

Fossil Wood of Subfamily Detarioideae (family Fabaceae) from the Paleogene of the Indian Subcontinent: Origin and Palaeo-dispersal Pathways

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ABSTRACT

A new fossil wood of *Hopeoxylon* i.e. *H. umarsarensis* sp. nov. showing close resemblance with the modern wood of *Sindora/Copaifera* of the subfamily Detarioideae (family Fabaceae) is described from the Umarsar lignite mine of Kutch basin, Gujarat that belongs to the Naredi Formation of the early Eocene age. Detarioideae is one of the reinstated subfamilies of the Fabaceae with diversity much higher in tropical Africa than in South America or Asia. The relics of this subfamily are known from the Paleocene onwards from various horizons of America, Africa, Europe, India and Southeast Asia. This is the oldest fossil record of the genus *Sindora/Copaifera* which contributes towards the understanding of the origin and palaeo-dispersal pathways of this early-diverging subfamily within the early branching Fabaceae.

INTRODUCTION

Palaeo-dispersal events have been closely related to plate tectonics. Many plant taxa thought to be originated on one continent reached far away from their origin point by using vicariance or dispersal mechanisms (Morley, 2000). The configuration of the Indian plate changed dramatically during the Late Jurassic and Cretaceous as the plate broke apart sequentially from Gondwana, East Gondwana, Madagascar, and finally from the Seychelles island (Chatterjee and Scotese, 1999). The island theory for the Indian subcontinent, being isolated for more than 100 million years until it docked with Asia, has been discarded as the Late Cretaceous Indian vertebrates are cosmopolitan and show faunal/floral similarities with those of South America, Madagascar, Africa, and Europe (Sahni and Bajpai, 1988; Briggs, 1989; Jaegger et al., 1989; Chatterjee and Scotese, 1999). Various landbridges have been proposed that opened up faunal/floral migration route between India and other continents. (Briggs, 1989; Krause et al., 1997; Chatterjee and Scotese, 1999).

The subfamily Detarioideae (Fabaceae), which is mainly distributed in tropical Africa with a less diverse representation in Asia and South America, has been hypothesized to be Afro-American in origin. It dispersed into Asia through the Indian subcontinent (Estrella et al., 2017) and this can be explained by the Out of India hypothesis (Datta and Karanth, 2009). This subfamily has ~81 genera and ca. 760 species with pantropical distribution (Steyermark et al., 1998; Herendeen, 2000; Bruneau et al., 2001; Gasson et al., 2003; Herendeen et al., 2003; LPWG, 2017; Estrella et al. 2018). The unequivocal fossil evidences of Detarioideae are from the Paleocene of Nigeria (Adegoke et al., 1978) and Oligocene-Miocene boundary in Central America (Hueber and Langenheim, 1986; Poinar and Poinar, 1999; Poinar and Chambers, 2015). The fossil being described in the present communication might be the oldest record of *Sindora/Copaifera* supporting the post Gondwanan origin possibly on the African

landmass and then dispersing eastwards through on the Indian subcontinent.

STUDY AREA AND AGE OF THE SUCCESSION

Umarsar lignite mine is situated in between Matanomadh and Brahma Nagar (latitude 23°42' to 23°47' N; longitude 68°51' to 68°53' E), Bhuj District, Gujarat (Fig. 1A). In the Kutch basin, there are several workable opencast lignite mines that have varied litho-stratigraphic thickness. Sedimentary deposits of these lignite mines are richly fossiliferous for micro and megafloreal records. The lignite-bearing succession of Kutch is well-developed in an almost peneplained terrain located south of the Rann of Kutch in Panandhro-Lakhpat area of the Kutch basin, Gujarat. Umarsar lignite mine is believed to be an extension of Panandhro lignite mine situated on the other side of the road (latitude 23°42' to 23°47' N; longitude 68°51' to 68°53' E). The lignite deposits of the Panandhro-Lakhpat region have also been designated as Panandhro Formation by Saraswati and Banerjee (1984). The depositional settings of Kutch lignites have been discussed in detail by Mukhopadhyay and Shome (1996). Recently, Agrawal et al. (2017), based on dinoflagellate cysts and associated spore-pollen assemblage, assigned an early Eocene (Ypresian; 56 – 48 Ma) age to the lignitic succession at Panandhro.

