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ABSTRACT

Wood of *Connaroxylon dimorphum* (Connaraceae, Oxalidales) from the Deccan Intertrappean Beds of India (KPg Boundary 65–67 MY BP) is described. It is characterized by parenchyma-like fiber bands alternating with normal fibers, septate and nonseptate fibers, vessel-ray pits with strongly reduced borders, uniseriate rays of square and upright cells, and radial tubules in the center of ray cells that are arranged in a herringbone pattern. The overall wood anatomy strongly resembles Melastomataceae *p. p.*, *Lagerstroemia p. p.* (Lythraceae) and *Connarus* (Connaraceae). However, the shared radial tubules of *Connarus* and the fossil strongly tilt the evidence of botanical affinities towards this genus. This would represent the second and by far the oldest fossil wood record of the Connaraceae, also considerably older than the earliest fossil records of the family's other plant parts, and one of the oldest fossils of the order Oxalidales.

Keywords: Parenchyma-like fiber bands, radial tubules, *Lagerstroemia*, Melastomataceae, *Connarus*.

INTRODUCTION

The Deccan Volcanic Province of India represents one of the largest continental flood basalts in Earth's history. The Deccan Traps were formed as a result of outpouring of lava due to volcanic eruptions in the Indian peninsula, associated with the movement of the Indian Plate over the Reunion hotspot (Chatterjee *et al*. 2013). Recent studies based on $^{40}Ar/^{39}Ar$ dating and magnetostratigraphy indicate that volcanism occurred from 67.5 ± 1–63 Ma with the bulk of the eruption at 65 ± 1 Ma, close to the K-Pg boundary (Chenet *et al*. 2009; Renne *et al*. 2015; Schoene *et al*. 2015; Shrivastava *et al*. 2015). The Deccan Intertrappean sediments were deposited during quiescent periods of the volcanic activity in lacustrine and fluviatile environments. These sedimentary deposits, referred to as the Deccan Intertrappean Beds, were deposited at a critical time in angiosperm history, are highly fossiliferous and contain diverse biota of Maastrichtian-Danian age (recently reviewed by Srivastava 2011 and Smith *et al*. 2015).

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The fossils described here initially were provisionally assigned to the Celastraceae because of the striking combination of distinct parenchyma-like fiber bands and almost exclusively uniseriate rays – attributes typical of several Celastraceae (Metcalfe & Chalk 1950; IAWA Committee 1989; InsideWood 2004-onwards). However, mismatching features such as intervessel pit size and nature of vessel-ray pits excluded Celastraceae and prompted a wider search of all possible woody angiosperms using InsideWood (InsideWood 2004-onwards; Wheeler 2011), the Leiden reference slide collection, and the wood anatomical literature.

The aims of this paper are to 1) contribute to an ongoing comprehensive review of the fossil woods from the Deccan Traps (Smith *et al*. 2015; Wheeler *et al*. 2017, in prep.); 2) attribute the fossil to the clade of its most likely living relative; and 3) briefly discuss its relevance for angiosperm phylogeny and paleoecology.

ORIGIN OF THE SAMPLES

The fossil woods described in the present communication were collected from the Mandla lobe outcrop of Dhangaon, Mandla District, Madhya Pradesh (N 22° 50' 57"; E 80° 26' 34.6") by one of us (RS) during field work in the Deccan Intertrappean Beds of central India in 2015. This locality occurs within a region where the bracketing basalts have recently been dated as lowermost Paleocene (Shrivastava *et al*. 2015).

Thin sections (cross, tangential and radial) of the fossil woods were prepared following the standard method of grinding, polishing and mounting in Canada balsam for permineralized material (Lacey 1963). The type slides are deposited in the museum of the Birbal Sahni Institute of Palaeosciences, Lucknow (BSIP). The thin sections were examined with an Olympus BX 50 light microscope and the photography was done with an Olympus DP 20 camera. The anatomical terms used in describing the wood follow the IAWA Hardwood List (IAWA Committee 1989).

