Surprisingly modern Latest Cretaceous–earliest Paleocene woods of India

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ABSTRACT

Background and approach – The Deccan Intertrappean Beds of Central India contain a diverse assemblage of fossil plants, including petrified woods from 15 localities. These beds are dated at c. 67–64 Ma, *i.e.* latest Cretaceous–earliest Paleocene and span the K-Pg boundary, a significant time in angiosperm history. At this time, the Indian tectonic plate was halfway on its journey from Gondwana to its collision with Asia, and relatively close to the equator. We provide descriptions in IAWA Hardwood List codes for 47 species of Deccan fossil woods, based on our examination of thin sections of these woods, mostly holotypes that are housed at the Birbal Sahn Institute of Palaeobotany, Lucknow, India. An appendix lists all validly published Deccan wood species of which we are aware, including 52 that we were not able to examine.

Main results – The Deccan fossil woods described herein include the oldest known occurrences of some orders, families or genera *viz.* Lamiales (Lamiaceae), Achariaceae (*Hydnocarpus*-like wood), Anacardiaceae, Simaroubaceae (*Ailanthus*-like and *Simarouba*-like woods), subfamily Leeoideae (Vitaceae), subfamily Myrtoideae (Myrtaceae), subfamily Planchoideae (Lecythidaceae), tribe Castilleae (Moraceae), tribes Grewioideae and Sterculioideae (Malvaceae). These first fossil records are discussed with reference to other macrofossil and pollen records of the same or related clades. They complement recent work on the oldest known *Olea* and Connaraceae also documented by Deccan woods.

For the Deccan woods we examined, we could confirm the earlier taxonomic assignment at least down to order or family level for 29 taxa. Ordinal level affinities are ambiguous for eight of the taxa. In two cases, we revised the taxonomic assignment to other families; for another eight, the original assignment was found to be incorrect, but we are unable to suggest alternative affinities.

Evolutionary implications – Only 3% of all Deccan woods have scalariform perforations and the incidences of so-called specialized features in the Baileyian sense are high, so these woods have a remarkably “modern” aspect. This is

anomalous in comparison with contemporaneous fossil woods from higher paleolatitudes, and seemingly they are more “derived” than the recent flora. In these respects, the Deccan woods constitute a unique assemblage. The low incidence of scalariform perforations suggests xeric conditions, while – in contrast – the low incidence of distinct growth ring boundaries suggests an aseasonal everwet climate. It is speculated that convergent xylem specialization, especially the selection for simple perforations, was enhanced by the climatic conditions found at low paleolatitudes with high temperatures as would characterize the Deccan Intertrappean Beds at the K-Pg boundary.

Keywords: Deccan Intertrappean Beds, functional traits, Maastrichtian, Danian, fossil woods.

INTRODUCTION

Since the 1920s numerous petrified woods have been reported from the Deccan Intertrappean Beds of India (lists in Chitale 1962; Lakhanpal *et al.* 1976; Srivastava 1991, 2011; Srivastava & Guleria 2006). Most were described and named during the 1950s to 1980s. At that time, it was thought that the Deccan Traps were younger (Eocene) and so, not surprisingly, the woods were identified by their general similarity with present-day Indian woods. Almost all Deccan woods were assigned either extant generic names or fossil wood generic names formed by adding *-oxylon* to an extant genus with similar wood anatomy.

Current understanding is that the Deccan Intertrappean Beds are older, c. 67–64 Ma, *i.e.*, late Maastrichtian–early Danian; chronos 30N–29N (Hooper *et al.* 2010; Keller *et al.* 2011; Smith *et al.* 2015). This represents an interesting time in the history of the angiosperms (~halfway between their initial radiation and the present day) and in the tectonic history of India (at that time the Indian plate was at a low paleolatitude on its journey from Gondwana to its collision with Asia). Hence, the Deccan wood assemblages take on additional significance. Some angiosperm taxa might have an Indian origin because their earliest records are known from these Maastrichtian–Danian sediments (*e.g.* Vitaceae, Manchester *et al.* 2013; Oleaceae, tribe Oleinae, Srivastava *et al.* 2015; Connaraceae, Baas *et al.* 2017). Woods can complement information from Deccan fossil fruits and seeds and provide data for reconstructing the biogeographic history of angiosperm families.

We recently examined thin sections of 47 Deccan woods, mostly holotypes, stored at the Birbal Sahni Institute of Palaeobotany, Lucknow, India. This work is part of a collaborative project with these objectives: 1) more broadly compare the woods’ combination of features to those of present-day woods globally in addition to those now native to India to better understand their relationships; 2) for woods that can be assigned to family or order, put them in context by referring to other early occurrences of the family or order, mainly using information from Friis *et al.* (2011) and referencing some age estimates, as summarized on the Angiosperm Phylogeny Website, v. 13 (Stevens 2001–onwards); 3) compare the incidences of selected functional traits of the Deccan woods to Maastrichtian woods from California, which is the most diverse late Cretaceous wood assemblage (Page 1981), to other late Cretaceous woods (almost all

from higher paleolatitudes than the Deccan woods), to Paleocene woods, and to modern woods from India and from the Old World tropics. The results of these comparisons will be discussed in the light of current hypotheses on adaptive xylem evolution in woody dicots; 4) prepare digital photographs of these woods and make them accessible on InsideWood (Wheeler 2011) for others to evaluate; and 5) augment the original published descriptions with information gathered during our study, so as to provide a consistent set of coded descriptions for these woods following the IAWA Hardwood List features (IAWA Committee 1989), and to make these descriptions accessible via the InsideWood website. For example, we have included new observations on vessel-ray parenchyma pits – a feature which was not included in many of the originally published descriptions, but which is often important in systematic assessments.

It is our intention in this paper to provide a general assessment of whether the samples we examined have features unique to the present-day taxa with which they originally were considered related. The comparative work that earlier studies represent is considerable; using more recently compiled wood anatomical information we could confirm many original conclusions about the fossils' affinities. As in the case of paleobotanical studies elsewhere in the world, we consider it is important to discuss the relative reliability of each taxonomic assignment, because of the important systematic, stratigraphic, and biogeographic implications that follow. Given that we were not able to access holotypes of all previously published Deccan woods, it is obvious that further work is needed, including recovery of the samples that were not available for our study, preparation of additional thin section slides to clarify some features, and the collection and analysis of new material. Data on the characteristics of the Deccan woods and their relationships to present-day taxa are important for climatic and biogeographic inferences and improving our understanding of the taxonomic composition of this important flora. Moreover, they can serve as calibration points for estimating ages in phylogenetic analyses.

GEOLOGIC SETTING

During the Cretaceous and Paleogene, the Indian subcontinent was geographically isolated as it migrated north from the east coast of Africa to later collide with Asia. As India passed over the Reunion Hotspot, the Deccan Traps were formed (Chatterjee *et al.* 2013; Smith *et al.* 2015). Figure 1 shows the position of India relative to other continents at this time. The Deccan volcanic province encompasses a series of continental flood basalts, or traps. They are estimated to have a volume greater than 1.3 million km³, cropping out over large areas of western and central peninsular India (Jay & Widdowson 2008; Schoene *et al.* 2015). Recent studies based on ⁴⁰Ar/Ar³⁹ dating and magnetostratigraphy indicate that volcanism occurred from 67.5 ± 1–63 Ma with the bulk of the eruption at 65 ± 1 Ma, the K-Pg boundary (Chenet *et al.* 2009; Renne *et al.* 2015; Schoene *et al.* 2015; Shrivastava *et al.* 2015). Sedimentary beds were deposited in lacustrine and fluvial environments during quiescent periods in volcanic activity. These sedimentary beds are highly fossiliferous and contain both flora and fauna. Fossil woods occur at multiple localities (Fig. 2); for many localities, there is

Figure 1. Map showing the estimated tectonic position of India 65 million years ago. Rectangular outline indicates the approximate area of Figure 2. Produced using Advanced Plate Tectonic Reconstruction Service, http://www.odsn.de/odsn/services/paleomap/adv_map.html

Figure 2. Map of central India showing areas of the Deccan Traps and the position of fossil wood localities. Abbreviations: AJ, Anjar; BA, Bharatwada; BE, Betul; DG, Dhangaon; GH, Ghughua; JA, Jhargad; KE, Keria; MK, Mohgaon Kalan; MO, Mohgaon; MZ, Mahurzari; NW, Nawargaon; PP, Parapani; PS, Palasunder; SG, Sagar / Phulsagar; SH, Shibli. Modified from Samant and Mohabey (2014).

uncertainty about whether they are Cretaceous or Paleocene. Questions about the ages of various Deccan localities and work that has been done to resolve those questions are summarized by Smith *et al.* (2015). Although controversy remains, in the opinion of author SRM, the Keria, Mohgaon Kalan, and Mahurzari localities are most likely late Maastrichtian, whereas those in the eastern part of the Mandla lobe, *e.g.*, Ghughua, Umaria, and Parapani, are within a sequence of basalt flows that have been dated as Danian (*e.g.*, Shrivastava *et al.* 2015).