MATERIAL AND METHODS

A petrified wood was collected from the middle seam of the Umarsar lignite mine (Fig. 1B) of Kutch district, Gujarat. Its preservation is satisfactory to reveal structural details. The fossil wood was cut into thin sections, i.e. transverse, tangential longitudinal and radial longitudinal for the anatomical study. Each section was polished and mounted in canada balsam (Haas & Rowe, 1999). These sections were studied with light microscopy (Leica DM2700 M) and photographed using a Leica DFC 290 digital camera. The fossil wood was compared not only with extant taxa by examining available wood slides at the xylarium of the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow, but also with published literature and the InsideWood database (<http://insidewood.lib.ncsu.edu/>; Wheeler 2011). While describing the fossil, the terminology of the IAWA Committee (1989) was followed. The figured specimen is deposited in the museum of the Birbal Sahni Institute of Palaeosciences, Lucknow.

RESULTS

Systematics

Family: Fabaceae

Subfamily: Detarioideae

Genus: *Hopeoxylon* Navale emend. Awasthi, 1977

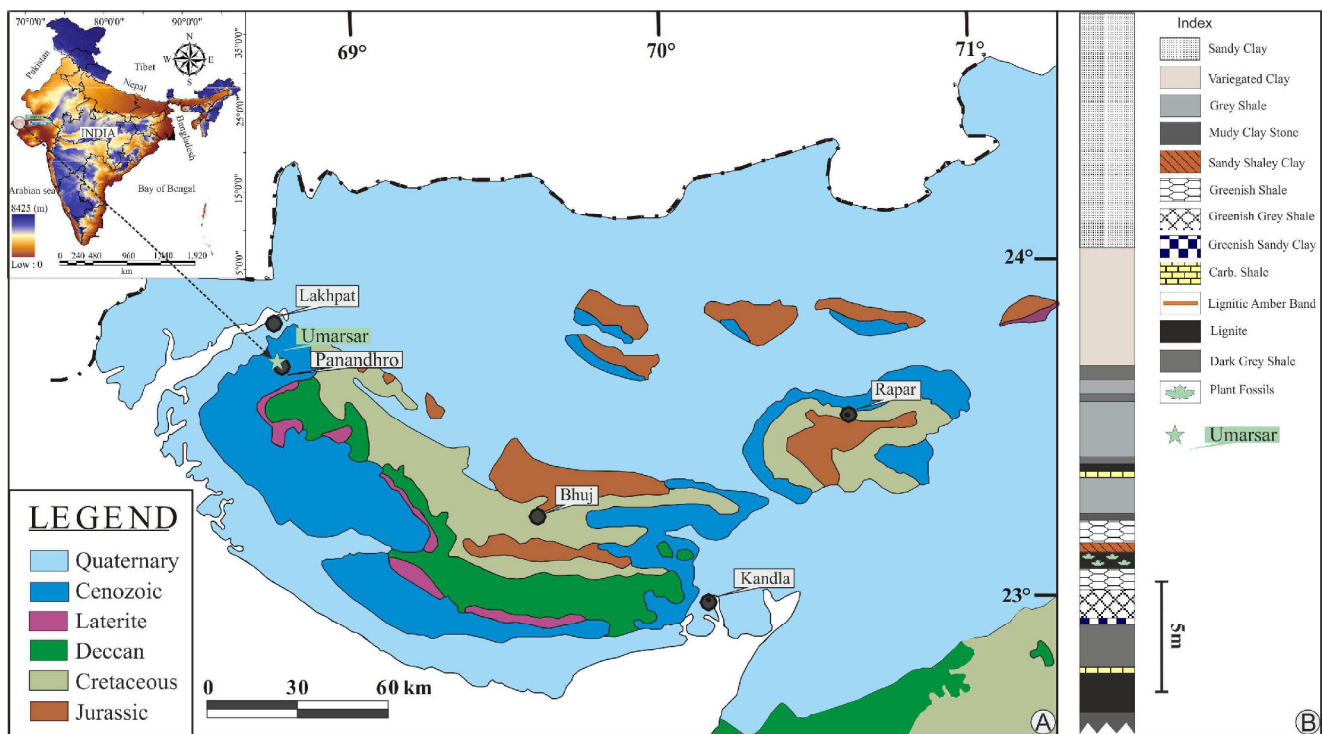


Fig. 1. (A) Geological map of the Kutch basin showing the fossil locality (marked by star) (after Roy and Jakhar, 2002); **(B)** Generalized lithology of the Umarsar lignite mine showing fossiliferous horizon from where the fossil wood was collected.