RESULTS AND DISCUSSION

Systematic description

Core-Eudicots
Order – Oxalidales
Family – Connaraceae
Genus – ***Connaroxylon*** Baas, Manchester, Wheeler & Srivastava, *gen. nov.*
Species – ***Connaroxylon dimorphum*** Baas, Manchester, Wheeler & Srivastava, *spec. nov*. Named for its dimorphic fibers
Holotype – BSIP Museum No. 40975
Paratype – BSIP Museum No. 40976
Stratigraphic horizon – Deccan Intertrappean Beds. Maastrichtian-lowermost Paleocene
Locality – Dhagaon, Mandla District, Madhya Pradesh: N 22° 50' 57"; E 80° 26' 34.6"
Material – Field accessions 22/8885; 30/8885. Two small samples of c. 4.2 cm diameter, containing pith; one stem contains a branch trace.

Diagnosis – Diffuse-porous wood. Vessels solitary and in radial multiples. Vessel elements with alternate intervessel pits and simple perforations. Vessel-ray pits with strongly reduced borders. Parenchyma very scanty. Fibers in alternating bands of thin-walled parenchyma-like fibers and thick-walled "normal" fibers. Rays almost exclusively uniseriate and composed of square to erect cells. Radial tubules present in some of the rays. Crystals in chambered ray cells and fibers.

Description (Fig. 1–9): *Growth rings* indistinct or faint and then marked by radially flattened fibers. *Vessels* diffuse (Fig. 1, 2), 20–25% solitary, remainder in radial multiples of 2–3 (–6 or very rarely more than 10; longest multiples in wood adjacent to pith), 14–30 per sq.mm, circular to oval when solitary, flattened at the place of contact when in radial multiples; tangential diameter 62 (29–115; SD 17) μm, radial diameter 79 (43–116; SD 23) μm. Vessel elements 387 (174–743; SD 159) μm long. Intervessel pits 8–10 μm, bordered with slit-like or round apertures (Fig. 3); vessel-ray pits mostly with strongly reduced borders and circular to elongate (Fig. 4). Thin-walled tyloses occasionally present. – *Fibers* of two types: 1) thin-walled and in parenchyma-like bands of varying widths alternating with 2) thick-walled in zones that vary from narrow to very wide (Fig. 1, 2). Most fibers nonseptate, but some septate. Fiber wall pitting not observed, probably minutely bordered to simple, typical of libriform fibers. Radial fiber diameter 20 (14–25; SD 4) μm. The parenchyma-like fiber bands are much more common in the juvenile wood than in the more mature wood towards the periphery of the samples. – *Axial parenchyma* scanty paratracheal, extremely sparse, strands of 5–6 cells, cells 16–30 μm in radial diameter. *Rays* almost exclusively uniseriate, but a few rays with short biseriate central portions (Fig. 5), 11–23 per mm, heterocellular, composed mainly of square or upright cells with a few procumbent cells present in biseriate portions, or upright, square and weakly procumbent cells mixed throughout the rays (Fig. 6). Height 2–20 cells or 539 (146–942; SD 241) μm. – *Crystals*. Prismatic crystals present in chambered upright ray cells (Fig. 6) and in chambered fibers (Fig. 7). – *Herringbone patterned rays and tubules*. In radial sections some of the rays show a herringbone pattern (Fig. 8) with cells converging towards narrow tubules with dark contents. [These tubules are very similar to the illustration of laticifers in *Croton* in the IAWA Hardwood List (IAWA Committee 1989; fig. 54 on p. 307).] – *Pith*. Both specimens contain a wide, more or less rounded to pentagonal pith with central large-celled parenchyma. The peripheral pith is small-celled, in some regions giving an impression of internal phloem, separated by some small-celled parenchyma layers from the protoxylem vessels (Fig. 9).

Coded descriptions following the IAWA Hardwood List (IAWA Committee 1989): 2, 5, 13, 22, 25v, 26, 27v, 31, 32, 41, 47, 48, 56v, 61, 65, 66, 67, 75, 78, 93, 96, 105, 109, 115, 116, 132, 136, 137v, 140, 143.