APPROACH

Each of the woods reviewed herein is described in concise form by listing the numerical codes for the IAWA Hardwood List features (IAWA Committee 1989) that we observed. In the code listing, a “v” following a feature number indicates a tendency towards a feature, *e.g.*, 7v, a tendency to a radial/diagonal vessel arrangement. Because the preservation of some samples was not good enough to observe certain features we use “?” after a feature number to indicate that we were unable to determine whether or not that feature was present; *e.g.*, a 61? indicates we could not determine if fiber pits were simple and a 62? indicates we could not determine if fiber pits were distinctly bordered.

For each taxon, we then specify the codings that we used to search InsideWood for taxa with combinations of features similar to the Deccan sample, followed by comments on the wood’s affinities. The search codings used are: “a” for absence of a feature, “p” for presence of a feature. We emphasize that, when searching for lists of woods with a similar combination of features, coding for the *absence* of a feature is as useful as coding for the presence of a feature. The results of the searches were validated by comparison with the literature and reference slides. Coded descriptions and photomicrographic images of all woods we examined are accessible on InsideWood (<http://insidewood.lib.ncsu.edu>) and can be retrieved with a keyword search for “Deccan”.

The acronym BSIP indicates that the cited sample is housed in the Birbal Sahni Institute of Palaeobotany, Lucknow, India. CMNH indicates a sample housed in the Cleveland Museum of Natural History, Ohio. Localities are presented as in the original text except where the political boundaries have changed. Hence, many of the sites originally indicated as being in the Mandla District have been revised to Dindori District, because the latter district was segregated from the former in 1999.

The taxa reviewed herein are arranged in alphabetical order by the generic name originally assigned to the wood. If the name was that of a present-day genus and we determined the Deccan wood did not have features unique to that genus, we place the generic name in quotes “...”. The figures provided herein emphasize the features that we consider needed to support our analysis of the woods; many additional images of these fossils are available in InsideWood (2004- onwards).

The original diagnoses of the species we examined were almost always accompanied by detailed comparisons with both modern (usually only Indian species) and fossil woods assigned to the family to which the Deccan wood was thought to belong. For this paper, we are forgoing such detailed comparisons and, instead, provide only a general assessment of the affinities of the Deccan species based on InsideWood searches, review of literature and examination of sections of extant woods.

RESULTS

Aeschynomenoxylon Müller-Stoll & Mädél 1967

Aeschynomenoxylon malwaense Bande 1978 [1981]

Examined: Holotype BSIP 35355; Locality: Agarwara, near Barwaha, Madhya Pradesh. – Fig. 3

Current taxonomic assessment: family unknown, not Fabaceae.

Description in IAWA Feature Numbers: 2 5 13 22 23v 25 31 42 46 52 61 66 68 79 80 82 89 97 104 115.

Figure 3. *Aeschynomenoxylon malwaense*, BSIP 35355. – A, B: Diffuse porous wood, vessel multiples uncommon, winged-aliform parenchyma, thin-walled fibers, TS. – C: Crowded alternate intervessel pits, TLS. – D, E: Vessel-parenchyma pits enlarged and with reduced borders, RLS. – F: Simple perforation plates, RLS. – G: Narrow rays, TLS. – H: Procumbent ray cells, RLS. — Scale bars: 200 μ m in A; 100 μ m in B, G; 50 μ m in C, D, F, H; 20 μ m in E.

***Aeschynomenoxylon tertiarum* (Prakash) Müller-Stoll & Mädel 1967**

Synonym: *Aeschynomene tertiara* Prakash 1962 [1963]

Examined: Holotype BSIP 10301; Locality: Mahurzari, Nagpur District, Maharashtra. – Fig. 4 A–E

Current taxonomic assessment: family unknown, not Fabaceae.

Description in IAWA Feature Numbers: 2 5 12 13 22 23 25v 26 27v 30 31 32v 41 46 52 61 63 66 68 79 80v 82v 86 89 96 109 115 136 142.

Three Deccan wood types have been assigned to *Aeschynomenoxylon*: *A. tertiarum* (Prakash) Müller-Stoll & Mädel (the type species), *A. malwaense* Bande, and *A. nawargaoense* Shete & Kulkarni (1982). Awasthi (1992) did not consider any of them “to match” *Aeschynomene* (Fabaceae).

Aeschynomenoxylon tertiarum – The very thin-walled imperforate elements (Fig. 4A) and exclusively uniseriate rays (Fig. 4E) of BSIP 10301 likely were the basis for Prakash (1962 [1963]) considering it related to the fabaceous genus *Aeschynomene*. Awasthi (1992) noted that its scanty paratracheal-vasicentric and narrow bands of axial parenchyma are not features of *Aeschynomene*. This wood has more in common with the basal stem/upper root wood of *Alstonia spatulata* (Apocynaceae; Ingle & Dadswell 1953; Baas, unpublished data). However, some vessel-ray parenchyma pits with reduced borders were observed (Fig. 4C, D) and this is not a feature of the Fabaceae nor of *Alstonia* and other Apocynaceae.

Prakash (1962 [1963]) noted that although pith was not present in the sample, the sample was from a region very near it. Multiple searches of InsideWood, using different combinations of features, did not return any matches for this sample. This wood type occurs at other localities (Chiraidongri, Bhutera, R. Srivastava, pers. obs.). These additional samples, especially if from more mature wood, might provide more information that would shed light on its affinities.

Aeschynomenoxylon malwaense and *A. nawargaoense* – Shete and Kulkarni (1982) noted that these two species were similar, but had “wide differences” with *A. tertiarum*. Winged aliform–confluent parenchyma occurs in these two species and their predominantly homocellular rays are not exclusively uniseriate. Certainly, these differences warrant the designation of different species; whether they should be in different genera deserves consideration. These axial parenchyma features, homocellular

Figure 4. — A–E: *Aeschynomenoxylon tertiarum*, BSIP 10301. — A: Very thin-walled imperforate elements in radial rows, few and widely spaced vessels, narrow parenchyma bands (AP), TS. — B: Simple perforation plate, crowded alternate intervessel pits, some with coalescent apertures, RLS. — C: Ray cells with circular pits with reduced borders, RLS. — D: Narrow band of axial parenchyma, ray cells square to barely procumbent, RLS. — E: Exclusively uniseriate very low rays, thin-walled imperforate elements, TLS. — F–J: *Ailanthoxylon indicum*, BSIP 5568. — F: Diffuse porous wood, vessels mostly solitary, winged aliform axial parenchyma, TS. — G: Vessel elements with simple perforation plates and crowded alternate intervessel pits, rays >4-seriate, TLS. — H: Multiseriate rays, uniseriate rays rare, TLS. — I: Simple perforation plates, rays composed of procumbent cells, RLS. — J: Vessel-parenchyma pits with reduced borders (arrows), RLS. — Scale bars: 200 µm in A, F, H; 100 µm in D, G, I; 50 µm in E; 20 µm in B, C, J.

rays, and very thin-walled short fusiform fibers occur in *Aeschynomene*. However, *Aeschynomenoxydon malwaense* has large vessel-ray parenchyma pits with reduced borders, again, a major argument against considering a wood to be a legume. We were unable to examine slides of *A. nawargaoense* Shete & Kulkarni (1982), a 2–3 cm axis with pith. Its vessel-ray parenchyma pits were not described or illustrated, so its affinities with the Fabaceae remain questionable.

It has long been known that species growing in swamps can have exceptionally low specific gravity wood (cork woods), *e.g.*, *Nyssa*, *Leitneria* (Trelease 1895), and basal stem wood of some *Alstonia* spp. (Baas, unpublished). Whether this was the preferred habitat for these woods with very thin-walled fibers remains to be determined.

Ailanthoxylon Prakash 1958 [1959]

Ailanthoxylon indicum Prakash 1958 [1959]

Examined: Holotype BSIP 5568; Locality: Mohgaon Kalan, Chhindwara District, Madhya Pradesh; BSIP 36525 described by Prakash, Verma, & Dayal 1967. – Fig. 4 F–J

Current taxonomic assessment: likely Simaroubaceae.

Description in IAWA Feature Numbers: 2 5 13 22 23 26 31 42v 43 46 52 61 66 68 69 79? 80 82 83 86v 91 92 93 98 102 104 114 121v.

Ailanthoxylon indicum shares a combination of features that appears to be unique to *Ailanthus*. Moreover, the relatively low percentage of vessel groups in *Ailanthoxylon indicum* resembles present-day diffuse porous species of *Ailanthus*, *e.g.*, *Ailanthus triphysa*. Yet the affinities of this fossil are problematic because its vessel-ray parenchyma pits do not match those of *Ailanthus*.

Prakash (1958 [1959]) described the vessel-ray parenchyma pits of this wood as “simple, small, rounded.” We also interpreted the vessel-parenchyma pits in BSIP 5568 as having reduced (simple) borders (Fig. 4J), which is not a feature of present-day *Ailanthus* or any other Simaroubaceae (*e.g.*, Pearson & Brown 1932; Lemmens *et al.* 1995). From another locality, Mahurzari, Shallom (1959a [1961]) described a second species, *Ailanthoxylon mahurzarii*, and noted “vessel-ray parenchyma pits are similar to intervessel pits.” She also noted that the *Ailanthoxylon mahurzarii* resembled *A. indicum*, except for the simple vessel-ray pitting in *A. indicum*. We were not able to examine slides of *Ailanthoxylon mahurzarii*, but its combination of features supports its assignment to the Simaroubaceae.