Synonymy: *Copaiferoxylon* Müller-Stoll et Mädell, 1967; *Sindoroxyton* Lemoigne et al., 1964; *Detarioxyton* Boureau et Louvet, 1975

Hopeoxylon umarsarensis Shukla et al., sp. nov. (Fig. 2A-F)

Specific diagnosis: Wood diffuse porous. Growth rings delimited by thin bands of marginal parenchyma enclosing gum canals situated at variable distance, bands 96–760 μm apart. Vessels round to oval, small to large-sized, tangential diameter range 80–200 μm , radial diameter 90–220 μm , solitary and in radial multiples of 2 to 3 (mostly 2), 22–30 per mm^2 , evenly distributed; vessel elements 250–385 μm in length with horizontal to oblique ends; perforations simple. Axial parenchyma both paratracheal and apotracheal; paratracheal vasicentric forming 1–2 celled sheath around the vessels; apotracheal in form of thin bands enclosing gum canals; solitary crystal present in chambered parenchyma cells. Xylem rays mainly 1–2 seriate, 6–9 cells or 250–435 μm high; ray tissue heterogeneous, procumbent cells 11–14 μm in tangential height; upright cells 40–54 μm in tangential height. Fibres polygonal in cross-section, thick-walled, non-septate. Gum canals normal, vertical in concentric rings and embedded in parenchyma bands, 110–156 μm in tangential diameter.

Holotype: Specimen no. BSIP 41705

Locality: Umarsar lignite mine, Kutch, Gujarat

Horizon and age: Naredi Formation; early Eocene

Remarks: The characteristic features of the fossil wood are concentric rings of gum canals situated at variable distance and embedded in thin marginal parenchyma bands, simple perforations, mostly biseriate rays with heterogeneous ray tissue, non-septate fibres and solitary crystal present in chambered parenchyma cells. All these features indicate its affinity with the xylotomically similar taxa *Copaifera* Lindl., *Detarium* Jussieu and *Sindora* Miquel of the Fabaceae (Metcalf and Chalk 1950; Normand 1950; Kribs 1959; Ilic 1991). Apart from these, fossil wood also shows some resemblance with other genera i.e., *Daniella* Benn. and *Sindoropsis* J. Léonard of

the Fabaceae and *Shorea* Roxb. ex C.F. Gaertn. of the Dipterocarpaceae. However, *Daniella* is distinct in having storied elements, *Sindoropsis* has intercellular canals in short tangential rows, while *Shorea* can be differentiated mainly in having vasicentric tracheids (<http://insidewood.lib.ncsu.edu/>). The fossil wood was compared in detail with anatomically similar genera i.e., *Copaifera*, *Detarium*, and *Sindora* and found similar to *Copaifera* and *Sindora* (<http://insidewood.lib.ncsu.edu/>) mainly in having 1-2 seriate rays and gum canals in concentric rings, while *Detarium* can be differentiated from our fossil in having more parenchyma.

Fossil woods resembling *Sindora* and allied forms, such as *Copaifera* and *Detarium* are usually placed under the fossil genus *Hopeoxylon* Navale emend. Awasthi (1977) and its nine species known from various parts of the world are: *H. aethiopicum* (Lemoigne et al.) Lalitha and Prakash (1980) from the Miocene of Ethiopia, *H. arcotense* Awasthi (1977) from the Neogene of south India, *H. assamicum* Lalitha and Prakash (1980) from the Miocene of Assam and West Bengal (Bera et al., 2001), *H. eosiamensis* Prakash (1981) from the Lower Siwalik of Uttarakhand, *H. indicum* (Navale) Awasthi (1977) from the Neogene of south India and Oligo-Miocene of Saudi Arabia (Prive-Gill et al., 1999), *H. libycum* (Boureau and Louvet) Lalitha and Prakash (1980) from the Paleogene of Libya, Algeria and Tunisia, *H. migiurtinum* (Chiarugi) Lalitha and Prakash (1980) from the Miocene of Somalia, *H. sindoroides* (Kramer) Lalitha and Prakash (1980) from the Tertiary of west Kalimantan and *S. speciosum* (Navale) Awasthi (1977) from the Neogene of south (Prakash et al., 1988) and northeast India (Mehrotra et al., 2005). Of them, *H. arcotense* was considered by Prakash et al. (1988) as synonym to *H. speciosum*. The present fossil was found different from all of them in having more frequent rows of gum canals, along with 1-2 seriate rays. Hence, this fossil wood is described under a new specific epithet i.e., *Hopeoxylon umarsarensis* Shukla et al., sp. nov.; the specific name is after the fossil locality. Although *H. indicum* (Navale) Awasthi (1977) is anatomically very similar to our fossil, yet it can be differentiated in having lesser number of rows of gum canals.

