during the period as all the nearest living relatives (NLRs) of the present and earlier described fossils are distributed in the evergreen to deciduous forests of the Indo-Malayan region (Lakhanpal *et al.* 1984; Shukla *et al.* 2012).

Dipterocarpaceae is an important family of tropical rainforests and to explain its origin two hypotheses exist; the first one advocates for the Malaysian origin, arguing that two-third of the total dipterocarp species occur there today and the region is also quite rich in its fossil records (Lakhanpal 1974; Sasaki 2006; Shukla *et al.* 2012). According to this, the family migrated from southeast Asia to India during the Neogene when the land connections were established between the two landmasses (Lakhanpal 1970; Awasthi 1994). The other hypothesis supports the Gondwanic origin based on phylogenetic studies comparing Dipterocarpaceae with the Sarcolaenaceae, a tree family endemic to Madagascar. These two also share a common ectomycorrhizal ancestor (Ducouso *et al.* 2004; Dutta *et al.* 2009; Rust *et al.* 2010; Beimforde *et al.* 2011). Recently, a few microfossils and chemical analysis of the resin (Dutta *et al.* 2009, 2011a, b) from the Eocene of western India supported the ‘Out of India’ hypothesis for the family. According to this hypothesis, the dispersal of the family into southeast Asia took place only when it came on rafting with the Indian plate from south to north. As far as the megafossil records of the family are concerned, its fossils are found in India only from the Early Miocene onwards (Guleria 1992b; Shukla *et al.* 2012), despite the fact that we have well established megafossil records from the Late Cretaceous to Palaeogene age from the Indian subcontinent (Mehrotra 2003). From the Palaeogene of India, the only fossil wood resembling Dipterocarpaceae was reported by Rust *et al.* (2010). The wood needs re-investigation as it lacks many important features of the family Dipterocarpaceae. The fossil wood shows very low and thin rays (Rust *et al.* 2010; figure S3E); such rays are not found in this family. Moreover, the authors ignored the presence of hyaline cells among the fibres (Rust *et al.* 2010; figure S3F) which look like the oil cells, characteristic feature of the family Lauraceae. In this family, thin and low rays are commonly found (Ghosh 1958; Kribs 1959; Hayashi *et al.* 1973; Miles 1978; Ilıc 1991). Further, the oil cells might have been misinterpreted by the

authors as gum canals in the cross-section of the fossil wood (Rust *et al.* 2010; figure S3A). Further discovery of reliable megafossil evidences from the early Palaeogene sediments would strengthen the 'Out of India' hypothesis.

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