To consider the effect of vessel-ray parenchyma pit features on the systematic placement of this fossil, we conducted searches without using this character. One search used the presence of most of the features listed above (2p 5p 13p 22p 23p 26p 43p 46p 52p 66p 70a 80p 82p 104p 114p), and the absence of storied rays and oil cells (118a 124–126a). Somewhat surprisingly, the only result of that search was *Ailanthus*.

Subsequently, we conducted more general searches, *e.g.*, diffuse porous woods with randomly arranged vessels that are solitary and in short radial multiples, simple perforation plates, alternate intervessel pitting not minute, vessels not narrow and not numerous, non-septate fibers without very thick walls, axial parenchyma winged aliform, homocellular rays 4- to 10-seriate, not numerous, and wood without oil cells, canals, or storied rays [5p 6a 7a 8a 9a 10a 11a 13p 14a 22p 24a 40a 41a 48a 49a 50a 80p 82r (required because the wings are obvious and narrow) 98p 104p 116a 118a 124a 125a 126a 127a 128a 129a 130a 132a].

Three families include some members with this combination of features: Bignoniaceae, Fabaceae (Caesalpinioideae, Mimosoideae, Papilionoideae), and Simaroubaceae.

ceae. All three families are characterized by vessel-ray parenchyma pits similar to intervessel pits. When we added rays > 1 mm as a search criterion, the only match was *Ailanthus*.

Corbett and Manchester (2004) reviewed the Northern Hemisphere fossil record for *Ailanthus*, concentrating on reports of the fruits, but also considered the foliage record. They concluded that the oldest known fossils of *Ailanthus* are early Eocene. Clayton *et al.* (2009) used two different methods to estimate the age and origin of the Simaroubaceae and suggested a North American origin for the family and estimated the age of the crown group as Maastrichtian. *Ailanthus*-type wood is common in Deccan Intertrappean exposures and occurs at multiple localities (e.g. Bhutera, Chiraidongri, Devrikhurd, Dhangaon, Ghughua; R. Srivastava, pers. obs.). The Deccan simaroubaceous woods raise questions about the geographic origin of the family and the possibility that it originated on the Indian subcontinent.

Amooroxylon Bande & Prakash 1979 (iss. 1984)

Amooroxylon deccanensis Bande & Prakash 1979 (iss. 1984)

Current taxonomic assessment: family unknown, not Meliaceae.

Examined: Holotype BSIP 35322; Locality: Nawargaon, Wardha District, Maharashtra.

Description in IAWA Feature Numbers: 2 5 13 22 23 25 26 31 32 43 46 47 52 56v 61 66 69 70 76 79 80 82 83 85 86 91 92 98 104 106 115.

This sample recently was redescribed, including reporting the peculiar feature of circular vessels, and its affinities reassessed (Baas *et al.* 2015). The presence of vessel-ray parenchyma pits with reduced borders precludes assigning *Amooroxylon* to the Meliaceae, but instead favors affinities with Urticales, especially Moraceae.

Anacardioxylon Felix 1894 [Tertiary, Antigua, West Indies]

Anacardioxylon semecarpoides Prakash & Dayal 1964b [1965]

Current taxonomic assessment: Anacardiaceae.

Examined: Holotype BSIP 32807; Locality: Mahurzari, Nagpur District, Maharashtra. – Fig. 5 A–F

Description in IAWA Feature Numbers: 2 5 12v 13 22 23 27 31v 32 42 46 47v 52 53 61 66 68 69 78 79 80 91 92 93 97 104v 106 114 115 136 137 138.

When Prakash and Dayal (1964b [1965]) described this wood they quoted Heimsch (1942) “from the xylem descriptions of the tribes of the Anacardiaceae it is evident that there are no characters or combinations of characters of the xylem which serve to differentiate one group from the other. It is true that there appear to be trends in each of [the] tribes, but these do not hold absolutely.” Prakash and Dayal compared this wood to genera of Anacardiaceae lacking radial canals and, based on the material available to them, concluded it showed “near resemblance” with *Semecarpus*. Consequently, they assigned it to *Anacardioxylon*, a genus for woods with features seen in the family Anacardiaceae, and gave it a specific epithet suggesting that the wood resembled *Semecarpus*.

We searched InsideWood using: 5p (diffuse porous), 13p (simple perforation plates), 22p 23p 27p (alternate intervessel pits, polygonal in outline and large), 32p

(vessel-ray parenchyma pits with reduced borders and horizontally elongate), vessels with tangential diameter 100–200 μm and less than 20/sq. mm (40a 48a 49a 50a), 61p 66p (fibers with simple pits and non-septate), axial parenchyma not diffuse-in-aggregates or winged aliform or banded or marginal (82a 85a 86a 89a), rays 1–3-seriate, with 1 row of square/upright marginal cells (97p 106p), and without sheath cells or tile cells (110a 111a), storied structure absent (118a 119a 120a 121a 122a), oil cells absent

(124a 125a 126a), canals and tubes absent (127a 128a 129a 130a 132a), cambial variants absent (133a 134a 135a), prismatic crystals in square/upright ray cells (136p 137p).

This search returned Anacardiaceae (6 genera – *Anacardium*, *Comocladia*, *Holigarna*, *Pseudospondias*, *Rhus*, *Semecarpus*), and one genus each in the Lauraceae (one species of *Persea* with confluent parenchyma and missing information for many features), Lythraceae (*Duabanga*; differing in having narrower, predominantly uniseriate rays), Moringaceae (*Moringa*; however, rays more numerous, often homocellular, and with a tendency to storied structure), and Urticaceae (*Musanga*; however, fibers very thin-walled, rays wider, fewer, and taller). The features of this wood match those of the Anacardiaceae, but are not unique to *Semecarpus*. Detailed information in Terrazas' (1994) comprehensive study of Anacardiaceae wood anatomy indicates that BSIP 32807's features are consistent with the subfamily Anacardioideae, a subfamily recognized in the cladistic analyses of Terrazas (1994) and Mitchell et al. (2006).

Artocarpoxylon Prakash & Lalitha 1978

Artocarpoxylon deccanense Mehrotra, Prakash, & Bande 1983 [1984]

Current taxonomic assessment: Moraceae.

Examined: Holotype BSIP 35536; Locality: Sylthar, Dindori District, Madhya Pradesh. – Fig. 5G–K

Description in IAWA Feature Numbers: 2 5 13 22 23 26v 27 31 42 46 47 52 53 61 66 68 69 76? 79 80 81 83v 92 93 98 102 106 107 108 110 114v 115 132.

We concur that BSIP 35536 is wood of Moraceae, but its combination of features is not diagnostic of *Artocarpus* or tribe Artocarpeae.

We used different criteria when searching InsideWood. One search used: 5p (diffuse porous wood), 13p (simple perforation plates), 22p 24a (alternate intervessel pits that are not minute), 30a (vessel-ray parenchyma pits not similar to intervessel pits), 40a 48a 49a 50a (mean tangential diameter not less than 50 µm, and vessel frequency not more than 20/sq. mm), 61p 66p (non-septate fibers with simple pits), 70a (fibers not very thick-walled), 77a 79p 85a 86a (axial parenchyma vasicentric, and not diffuse-in-aggregates or banded), 98p 102p 104a 105a (wider rays frequently >4-seriate, not homocellular), 110p 111a (sheath cells present, tile cells absent), 118a 119a 120a (storied structure absent), 124a 125a 126a 127a 128a 129a (oil cells and axial canals absent), 132p (laticifers/tanniferous tubes present), 133a 134a 135a (cambial variant structure

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Figure 5. — A–F: *Anacardioxylon semecarpoides*, BSIP 32807. — A: Diffuse porous wood, vessels solitary and in short multiples, paratracheal parenchyma, TS. — B: Simple perforation plates, RLS. — C: Crowded alternate intervessel pits, TLS. — D: Vessel-ray parenchyma pits with reduced borders, mostly horizontally elongate, RLS. — E: Rays with procumbent body cells, axial parenchyma strands to right of vessel, RLS. — F: Rays 1–2-seriate, mostly 2-seriate, TLS. — G–K: *Artocarpoxylon deccanense*, BSIP 35536. — G: Vessels solitary and in radial multiples, fiber walls thin to medium thick, TS. — H: Vessel elements with simple perforation plates, TLS. — I: Crowded alternate intervessel pits, TLS. — J: Rays with 1–4 marginal rows of square/upright cells, tubes in rays (arrows), TLS. — K: Detail of ray with sheath cells and tube (arrow), TLS. — Scale bars: 500 µm in A; 200 µm in B, C, G, H; 100 µm in E, J; 50 µm in D, F, I, K.

absent). Only species in the Moraceae had this combination of features (*Antiaris*, *Castilla*, *Maquira* in the tribe Castilleae; *Poulsenia* of tribe Moreae), but *Artocarpus* was not recovered.

Another search using fewer features (13p 22p 24a 25a 31p 79p 80p 81p 98p 102p 106p 107p 110p 132p) returned only *Antiaris* and *Maquira*, both in tribe Castilleae.

Atalantioxylon Lakhanpal, Prakash, & Bande 1976 [1978]

Atalantioxylon indicum Lakhanpal, Prakash, & Bande 1976 [1978]

Current taxonomic assessment: Sapindales.