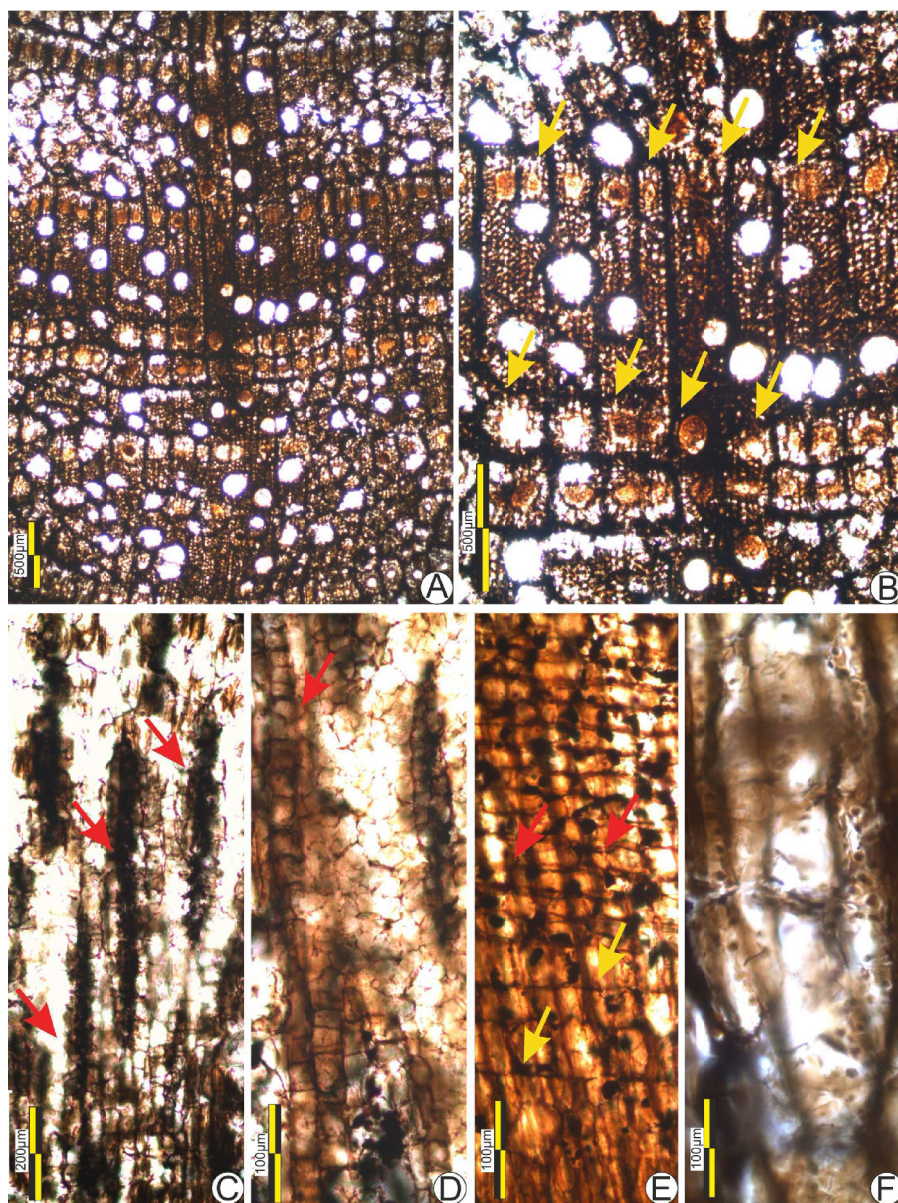


Fig. 2. A–F. *Hopeoxylon umarsarensis* Shukla et al., sp. nov. (A) Cross section of the fossil wood showing arrangements of vessels and rows of gum canals; (B) Magnified cross section of the fossil wood showing rows of gum canals at variable distance (yellow coloured arrows); (C) Tangential longitudinal section of the fossil wood showing 1–2 seriate rays (mostly uniseriate) (red coloured arrows); (D) Tangential longitudinal section of the fossil wood showing chambered parenchyma cells (red coloured arrows); (E) Radial longitudinal section of the fossil wood showing heterocellular rays (upright cells marked by yellow coloured arrows and procumbent cells by red coloured arrows); (F) Radial longitudinal section of the fossil wood showing intervessel pits.