Comparison with extant and fossil woods

Striking features of this fossil are the parenchyma-like, thin-walled fiber bands alternating with zones of thick-walled fibers, almost exclusively uniseriate rays, vessel-ray pits with reduced borders and chambered ray parenchyma and fibers with prismatic crystals. Other features such as diffuse porosity, simple perforation plates, and alternate

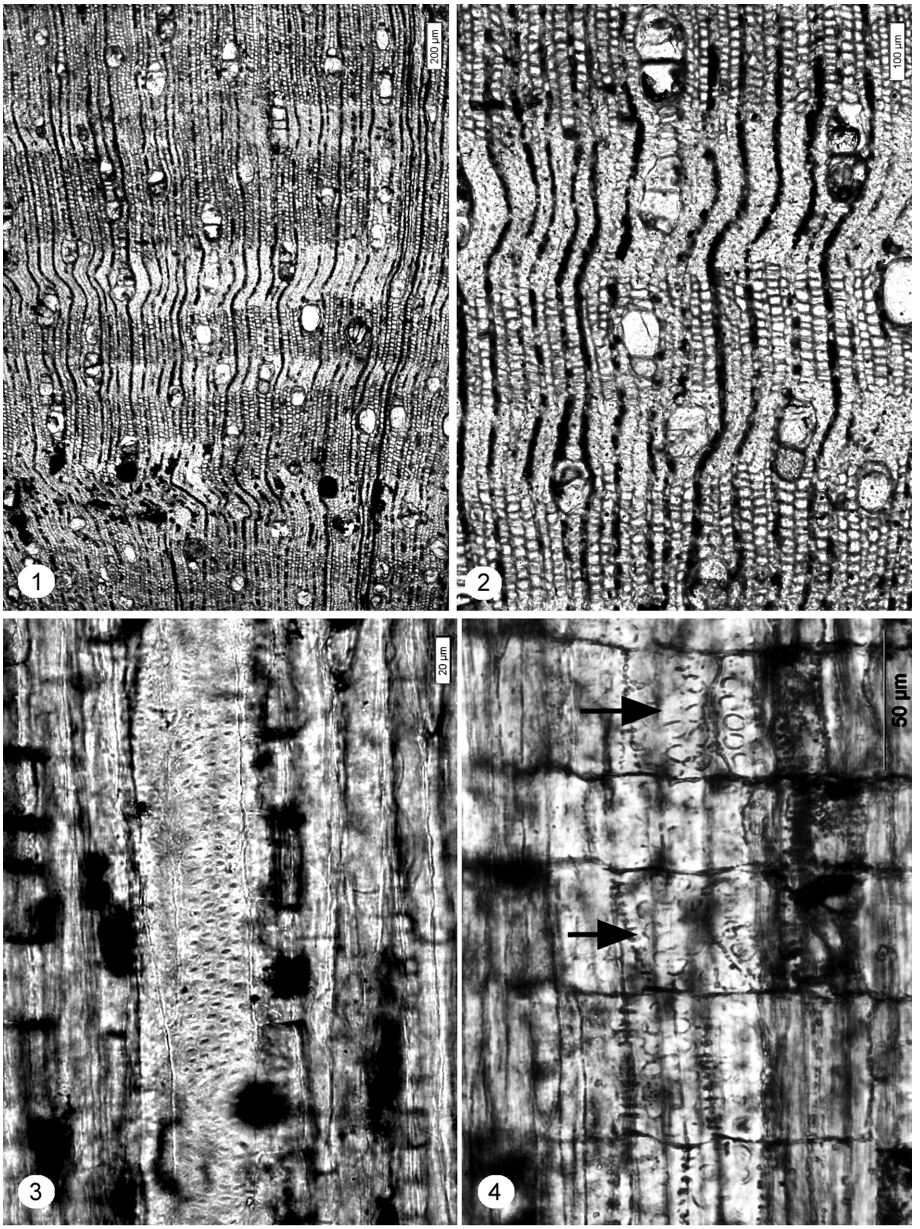

Figure 1–4. *Connaroxylon dimorphum*. – 1 & 2: Diffuse-porous wood, alternating zones of thin-walled and thick-walled fibers, TS. – 3: Alternate intervessel pits, RLS. – 4: Vessel-ray parenchyma pits with reduced borders (arrows), RLS. — Scale bars: 200 µm in 1; 100 µm in 2; 20 µm in 3 & 4.