Examined: Holotype BSIP 63/1505; Locality: Mohgaon, Dindori District, Madhya Pradesh. – Fig. 6A–D

Description in IAWA Feature Numbers: 1v 2 5 13 22 24v 25 30 41 48 52 53v 56v 61 66 75 78 97 104 115.

Lakhanpal *et al.* (1976 [1978]) reported diffuse and marginal parenchyma for this sample, but we did not observe those features. We searched for: diffuse porous (5p), vessels solitary and in short radial multiples randomly arranged (6a 7a 8a 9a 10a 11a), simple perforation plates (13p), minute to small alternate intervessel pits (22p 26a 27e), vessel-ray parenchyma pits similar to intervessel pits (30p 32a 33a), vessels not wide and not < 5 per sq.mm or > 100 per sq.mm (43a 46a 50e), vessel elements < 800 μ m (54a), non-septate fibers with simple pits (61p 66p), axial parenchyma not common (77a 78p 80a 83a 85a 86a), rays mostly 3-seriate and homocellular (96a 97p 104p), storied structure absent (118a 120a). This combination of features occurs in the families Meliaceae, Rutaceae (including *Atalantia*) and Sapindaceae, all in the order Sapindales. There also are one to two records in the families Asteraceae, Bignoniaceae, Combretaceae, Fabaceae and Oleaceae, all of which are less likely to have any relationships to this fossil because of some differences in axial or ray parenchyma features. When we added the features that Lakhanpal *et al.* (1976 [1978]) observed but we did not [diffuse axial parenchyma (76p) and marginal parenchyma (89p)], this search returned Rutaceae (6 genera, including *Atalantia*) and Sapindaceae (3 genera).

As did Lakhanpal *et al.* (1976 [1978]), we observed tyloses in some vessels, which is unusual for woods with vessel-ray parenchyma pits similar to small intervessel pits (Chattaway 1949; Bonsen & Kučera 1990; Saitoh *et al.* 1993; De Micco *et al.* 2016). Gums are the usual vessel occlusion in the Rutaceae; tyloses common occurs in 3 records (one of which is *Atalantia*), while gums present occurs in 52 records of the 135 Rutaceae records in InsideWood. Fiber walls of *Atalantia* are very thick-walled unlike this Deccan sample. The original work on this Deccan wood was restricted to comparisons with Indian species. We think it probable this wood is Sapindales, but wood anatomy of several genera of these three sapindalean families overlaps, making it nearly impossible to assign this wood to a single family or genus confidently. Among these families, Rutaceae may be the most likely candidate, because “tyloses common” has not been reported for either Meliaceae or Sapindaceae.

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Figure 6. — A–D: ***Atalantioxylon indicum***, BSIP 63/1505. — A: Diffuse porous wood, vessels solitary and in radial multiples of 2–3(–4), axial parenchyma rare, TS. — B: Alternate intervessel pits, vessel-axial parenchyma pits, RLS. — C: Simple perforation plate, rays composed of procumbent cells, RLS. — D: Rays mostly 3-seriate, TLS. — E–J: ***Barringtonioxylon mandlaense***, BSIP 35315. — E, F: Diffuse porous wood, vessels solitary and in radial multiples, vasicentric parenchyma, TS. — G: Crowded alternate intervessel pits, simple perforation plates, TLS. — H: Vessel-axial parenchyma pits, some similar in size to intervessel pits, some horizontally enlarged with reduced borders (arrow), simple perforation plate, RLS. — I: Heterocellular multiseriate rays, TLS. — J: Heterocellular rays more than 4-seriate with sheath cells (arrows), TLS. — Scale bars: 200 μ m in A, E, I; 100 μ m in D, F, J; 50 μ m in B, C, G, H.

There is another report of rutaceous wood from the Deccan Intertrappean Beds. Chitale and Khubalkar (1974) described *Rutaceoxylon mahurzari* from Mahurzari, but we were unable to locate the sections of this species. The description of this wood lacks information on vessel-ray parenchyma pits and ray cellular composition, so it is not possible to determine whether this wood belongs to the Rutaceae or to the Sapindales, or to yet another order.

***Barringtonioxylon* Shallom 1960a**

***Barringtonioxylon deccanense* Shallom 1960a**

Current taxonomic assessment: probably Lecythidaceae.

Examined: Holotype CMNH Microslides 1572 (transverse), 1589 (tangential), no radial section available; Locality: Mahurzari, Nagpur District, Maharashtra. – Fig. 7A–F Description in IAWA Feature Numbers: 2 5 13 22 23 27 31 41 47 52 53 56 61 66 69 71? 72? 73? 76 77 86v 92 98 103v 106 107 108 110v 115.

We did not have access to the radial section of this sample, but Shallom's (1960a) paper illustrated vessel-ray parenchyma pits rounded to oval in outline and apparently with reduced borders and rays composed of square and barely procumbent cells.

We searched InsideWood for diffuse porous wood with randomly arranged vessels that are solitary and in short radial multiples (5p 6a 7a 8a 9a 10a 11a), simple perforation plates (13p), alternate intervessel pits that are polygonal in outline and large (22p 23p 27p), tyloses commonly present (56p), non-septate fibers with simple pits (61p 66p), axial parenchyma diffuse-in-aggregates and not aliform or confluent or in broad bands (77p 80a 83a 85a), widest rays >4-seriate and not homocellular (98p 104a 105a), storied structure, oil cells, canals, and cambial variants all absent (118–120a, 124–135a). This search returned Cornaceae (*Alangium*), Cunoniaceae (*Geissois*), Euphorbiaceae (*Discoglyprena*), Lecythidaceae (*Asteranthos*, *Barringtonia*, *Careya*, *Cariniana*, *Grias*), Phyllanthaceae (*Aporosa*, *Uapaca*). The Cunoniaceae usually have some scalariform perforation plates in addition to simple ones and fiber pits are more obvious, so we believe this family can be excluded. Ray features suggest that this wood is similar to *Barringtonia*, especially to *B. acutangula* and *B. racemosa*, which have axial parenchyma diffuse-in-aggregates and in uniseriate lines. *Discoglyprena* (Euphorbiaceae)

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Figure 7. — A–F: *Barringtonioxylon deccanense*. — A, B: CMNH Microslide 1572. Diffuse porous wood, vessels solitary and in radial multiples, diffuse-in-aggregates axial parenchyma, TS. — C–F: CMNH Microslide 1589, TLS. — C: Crowded alternate intervessel pits, pits angular in outline, some with coalescent apertures, axial parenchyma strand adjacent to vessel, possible vessel-axial parenchyma pits. — D: Rays tending to two sizes: tall uniseriate rays composed of upright cells, heterocellular multiseriate rays. — E: Multiseriate rays with a variable number of marginal ray cells, simple perforation plates, alternate pits. — F: Multiseriate rays, some with tendency to sheath cells, tyloses common. — G–L: *Barringtonioxylon eopterocarpum*, BSIP 32778. — G, H: Diffuse porous wood, vessels solitary and commonly in radial multiples, apotracheal parenchyma abundant, TS. — I: Vessel-ray parenchyma pits appear to have weakly reduced borders, RLS. — J: Crowded alternate intervessel pits, TLS. — K: Rays with sheath cells, vessel elements with simple perforation plates and crowded alternate intervessel pitting, TLS. — L: Ray with sheath cells, abundant tyloses in vessel, TLS. — Scale bars: 200 µm in A, D, G; 100 µm in B, E, F, H, K, L; 50 µm in C, I, J.

differs in having cells in the body of the ray that are circular in outline in tangential section and a much lower vessel density. *Phyllanthaceae* consistently have markedly taller rays. *Alangium* rays consist of well-defined procumbent cells and square and upright cells. The ray cellular structure that Shallom (1960a) described and illustrated (rays with barely procumbent cells and square cells of similar height) is similar to *B. acutangula* and *B. racemosa*. Her conclusion of likely affinities to *Barringtonia* remains

plausible. This species was subsequently reported from another Deccan locality in Yavatmal District, Maharashtra (Srivastava *et al.* 2009), this sample was noteworthy for being infected with fungal conidia and mycelia. *Barringtonioxylon deccanense* also occurs in the Lameta Formation, which is accepted as being Maastrichtian in age (Kar *et al.* 2004). Additional work and collections may indicate that this wood type is an indicator of latest Cretaceous age and that Mahurzari is indeed latest Cretaceous or that this wood survived throughout K-Pg boundary event and Mahurzari is early Paleocene.

***Barringtonioxylon eopterocarpum* Prakash & Dayal 1964a [1965]**

Current taxonomic assessment: Lecythidaceae.

Examined: Holotype BSIP 32778; Locality: Mahurzari, Nagpur District, Maharashtra. – Fig. 7G–L

Description in IAWA Feature Numbers: 2 5 10v 13 22 27 30? 31 32v 42 43 46 47 53 56 61? 62? 65? 66? 76 77 78 92 93 98 102 103v 106v 107 108 110 115.