DISCUSSION

Palaeobiogeography and Palaeo-dispersal Pathways for Detarioideae

Historical biogeography analyzes the geographic distribution of organisms in relation to space and time and attempts to reconstruct distribution patterns of organisms (Lieberman, 2000). The diverse legume family supposed to have an ancient origin is highly debatable and hypothesized by different theories of origin and dispersal. Some workers believe that the family originated in west Gondwana with subsequent vicariance events involving South American and African lineages (Raven and Axelrod, 1974; Morley, 2000), but phylogenetic analyses of various groups of Fabaceae discard this explanation for

the origin of legume clades (Lavin et al., 2000, 2004; Bruneau et al., 2008; Simon et al., 2009). Another theory i.e. Tethys Seaway hypothesis (Laurasian origin) (Ramdhani et al., 2010; Yahara et al., 2013) has also been discarded based on recent fossil evidences (Pan et al., 2010; Moya and Brea, 2015). Estrella et al. (2017) concluded that Detarioideae probably originated in Africa, followed by a rapid succession of dispersal events involving other Gondwana regions that were already separated (South America, Antarctica, Madagascar and India). Although the landmasses forming Gondwana were already drifting apart at that time (Scotese, 2004), yet dispersal routes were available among the different units that once formed Gondwana (Morley, 2003). The present fossil wood of the subfamily from the early Eocene (56–48 Ma) horizon is congruent with this hypothesis and would support that the subfamily originated in the African continent and dispersed over the Indian subcontinent through Oman-Kohistan-Ladakh (OKL) Arc (Chatterjee and Scotese, 2010). As far as the time of origin of Detarioideae is concerned, there are two schools of thoughts. According to Bruneau et al. (2008) it originated in the early to middle Eocene, while Esterella et al. (2017) suggested its origin in the early Paleocene. The present finding from the Ypresian age supports the latter view.

Most plate reconstructions suggest that India was an isolated island continent until it docked with Asia (Barron and Harrison, 1980; Smith, 1988). In contrast, the Late Cretaceous Indian vertebrates are cosmopolitan and show faunal similarities with those of South America, Madagascar, Africa, and Europe (Sahni and Bajpai, 1988; Briggs, 1989; Jaegger et al., 1989; Chatterjee and Scotese, 1999). Many landbridges have been proposed to trace the possibilities of faunal/floral migration routes between India and other Gondwanan continents (Briggs, 1989; Krause et al., 1997; Chatterjee and Scotese, 1999). The Oman-Kohistan-Ladakh (OKL) arc serves as an important biotic corridor between India and Africa (Chatterjee and Scotese, 2010; Chatterjee et al., 2013). The OKL arc was accreted to the Indian plate around 70 Ma and formed a biotic dispersal corridor for the migration of Gondwana dinosaurs during the Maastrichtian (Chatterjee and Scotese, 2010). This hypothesis (Chatterjee and Scotese, 2010; Chatterjee et al., 2013) may account for the occurrence of similar family-level taxa in India, Madagascar and South America during the latest Cretaceous. Many plant families reached Eurasia by rafting on the Indian plate when it got bumped into the Eurasian plate at approximately 55 ± 10 Ma (Wang et al., 2014). However, a recent study (Hu et al., 2016) proposed that the initial collision occurred in the central-eastern Himalaya at 59 ± 1 Ma. The above conclusion is supported by the presence of modern analogs of the fossil in the tropical forests of Southeast Asian regions.

The palaeocontinental position of the Indian subcontinent during the early Eocene (~55–52 Ma) (Scotese and Golonka, 1992; Molnar and Stock, 2009; Chatterjee et al., 2013) has been evident by the

presence of luxuriant tropical forests (Shukla and Mehrotra, 2018). The Panandhro lignite mine was exposed to the palaeoequatorial scenario during the time of deposition of the sediments as the lignite deposits of this mine have been formed from an angiosperm dominant luxuriant mixed forest ecosystem under a humid tropical climatic condition (Agarwal et al., 2017). A palynoassemblage described from this mine shows the presence of mangrove pollen and dinoflagellate cysts, along with moderate sulfur contents. This suggests the deposition of lignite mainly in a near shore setting or marine influenced setting (Mathews et al., 2018). A few plant megafossils comparable to *Syzygium*, *Lagerstroemia speciosa*, *Cinnamomum zeylanicum*, *Ficus tomentosa*, and *Pandanus* spp. described from this mine indicate the existence of tropical evergreen to semi evergreen forests in and around the localities during the early Eocene (Lakhanpal and Guleria, 1981). The Umarsar lignite mine is a newly opened mine considered to be an extension of the Panandhro lignite mine and hence might have been experiencing the same kind of climatic conditions during the early Eocene time.

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