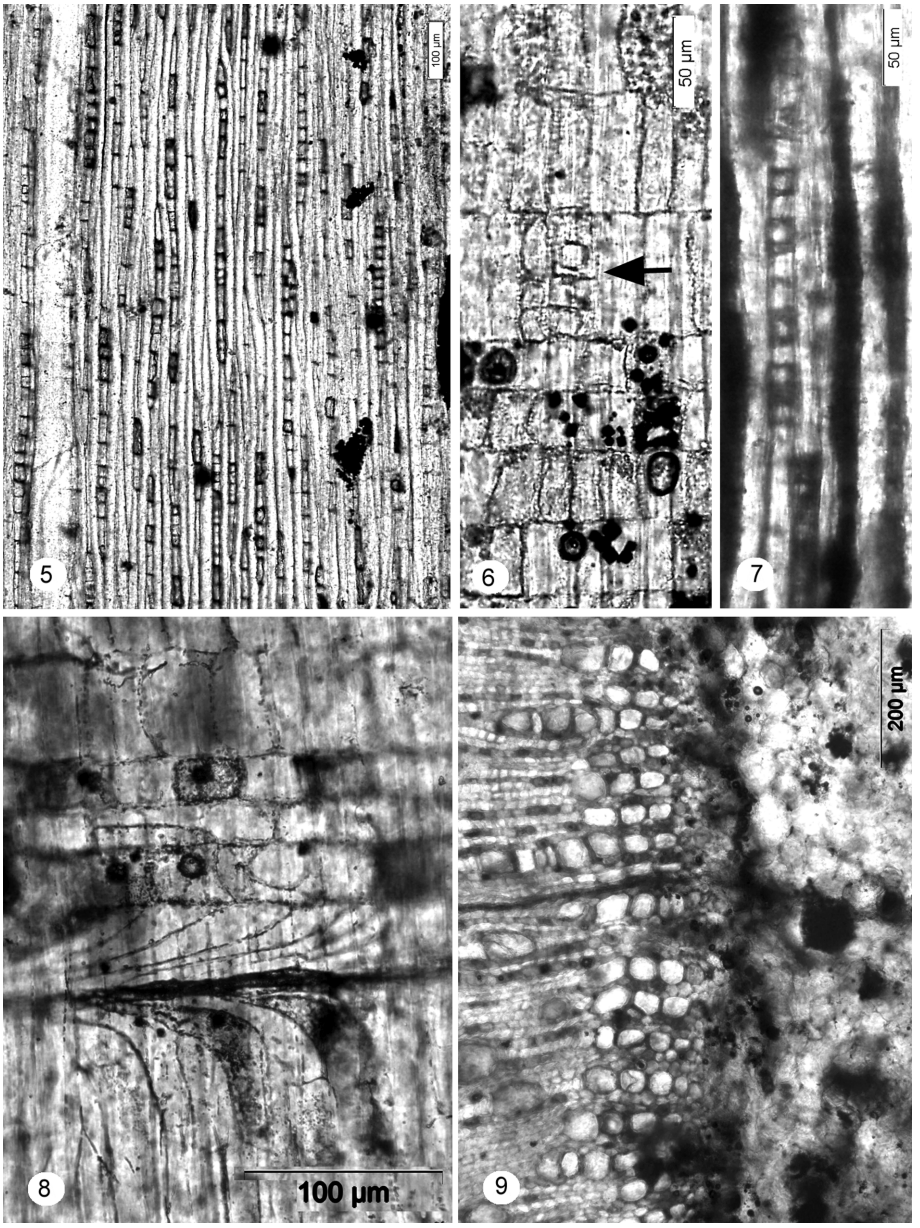

Figure 5–9. *Connaroxylon dimorphum*. – 5: Rays predominantly uniseriate, TLS. – 6: Prismatic crystals in chambered upright ray cells (arrow), RLS. – 7: Prismatic crystals in chambered fibers. – 8: Radial tubule situated in between modified ray cells arranged in a herringbone pattern, RLS. – 9: Pith, primary xylem and juvenile secondary xylem, suggesting absence of internal phloem, TS. — Scale bars: 200 µm in 9; 100 µm in 5 & 8; 50 µm in 6 & 7.

medium-sized to large intervessel pits are of less diagnostic significance because they occur in the majority of woody dicots (Wheeler *et al*. 2007). The occasional presence of tubule-like structures (laticifers or tanniniferous tubules in the center of the herringbone ray cell patterns) and presence or absence of intraxylary or internal phloem is of much greater diagnostic weight.