Although *Barringtonioxylon deccanense* from Nagpur and *B. eopterocarpum* from Mahurzari are from the same area, as noted below, they are different enough to consider them separate species. One of our searches of InsideWood only returned *Barringtonia acutangula*. The features we used in that search were diffuse porous wood with vessels that are solitary and in radial multiples and randomly arranged (5p 6a 7a 8a 9a 11a), simple perforation plates (13p), large alternate intervessel pits (22p 27p), vessels with a mean tangential diameter of >100 µm and <40/sq. mm (40a 41a 49a), tyloses commonly present (56p), non-septate fibers with simple pits (61p 66p), axial parenchyma diffuse-in-aggregates and not vasicentric, aliform, confluent or in broad bands (77p 70a 80a 83a 85a), widest rays >4-seriate and not homocellular (98p 104a 105a), sheath cells present (110p), tile cells and storied structure absent (111a 118a 120a).

Of the extant species that Prakash and Dayal (1964a [1965]) examined, they thought this sample most similar to *Barringtonia pterocarpum*, hence its specific epithet. We observed that *Barringtonia racemosa* is also similar, but has more regular uniseriate lines of axial parenchyma. Prakash and Dayal assigned this sample to *Barringtonioxylon* because they considered it similar to the genus *Barringtonia*, although they noted differences between it and the type species, *Barringtonioxylon deccanense* (reviewed above). Compared to *B. deccanense*, *B. eopterocarpum* consistently has more vessels per radial multiple, fewer uniseriate rays, wider (to 8-seriate) and higher (to 4 mm) rays. Future work and additional samples might show that there is a continuum between these features, and that *B. deccanense* and *B. eopterocarpum* are conspecific.

***Barringtonioxylon mandlaense* Bande & Khatri 1980**

Current taxonomic assessment: Lecythidaceae/subfamily Planchoidae.

Examined: Holotype BSIP 35315; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 6E–J

Description in IAWA Feature Numbers: 2 5 13 22 23 27 31 42 47 52 56 61 66 70 76 79 80v 81v 93 98 102 103v 107 108 110 115.

Bande and Khatri (1980) noted that the holotype (BSIP 35315) was taken from a large log, although they did not provide measurements, and that its “medium sized vessels

with simple perforations, paratracheal vasicentric and diffuse to diffuse-in-aggregates parenchyma, fine to broad rays of two distinct types and moderately thick-walled, non-septate fibers clearly indicates the affinities of this wood to the living genus *Barringtonia*.” By two distinct types, they seem to have meant uniseriate rays composed of upright cells only and multiseriate rays with procumbent body cells and marginal rows of square and upright cells. However, a search of InsideWood for those features plus the presence of diffuse porous wood and absence of broad parenchyma bands (5p 13p 42p 66p 69p 76p 77p 79p 85a 98p 104a) indicates those features, while present in *Barringtonia*, are not unique to it and also occur in *Petersianthus* (Lecythidaceae) and nine other families.

Consequently, we used more features and searched for diffuse porous woods with randomly arranged vessels that are solitary and in short radial multiples (5p 6a 7a 8a 9a 10a), simple perforation plates, large alternate intervessel pitting and vessel ray parenchyma pits with reduced borders (13p 22p 27p 31p), vessels with mean tangential diameters of 100–200 μm and between 5–20 vessels/sq. mm (42p 47p), non-septate fibers that are not very thin-walled (61p 66p 68a), axial parenchyma diffuse (we did not observe diffuse-in-aggregates parenchyma, so did not use that feature) and vasicentric, absence of broad bands of parenchyma, with 5–8 cells/strand (76p 79p 85a 93p), wider rays more than 4-seriate and commonly > 1 mm high, some rays with 2–4 marginal rows of upright cells and occasional sheath cells (98p 102p 107p 110p), storied structure, canals, oil cells, and cambial variant structure all absent (118a 119a 120a 124a 125a 126a 127a 128a 129a 132a 133a 134a 135a). This particular combination of characters returned Cannabaceae (*Gironniera*), Lecythidaceae (*Petersianthus*), and Phyllanthaceae (*Uapaca*). The vessel-ray parenchyma pits in this wood are the same size as the intervessel pits and because in the literature such pits have been described as similar to intervessel pits (feature 30), we repeated the above search, substituting 30p for 31p. This search returned Cannabaceae (*Gironniera*) and Lecythidaceae (*Petersianthus*). In InsideWood these two genera are coded as having both types of vessel-ray parenchyma pitting.

Based on the material available to us, we consider it probable that this wood belongs to the Lecythidaceae, rather than the Cannabaceae, based on vessel-ray parenchyma pit appearance and axial parenchyma distribution. It lacks the banded parenchyma that occurs in most members of the Lecythidaceae and so resembles some species of *Barringtonia* and *Petersianthus*. Both are in the subfamily Planchonideae, in the *Petersianthus-Chydenanthus-Barringtonia* clade of Old World genera (Mori et al. 2007). It has been suggested that these three genera should be recognized as the Barringtoniaceae (e.g., Mori et al. 2007); we note that the axial parenchyma distribution is another character that may support that suggestion.

Bischofinium Bande 1974

Bischofinium deccanii Bande 1974

Current taxonomic assessment: Phyllanthaceae, similar to *Bridelia*.

Examined: Holotype BSIP 35152; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 8A–F

Description in IAWA Feature Numbers: 2 5 13 22 23 25v 26 31 32 36v 37v 42 47 48v 52 56 61 66 69 78 79 92 93 98 102 106 107 108v 110 115.

Awasthi (1988 [1989], p.150) did not think that this wood had affinities with *Bischofia* because *B. javanica* has absent to rare axial parenchyma, while this wood has vasicentric parenchyma. He did not suggest alternative affinities. A search for diffuse porous wood (5p), simple perforation plates (13p), small alternate intervessel pitting

(22p 26p), vessel-ray parenchyma pitting not similar to intervessel pitting (30a), mean tangential diameter of vessels 100–200 μm and 5–20 per sq. mm (42p 47p), tyloses abundant (56p), thick-walled non-septate fibers with simple pits (61p 66p 69p), vasicentric parenchyma (79p), heterocellular rays >4-seriate, >1 mm tall, with some sheath cells and 4–12 per linear mm (98p 102p 104a 105a 110p 115) and no canals (127–130a) or oil cells (124–126a) returned *Bridelia* (Phyllanthaceae) as a match for this combination of features. Two other searches, one using rays not exclusively uniseriate or >10-seriate (96a 99a) rather than 98p and the other using scanty paratracheal (78p) rather than vasicentric, also returned *Bridelia*. We did not observe septate fibers in this sample; present-day *Bridelia* have septate fibers, either as the only fiber type or in combination with non-septate fibers. This wood has features found in the Phyllanthaceae, but given we did not observe septate fibers and the considerable overlap in features of extant genera in this family, it seems prudent not to consider it equivalent to a single extant genus.

We have examined peels of the permineralized trilocular fruit capsule bearing two seeds per locule described by Mistri *et al.* (1992). It provides confirmation that Phyllanthaceae occur in the Deccan flora, but we do not know if this fruit from Singpur represents the same taxon as this wood from Parapani. Being capsular, rather than fleshy, the fruit of Mistri *et al.* (1992) does not correspond to the genus *Bischofia*.

***Bridelioxylon* Ramanujam 1956**

***Bridelioxylon krauselii* (Prakash) Mädel 1962**

Synonym: *Euphorbioxylon krauselii* Prakash 1957 [1959]

Current taxonomic assessment: Malpighiales / Salicaceae–Euphorbiaceae clade.

Examined: Holotype BSIP 5587 of Prakash 1950; Locality: Keria, near Mohgaon Kalan, Chhindwara District, Madhya Pradesh. – Fig. 8G–L

Description in IAWA Feature Numbers: 1 5 10 13 22 23 26 31 42 45v 47 52? 53? 54? 61? 65 66? 69 70 75 78 92 97 98v 106 107 108v 109v 115 136 137 138.

The combination of features of this wood occurs in the Achariaceae and Phyllanthaceae, both in the Malpighiales. Additional comparative work seems warranted to determine whether its affinities are only with the Phyllanthaceae. Some Phyllanthaceae

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Figure 8. — A–F: *Bischofinium deccanii*, BSIP 35152. — A, B: Diffuse porous wood, vessels solitary and in occasional multiples of 2, thick-walled fibers, TS. — C: Simple perforation plates in side view, crowded alternate intervessel pits, TLS. — D: Vessel-ray parenchyma pits with reduced borders, variable in shape (arrows), simple perforation plates, RLS. — E: Rays >4-seriate, sheath cells present, TLS. — F: Heterocellular ray, RLS. — G–L: *Bridelioxylon krauselii*, BSIP 5587. — G: Indistinct growth ring marked by change in frequency of long radial multiples, diffuse porous, vessels solitary and in radial multiples, TS. — H: Vessels in radial multiples, some with >4 per multiple, and a tendency to two diameter classes, TS. — I: Crowded alternate intervessel pits, angular in outline (IVP, arrow), RLS. — J: Simple perforation plate, vessel-ray parenchyma pits appearing to have reduced borders, RLS. — K: Heterocellular rays, mostly 2–3-seriate, simple perforation plates in side view, and alternate intervessel pits (IVP), TLS. — L: Rays mostly 2–3-seriate, ray cells with walls of different thicknesses, septate fibers, TLS. — Scale bars: 200 μm in A, G; 100 μm in B, E, F, H, K; 50 μm in C, D, I, J, L.

have been reported to have a tendency to IAWA feature 45 (vessels of two distinct diameter classes, wood not ring porous) as seen in BSIP 5587. The silicified trilocular capsular fruit of phyllanthaceous affinity mentioned above is from another locality (Singpur) of the Deccan Intertrappean Beds (Mistri *et al.* 1992).