Searches of InsideWood (2004-onwards; Wheeler 2011) for the combination of vessel-ray pits with reduced borders, parenchyma-like fiber bands and uniseriate rays (31, 67, 96) yield Connaraceae (3 genera), Melastomataceae (23 genera), and one genus of the Lythraceae, *Lagerstroemia p.p*. This combination of taxa also is retrieved when adding intervessel pits alternate and 7–10 μm in diameter (26) and septate fibers present (65). Searches for complete codes of the fossil wood (including, for instance, presence of both septate and nonseptate fibers (65 and 66), crystals also occurring in chambered upright ray cells (140), all ray cells square to upright (105) in InsideWood) do not result in any matches, but if one or two mismatches are then allowed for the InsideWood search, the same Connaraceae, Lythraceae and Melastomataceae are retrieved repeatedly as best matches. Even when parenchyma-like fiber bands are not coded present, these three families are retrieved.

Detailed comparison with slides from the Naturalis reference collection (Lw and Uw), full descriptions in InsideWood (2004-onwards; cf. Wheeler 2011) and monographs of the wood anatomy of Connaraceae (Heimsch 1942; Dickison 1972; Den Outer & Van Veenendaal 1989), Melastomataceae (Van Vliet 1981; Ter Welle & Koek-Noorman 1981) and Lythraceae (Baas & Zweypfenning 1979) show striking similarities, but also some differences with the fossil. *Lagerstroemia* has species with or without distinct fiber dimorphism, but its overall anatomy, including the presence of chambered crystalliferous fibers and its vessel-ray pitting is quite similar to the fossil. One persistent difference is the ray composition: typically composed of procumbent cells only in mature *Lagerstroemia* wood, and typically composed of square to upright cells in the Deccan fossil. High proportions of upright and square ray cells were only found in thin herbarium twigs of *L. loudonii* by Baas and Zweypfenning (1979), although some other genera of Lythraceae have rays mainly composed of upright and square cells.

Ray width and composition in the Melastomataceae closely matches that of the fossil, but most Melastomataceae lack chambered crystals and typically show intervessel and vessel-ray pits that are larger and coarser than those of the fossil. The few Melastomataceae that have chambered crystals (*Graffenrieda* and *Huilaea* from the New World – cf. Ter Welle & Koek-Noorman 1981) differ from our fossil in having vasicentric and/or diffuse or reticulate parenchyma.

Despite the fairly great similarities of the fossil wood with some species of Lythraceae and Melastomataceae there are two circumstantial reasons against attribution of the fossil to the order Myrtales to which these two families belong: 1) all Myrtales have internal phloem, usually conspicuous, derived from the bicollateral vascular bundles of their primary plant body (Van Vliet & Baas 1984) – in the fossil the presence of internal phloem is not clearly evident, although its existence cannot be completely excluded; 2) the more or less pentagonal shape of the pith suggests a spiral leaf arrangement

with the corners of the pith linked to the alternating leaf gaps in the stem. Myrtales typically have opposite leaves with an oval or quadrangular pith with the leaf gaps in opposite positions.

From the Connaraceae, the genera *Connarus, Hermandradenia*, and *Jollydora* are retrieved in several InsideWood searches. *Connarus* is wood anatomically a very diverse genus, with its climbing species showing vessel dimorphism and vascular/vasicentric tracheids (Heimsch 1942; Dickison 1972; Den Outer & Van Veenendaal 1989), while its erect species are variable for distinctness of fiber dimorphism and ray cell composition.

If the presence of radial tubules is considered and feature 132 (tubules present) is included in an InsideWood search in combination with diffuse porosity, simple perforation plates, simple vessel-ray pits and uniseriate rays (5, 13, 31 and 96), searches only yield Euphorbiaceae (13 genera) and Myristicaceae (*Otoba* sp.). These taxa differ very strongly in parenchyma distribution and ray composition and cannot be serious candidates for close affinity. However, the genus *Connarus* also has tube-like structures in the rays (Heimsch 1942; Dickison 1972; Den Outer & Van Veenendaal 1989) – a feature overlooked in the InsideWood coding 2004–2015. In the Naturalis reference slide collections we noticed tubules associated with ray cell patterns reminiscent of the herringbone pattern in the fossil (mainly in slides of *C. pachyneurus* and *C. perrottetii* from the Utrecht collection: Uw). The connaraceous genera *Hermandradenia* and *Jollydora* lack radial tubes or tubules (Dickison 1972; Den Outer & Van Veenendaal 1989). Radial tubules (either containing latex or tannin-like substances) are of very rare occurrence, and therefore highly diagnostic in angiosperm woods. Their unambiguous presence in the fossil (Fig. 8), in combination with all other features tilts the evidence strongly in favor of a close affinity of the fossil with modern *Connarus*.