A search for 5p 10p (diffuse porous wood with radial multiples of 4 or more common), 13p 22p 24a 30a (simple perforation plates, alternate pitting that is not minute, vessel-ray parenchyma pits not similar to intervessel pits), 42p 47p (vessel mean tangential diameter of 100–200 μm and 5–20 vessels per sq. mm), 65p (septate fibers), 75p (axial parenchyma rare), 97p 104a 105a (rays 1–3 cells wide and not homocellular) returned only Achariaceae (*Eleutherandra*, *Ryparosa*) of the Malpighiales and Elaeocarpaceae of the Oxalidales. Another search using 5p 10p 13p 22p 24a 30a 42p 47p 65p 78p (scanty paratracheal) 97p 107p returned Phyllanthaceae (*Bridelia*), also Malpighiales.

There are differences in ray structure between this Deccan wood and the Elaeocarpaceae, Achariaceae, and Phyllanthaceae. Rays in Elaeocarpaceae often are of two distinct sizes and uniseriate rays are common. Rays of Achariaceae almost always are over 1 mm high. High rays also occur in many Phyllanthaceae.

Burseroxylon Prakash & Tripathi 1973 [1975]

Burseroxylon preserratum Bande & Prakash 1982 [1983]

Current taxonomic assessment: Sapindales.

Examined: BSIP 35374 (not holotype); Locality: Ghughua, Dindori District, Madhya Pradesh. – Fig. 9A–E

Description in IAWA Feature Numbers: 2 5 13 22 23 25 26 31 42 47 48 52 53 56 61 65 68v 69 78 79v 92 97 104? 106? 115 136? 138?.

The features of this sample are not unique to the Burseraceae, but also occur in the Anacardiaceae and Kirkiaceae. These three families are in the Sapindales. Determining whether an isolated piece of wood belongs to the closely related Anacardiaceae or Burseraceae has long been a problem. The timing of divergence of the Anacardiaceae and Burseraceae has different estimates based on molecular analyses, ranging from c. 60 Ma to 91 Ma to 120 Ma (see Stevens 2001-onwards; Weeks *et al.* 2014).

Figure 9. — A–E: ***Burseroxylon preserratum***, BSIP 35374. — A: Diffuse porous, vessels solitary and in short radial multiples, TS. — B: Crowded alternate intervessel pits, angular in outline, simple perforation plate in side view, TLS. — C: Vessel–axial parenchyma pits with reduced borders, TLS. — D: Rays mostly 2-seriate, vessels with tyloses, TLS. — E: Rays mostly 2-seriate, septate fibers, TLS. — F–H: ***Callistemonoxylon deccanense***, BSIP 35884. — F: Vessels exclusively solitary, fiber walls thick, TS. — G: Simple perforation plates, vasicentric tracheids, RLS. — H: Rays 1–3-seriate, heterocellular, TLS. — I–M: ***Calophylloxylon dharmendrae***, BSIP 35373. — I, J: Solitary vessels in radial to diagonal arrangement, variation in vessel density across growth rings, TS. — K: Vasicentric tracheids (VT) and simple perforation plate, RLS. — L: Narrow rays, mostly uniseriate, simple perforation plates in vessels, TLS. — M: Rays composed of procumbent cells with a single marginal row of square cells (bottom ray), chambered crystalliferous axial parenchyma strands, RLS. — Scale bars: 200 μm in A, F, I, J; 100 μm in D, G, H, L; 50 μm in B, C, E, K, M.

A search for 5p 6a 7a 8a 9a (diffuse porous, vessels randomly arranged and in short multiples), 13p 22p 23p 24a (simple perforation plates, alternate intervessel pits that are polygonal in outline and not minute), 30a (vessel-ray parenchyma pits not similar to intervessel pits), 42p 46a 49a 50a (vessel mean tangential diameter 100–200 μm and not less than 5/sq.mm or more than 40 per sq.mm), 56p (tyloses common), 61p 65p 70a (septate fibers with simple pits and not thick-walled), 77a 78p 80a 83a 85a 86a

(axial parenchyma scanty paratracheal, and not diffuse-in-aggregates, aliform, confluent, or banded), 97p 104a 105a 115p (rays 1–3-seriate, not homocellular, 4–12 per mm), 124a 125a 126a 130a 132a 133a 134a 135a (oil cells, canals, and cambial variants absent) yielded Anacardiaceae (6 genera), Burseraceae (8 genera), Kirkiaceae (1 genus), and Phyllanthaceae (*Bridelia*, *Margaritaria*). Ray structure in the Phyllanthaceae differs; rays are markedly heterocellular in Phyllanthaceae, but not in *Burseroxylon*. Hence, the assignment to order Sapindales is preferred.

Callistemonoxylon Bande, Mehrotra, Prakash 1986 [1987]

Callistemonoxylon deccanense Bande, Mehrotra, Prakash 1986 [1987]

Current taxonomic assessment: Myrtaceae.

Examined: Holotype BSIP 35584; Locality: Ghughua, Dindori District, Madhya Pradesh. – Fig. 9 F–H

Description in IAWA Feature Numbers: 2 5 9 13 22 26 30? 300? 42 47 48 52 53 60 61 66 78 93 97 106 107 115.

We searched InsideWood for diffuse porous wood with solitary vessels (5p 9p), simple perforation plates (13p), alternate intervessel pits that are not minute (22p 24a), vessels 100–200 µm in tangential diameter and not less than 5/sq.mm or more than 40/sq.mm (42p 46a 49a 50a), vasicentric tracheids and non-septate fibers present (60p 66p), axial parenchyma scanty paratracheal and not diffuse-in-aggregates, aliform-confluent or banded (77a 78p 80a 83a 85a 86a), rays 1–3-seriate that are not homocellular (97p 104a 105a), oil cells, canals, and cambial variant structure absent (124a 125a 126a 130a 132a 133a 134a 135a).

This combination of features was found in 4 genera of Myrtaceae (*Eucalyptus*, *Lophostemon*, *Syncarpia*, *Tristaniopsis*), but not *Callistemon*. We did not observe vessel-ray parenchyma pit type in this wood, which is not well preserved, and that feature was not described by Bande *et al.* (1986 [1987]). Without information on vessel-ray parenchyma pits, it is not possible to assign this wood to a particular genus. According to Ingle and Dadswell (1956) and Metcalfe and Chalk (1950), vessel-ray parenchyma pits in *Callistemon* are similar to intervessel pits and it has diffuse axial parenchyma, which we did not observe. We concur with the assignment of this wood to the Myrtaceae, but do not think that it represents *Callistemon*. The generic name *Callistemonoxylon* still has priority for this wood, but its similarity to extant *Callistemon* is not sufficient to imply close relationship.

Calophylloxylon Lakhanpal & Awasthi 1964 [1965]

Calophylloxylon dharmendrae Bande & Prakash 1980

Current taxonomic assessment: Myrtaceae.

Examined: Holotype BSIP 35373; Locality: Shahpura, Dindori District, Madhya Pradesh. – Fig. 9 I–M

Description in IAWA Feature Numbers: 1 2 5 7 9 13 22 26 30? 31? 32? 42 47 60 61? 62? 65 66 76 96 104 106 115 116 136 142.

The vessels in this wood have an obvious radial to diagonal arrangement, with variation in the spacing of the vessels (Fig. 9 I, J). Bande and Prakash (1980) considered this

wood similar to *Calophyllum* because it has “vessels arranged in characteristic oblique pattern, vasicentric tracheids, tangential bands of parenchyma and mostly uniseriate rays.” Mehrotra (1989) suggested that this wood has features of *Eucalyptus dharmendrayae* (Bande et al. 1986 [1987]). We concur with Mehrotra and agree that this wood is more likely to have affinities with the Myrtaceae than with the Calophyllaceae. We are not sure whether or not it is conspecific with *Eucalyptus dharmendrayae*, collected from the same locality. There is variation in the cross-sectional appearance (compare Fig. 9 I, J with Fig. 12 A, B), but this type of variation may occur within a species.

A search of InsideWood for the combination of features that Bande and Prakash (1980) remarked upon (7p, 60p, 85p, 96p) indicates that these features are not unique to *Calophyllum* (Calophyllaceae, Malpighiales), but also occur in *Eucalyptus* (Myrtaceae, Myrtales). Bande and Prakash also reported that there were 3–4-seriate widely spaced bands of axial parenchyma. However, we are not sure if bands are present; one area of the transverse section looked as if bands might be present, but we did not see any evidence of bands in the radial section. One tangential section intersected a group of subdivided cells that might represent axial parenchyma strands; it is possible that these are strands in a parenchyma band. Apotracheal bands of axial parenchyma are a defining feature of *Calophyllum* and are obvious in the type species of the genus *Calophylloxyton*, *C. indicum* from the Miocene Cuddalore Series (Lakhanpal & Awasthi 1964 [1965]). Without being able to confirm the presence of such bands it is not possible to verify the assignment of BSIP to the Calophyllaceae. We were not able to determine vessel-ray parenchyma pit type, intertracheary pitting appears to be alternate, and in some regions it looked as if there are coalescent apertures (Fig. 9 K).

***Dracontomeloxylon palaeomangiferum* Prakash 1979**

Current taxonomic assessment: Anacardiaceae.

Sample examined: BSIP 5875; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 10A–E

Description in IAWA Feature Numbers: 1v 2 5 13 22 23 27 31 32 42 43 46 47 52? 53? 54? 56 61? 65 66 69 78v 79 80 81 83v 91 92 93v 97 98 106 107v 110v 115.

In 1979, Ghosh and Roy proposed the genus and species *Dracontomelumoxylon mangiferumoides* for a Miocene wood they considered similar to the extant Indian species *Dracontomelon dao* [synonym *Dracontomelon mangiferum*]. However, they did not designate a holotype, so it is a *nomen nudum*. Also in 1979, Prakash described a Miocene wood from the Siwalik sediments of India, also said to resemble *Dracontomelon*, and named it *Dracontomeloxylon palaeomangiferum*. A holotype was designated, so this would be a valid name.

Subsequently, Bande and Khatri (1980) described a sample (BSIP 5875) from Parapani they considered “almost identical” to *Dracontomeloxylon palaeomangiferum* Prakash, and assigned it to that species; we examined this sample. Bande and Prakash (1982 [1983]) described another sample from Shahpura, which they assigned to the invalid genus *Dracontomelumoxylon*. They commented that it was nearly identical to Bande and Khatri’s Parapani sample and thus implied that the Parapani and Shahpura samples were conspecific, making this one of the few wood types described from

more than one Deccan locality. This wood type also occurs at Ghansor, Seoni District, Madhya Pradesh (Srivastava 2010). Bande and Prakash (1982 [1983]) commented on differences between the Miocene and Deccan samples in growth ring distinctiveness (indistinct – absent in the Deccan samples; present in the Miocene samples) and in how common septate fibers were (less common in the Deccan samples). They considered this variation to be consistent with that seen within present-day *Dracontomelon*.

The combination of features in this wood indeed occurs in *Dracontomelon*, but is not unique to it. These features occur in other Paleotropical Anacardiaceae, e.g., *Haemastaphis*, *Mangifera*, and *Pseudospondias*. Present-day *Dracontomelon* tends to have wider rays (some to 4-seriate) than do the aforementioned genera (rays to 3-seriate), but we hesitate to use that difference to assert that this wood represents *Dracontomelon* because of the overlap in ray sizes we observed.

We searched for diffuse porous woods with randomly arranged vessels that are solitary and in short radial multiples (5p 6a 7a 8a 9a 10a 11a), exclusively simple perforation plates (13p 14a), large alternate intervessel pits polygonal in outline (22p 23p 27p), vessel-ray parenchyma pits not similar to intervessel pits (30a), vessel diameters >100 µm and fewer than 20 vessels/sq.mm (40a 41a 48a 49a 50a), fibers septate and non-septate with walls thin to thick (65p 66p 69p), axial parenchyma vasicentric to aliform and not in bands (79p 80p 85a 86a), rays not exclusively uniseriate and not >10-seriate, not of two distinct sizes (96a 99a 100a 103a), rays with procumbent body cells and with one marginal row of square to upright cells (106p), tile cells, storied structure, oil cells, canals all absent (111a 118a 120a 124a 125a 126a 127a 128a 129a 130a 133a 134a 135a). This combination of features occurs in Anacardiaceae and Moraceae. The shape of the ray cells and ray spacing are consistent with those seen in the Anacardiaceae.

Elaeocarpoxyylon Prakash & Dayal emend. Prakash & Tripathi 1973 [1975]

Elaeocarpoxyylon antiquum Prakash & Dayal 1963 [1964]

Current taxonomic assessment: possibly Elaeocarpaceae, but also possibly Malpighiales, families Achariaceae, Phyllanthaceae, Salicaceae.

Examined: Holotype BSIP 32734; Locality: Mahurzari, Nagpur, Maharashtra.

Fig. 10F–K

Description in IAWA Feature Numbers: 2 5 10v 13 21v 22 23v 26 27 31 32 41 47 53 61 65 69 75 78 92? 93? 97 107 108 116 136? 137?.

There is overlap in the wood anatomy of some malpighiale families and the Elaeocarpaceae. We examined samples of three *Elaeocarpoxyylon* species described from the Deccan Beds; BSIP 32734 is the only one with a combination of features found in the Elaeocarpaceae. The first group of features we used to search InsideWood was: diffuse porous wood with vessels solitary and in radial multiples not arranged in any pattern (5p 6-9a), simple perforation plates (13p), alternate intervessel pitting that is

←

Figure 10. — A–E: *Dracontomeloxylon palaeomangiferum*, BSIP 5875. — A, B: Diffuse porous wood; vessels solitary and in short radial multiples; scanty paratracheal parenchyma. — C: Crowded alternate intervessel pits, polygonal in outline, TLS. — D: Body of ray composed of procumbent cells; vessel-ray parenchyma pits barely visible, RLS. — E: Rays mostly 3(–4)-seriate, TLS. — F–K: *Elaeocarpoxyylon antiquum*, BSIP 32734. — F, G: Diffuse porous wood; vessels solitary and in radial multiples, randomly arranged; axial parenchyma rare, TS. — H: Crowded alternate intervessel pits; simple perforation plates, RLS. — I: Vessel-ray parenchyma pits (arrow), RLS. — J: Narrow heterocellular rays, uniseriate rays abundant, TLS. — K: Ray cellular composition, RLS. — Scale bars: 200 µm in A, F; 100 µm in B, E, G, J; 50 µm in C, D, H, I, K.

medium-large (22p 24a 25a), vessel-ray parenchyma pitting not similar to intervessel pitting (30a), septate fibers without obvious pits (61p 65p), rare-scanty paratracheal parenchyma (77a 79-86a), numerous markedly heterocellular rays not exclusively uniseriate or >10-seriate (96e 99e 108p 116p), storied structure absent (118-122a), oil cells absent (124-126a), canals and cambial variants absent (127-135a). This returned members of the Achariaceae (5 genera), Calophyllaceae (1 species, unlikely because some diffuse parenchyma, not scanty paratracheal), Euphorbiaceae (*Acalypha*), Phyllanthaceae (3 genera), and Salicaceae (7 genera), all Malpighiales; and Elaeocarpaceae (12 species of *Elaeocarpus* and 1 of *Aristotelia*), Oxalidales.

A second search including presence of scanty paratracheal parenchyma (78p) and rays 1–3-seriate (97p) returned Achariaceae (1 species), Phyllanthaceae (1 species), and Salicaceae (1 species), all Malpighiales, and Elaeocarpaceae (8 species of *Elaeocarpus* and 1 of *Sloanea*). Radial multiples of 4 or more are relatively easy to find in BSIP 32734; all four of the aforementioned families have some species with that feature or a tendency to it.

A feature of many samples of present-day species of *Elaeocarpus* we examined was a high ratio of tall 1-seriate rays to 2–3-seriate rays (e.g., *E. dentatus*, *E. dolichostylus*, *E. elatus*, *E. grandis*, *E. polydactylus*, *E. tuberculatus* images in InsideWood). Tall uniseriate rays composed of upright cells also occur in Achariaceae, Phyllanthaceae, and Salicaceae, but it appears that the 1-seriate: 2–3-seriate ray ratio is not as high as it is in the Elaeocarpaceae. It is possible that this wood belongs to the Elaeocarpaceae, but we cannot be confident about that relationship because it shares features with some Achariaceae, Phyllanthaceae, and Salicaceae.

Elaeocarpoxyylon ghughuense Awasthi, Mehrotra, Srivastava 1995 [1996]

Current taxonomic assessment: family unknown.

Examined: Holotype BSIP 37373; Locality: Ghughua near Shahpura, Dindori District, Madhya Pradesh. – Fig. 11A–E

Description in IAWA Feature Numbers: 2 5 10v 13 22 23 26 31 32v 41 47 52 61 65? 66 68 69 75 78 92 93v 97 98v 106v 107 115.