A comparison with fossil woods from the Indian subcontinent yielded no matches at all (see also the forthcoming review in Wheeler *et al*. 2017).

Connaroxylon in context

Connaraceae (Oxalidales) are a pantropical family of trees, shrubs and lianas including 12 genera and 180 species (Mabberley 2008). The family is best represented in Africa, much less so in Asia and the Neotropics (Mondal & Guha 2000). The modern genus *Connarus* numbers 77 species (Mabberley 2008). In the present-day flora of India, the family is represented by 4 genera: *Cnestis, Connarus, Ellipanthus,* and *Rourea*, of which *Connarus* is the most species-rich with 9 or 10 species (Mondal & Guha 2000).

The fossil record of the Connaraceae is very poor. In her review Collinson *et al*. (1993) mentioned an early record of an inflorescence of *Connaracanthium roureoides* Conwentz 1886 from the Lower Tertiary of West Prussia, Germany. Van Steenis (1962) discussed this fossil and mentioned that the monographer of Indo-Malesian Connaraceae, P.W. Leenhouts, considered the flowers to be misidentified and to belong to Caesalpinioideae instead. Fruits such as those of modern *Cnestis* have been recorded from the Lower Miocene of Kenya (Chesters 1957). Very recently Khan and Bera

(2016) attributed a well-preserved leaflet impression from the middle-upper Miocene of NE India to the connaraceous genus *Rourea*. The family is not represented in the fossil pollen record. Bande *et al*. (1987) attributed one fossil wood from the lower Miocene of Zaire (Central Africa) to the Connaraceae: *Byrsocarpus tertiara* Bande, Dechamps, Lakhanpal & Prakash. Its anatomy shows two significant differences with *Connaroxylon* (cf. InsideWood 2004-onwards) in lacking parenchyma-like fiber bands and having vasicentric parenchyma.

Friis *et al*. (2011) did not mention Connaraceae in their review of the angiosperm fossil record and discussed only two families from the order Oxalidales: Elaeocarpaceae with earliest occurrences in Australia during the Eocene, and Cunoniaceae with earliest records in Maastrichtian palynofloras of Australia and New Zealand. Various molecular clock analyses summarized by Stevens (2016), date the whole order of the Oxalidales (including Huaceae) between 93–89 (105–78) Ma, and the age of the node giving rise to the core families of the order, including the sister families Connaraceae and Oxalidaceae between 77–59 (80–40) Ma. These age estimates are not in conflict with the Deccan age of *Connaroxylon* as early representative of the Connaraceae.

If our attribution of *Connaroxylon dimorphum* to the Connaraceae is correct, this would be the oldest fossil record of the family, provisionally suggesting an origin in the Indian subcontinent, or its East-Gondwanic precursor. It is becoming apparent that the Deccan flora contains many first records of clades that have become widespread in modern floras, *e.g*. *Indovitis* (Manchester *et al*. 2013), *Oleoxylon* (Srivastava *et al*. 2015), and several Deccan taxa revisited by Wheeler *et al*. (2017). This is perhaps not surprising for a drifting continent halfway between arctic Gondwana and Laurasia (cf. Srivastava 2011; Smith *et al*. 2015). This strengthens "out-of-India" scenarios for the diversification of certain angiosperm clades in Laurasia and the adjoining Malesian region as advocated by Manchester *et al*. (2013) for Vitaceae.

Presence of *Connaroxylon* along with a number of pantropical and tropical families and taxa, *viz*. Achariaceae (formerly Flacourtiaceae), Anacardiaceae, Annonaceae, Euphorbiaceae, Lecythidaceae, Malvaceae, Moraceae, Oleaceae, Phyllanthaceae, Simaroubaceae, Vitaceae etc. fits with its remarkably "modern" appearance, and suite of functional traits typical for modern tropical lowland floras (cf. Wheeler *et al*. 2017). The very low incidence of scalariform perforations in the Deccan flora suggests a xeric forest type, but the absence of distinct growth rings suggests continuous growth, which in modern floras is more typical of mesic tropical conditions.

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