When *Elaeocarpoxyylon ghughuense* was described, the features used to establish its similarities with *Elaeocarpus* were not explicitly discussed; it was mentioned that it was distinct from all other species of *Elaeocarpoxyylon*. We do not consider BSIP 37373 a reliable record for Elaeocarpaceae. The combination of features used to diagnose this

Figure 11. — A–E: *Elaeocarpoxyylon ghughuense*, BSIP 37373. — A, B: Diffuse porous wood; vessels solitary and in radial multiples, some of 4 or more, randomly arranged, TS. — C: Crowded alternate intervessel pits, TLS. — D: Vessel-ray parenchyma pits with reduced borders, RLS. — E: Series of vessel elements with simple perforation plates; narrow heterocellular rays, TLS. — F–K: *Elaeocarpoxyylon mandlaense*, BSIP 37354. — F, G: Diffuse porous wood; vessels solitary and in radial multiples, randomly arranged, TS. — H: Simple perforation plates (arrows), TLS. — I: Vessel-ray parenchyma pits (arrow, VRP), RLS. — J: Multiseriate rays often 6–8 cells wide, TLS. — K: Rays with many square and upright cells, RLS. — Scale bars: 500 µm in A; 200 µm in B, E, F, J; 100 µm in G, K; 50 µm in C, D, H, I.

species: diffuse porous (5p), vessels small to medium (40a 43a), 16–20 vessels/sq. mm (46a 49a 50a), perforations simple (13p), alternate intervessel pits 4–6 μ m across (22p 24a 27a), vessel-parenchyma pits slightly larger than intervessel pits (we observed reduced borders, 31p), fibers without obviously bordered pits (61p), axial parenchyma very sparse with a few cells associated with the vessels (one search with 75p, one with 78p), rays 1–3-seriate with 1–4 rows of upright cells (97p 104a 105a 108a) is

not diagnostic of the Elaeocarpaceae. This combination is not unique to a particular family or order, as it occurs in the Achariaceae, Phyllanthaceae (Malpighiales), Anacardiaceae, Burseraceae, Kirkiaceae (Sapindales), Cannabaceae (Rosales), Lamiaceae, Verbenaceae (Lamiales).

The diagnosis of *Elaeocarpoxydon ghughuense* describes the fibers as septate and non-septate, but we were not able to confirm the presence of septate fibers in BSIP 37373. Given that the fibers appear to be predominantly non-septate in BSIP 37373, it seems unlikely this wood has relationships with the Achariaceae, Burseraceae, Kirkiaceae, Lamiaceae, Phyllanthaceae, or Verbenaceae in which fibers are commonly, or exclusively septate. However, the preservation of this sample is not good, so relying on the presence/absence of septate fibers to determine affinities is questionable. We hesitate to say anything about the affinities of BSIP 37373 other than that a relationship with Elaeocarpaceae is highly unlikely. Three well-preserved twigs from Ghansor, another Deccan locality, were assigned to this species (Srivastava 2010), septate fibers are present in these samples and rays are markedly heterocellular with >4 marginal rows of upright cells. Their combination of characteristics occurs in the Malpighiales (Malpighiaceae, Phyllanthaceae, Salicaceae).

Elaeocarpoxydon mandlaense Lakhanpal, Prakash, & Bande 1976 [1978]

Current taxonomic assessment: family unknown.

Examined sample: BSIP 37354, holotype not available; Locality for BSIP 37354:

Mohgaon Kalan, Chhindwara District, Madhya Pradesh. – Fig. 11 F–K

Description in IAWA Feature Numbers: 2 5 13 22 24 25 30 41 42 47 52 53 61? 62? 65? 66? 75? 78 79? 92 93 98 99v 102 105v 108v 110.

We did not see the type specimen for this species, but another sample from Mohgaon Kalan which was figured but not described by Awasthi *et al.* (1995 [1996]). They noted that this specimen (BSIP 37354) differed from Lakhanpal *et al.*'s original 1976 [1978] description in having narrower vessels and lower rays. Moreover, this sample differs from the Elaeocarpaceae in having all vessel-ray parenchyma pits similar to intervessel pits and minute-small intervessel pitting. *Elaeocarpus* has vessel-ray parenchyma pits that are exclusively or mostly with reduced borders and medium to large intervessel pits. It may be that the type, which we were not able to see, has features of Elaeocarpaceae, but this sample does not. It was not possible to determine fiber type and fiber pitting making it difficult to determine the affinities of this wood.

We searched for diffuse porous wood (5p), vessels solitary and in short radial multiples, randomly arranged (6a 7a 8a 9a), 13p (simple perforation plates), alternate intervessel pits not medium–large (22p 26a 27a), vessel-ray parenchyma pits similar to intervessel pits (30p), vessels not very narrow or very wide and not >40 vessels/sq. mm (40a 43a 49a 50a), axial parenchyma not obvious (77a 80a 83a 85a 86a 89a), rays >4 cells wide and commonly >1 mm high (96a 97a 102p), not abundant and not composed exclusively of procumbent cells (104a 116a), storied structure and canals absent (118a 119a 120a 127a 128a 129a 130a). This general pattern is of wide occurrence, found in some species of 13 orders and 16 families: Apocynaceae, Rubiaceae (Gentianales), Asteraceae (Asterales), Boraginaceae (Boraginales), Capparaaceae

(Brassicales), Gesneriaceae, Stilbaceae (Lamiales), Malvaceae (Malvales), Meliaceae, Sapindaceae (Sapindales), Onagraceae (Myrtales), Primulaceae (Ericales), Sabiaceae (Proteales), Salicaceae (Malpighiales), Stemonuraceae (Aquifoliales), Urticaceae (Rosales). Hence, a confident familial or ordinal assignment is not warranted.

“*Eucalyptus*” *dharmendrae* Bande, Mehrotra, & Prakash 1986 [1987]

Current taxonomic assessment: Myrtaceae, subfamily Myrtoideae.

Examined: Holotype BSIP 35882; Locality: Ghughua, near Shahpura, Dindori District, Madhya Pradesh. – Fig. 12 A–F

Description in IAWA Feature Numbers: 2 5 7 9 13 22 25 30? 31? 32? 42 47 52 53 56 60 61 65? 76 78 96 104 106v 116 136 142.

The features of this wood are unique to Myrtaceae. Unfortunately, vessel-ray parenchyma pits could not be discerned in this specimen, yet this is a character important for distinguishing genera in Myrtaceae. Consequently, we hesitate to treat this as a record for the genus *Eucalyptus*, but agree with Bande *et al.* (1986 [1987]) that it most probably represents an Australian element in the Deccan Intertrappean Beds because the anatomically similar genera *Lophostemon* and *Eucalyptus* are found primarily in Australia today. A search for diffuse porous woods with exclusively solitary vessels in a radial/diagonal arrangement (5p 7p 9p), simple perforation plates (13p), vasicentric tracheids (60p), diffuse and scanty paratracheal axial parenchyma (76p 78p), exclusively uniseriate homocellular rays (96p 104p) returned Chrysobalanaceae, which can be eliminated because of its more abundant, usually banded, axial parenchyma, and *Eucalyptus* and *Lophostemon* of the Myrtaceae.

Bande *et al.* (1986 [1987]) reported septate fibers for this species, but they are not obvious in the slides we examined. Septate fibers are rare in the Myrtaceae; Metcalfe and Chalk (1950) noted that gum plugs in fibers in the heartwood can easily be confused with septate fibers. According to Mehrotra (1989), the wood described as *Calophylloxylon dharmendrae* (Bande & Prakash 1980) should be transferred to this species.

More recently, another sample from the same locality was described as a new species, *Eucalyptus ghughuensis* Shukla *et al.* (2012). Unfortunately, in the description of this species, vessel-ray parenchyma pits are not described. Moreover, the criteria used to distinguish extant *Eucalyptus* from extant *Tristania*, now synonymized with *Lophostemon*, are not valid. It was stated that extant *Lophostemon* (*Tristania*) does not have diagonal pore arrangement as seen in the fossil. However, Ingle and Dadswell (1956) and Sosef *et al.* (1998) noted the occurrence of this pattern in the genus, and the low magnification transverse section of *Lophostemon confertus* on InsideWood (FPAw a.151, photo by J. Ilic) shows a diagonal pore arrangement. Shukla *et al.* (2012) used the semi-ring porous appearance of the wood closest to the pith and a higher vessel frequency to differentiate this sample from *E. dharmendrae* and as reasons to assign it to a new species. However, wood farther from the pith in the sample is diffuse porous (R. Srivastava, pers. obs.) and the difference in vessel frequency is variation that would be expected when comparing wood from a young cambium and next to the pith with wood produced by an older cambium.

Figure 12. — A–F: *Eucalyptus dharmendrae*, BSIP 35882. — A, B: Diffuse porous wood, exclusively solitary vessels in radial/diagonal arrangement, TS. — C: Vasicentric tracheids, rays with procumbent cells, RLS. — D: Bubble-like tyloses, TLS. — E: Uniseriate rays, vessel with tyloses, TLS. — F: Rays composed of procumbent cells, strand of chambered crystalliferous axial parenchyma (arrow), RLS. — G–J: *Euphorioxylon deccanense*, BSIP 35895. — G: Diffuse porous wood, vessels solitary and in short multiples; growth ring boundaries distinct, TS. — H: Simple perforation plates, crowded alternate intervessel pits, TLS. — I: Vessel-ray parenchyma pits similar to intervessel pits, rays with procumbent cells, RLS. — J: Rays uniseriate, TLS. — Scale bars: 200 μm in A, B, G; 100 μm in E, J; 50 μm in C, D, F, H, I.

Euphorioxylon Awasthi, Guleria, & Lakhanpal 1981 [1982]

Euphorioxylon deccanense Mehrotra 1986 [1987]

Current taxonomic assessment: Sapindaceae.

Examined: Holotype BSIP 35895; Locality: Ghughua, Dindori District, Madhya Pradesh. – Fig. 12 G–J

Description in IAWA Feature Numbers: 2 5 13 22 23 25 26 30 42 47 52 61 65? 66 68 69 75 78 91? 92? 96 97v 104 106? 115.

The Plant List (Version 1.1 (September 2013) indicates that *Euphoria* species names are either unresolved or synonyms of species of *Allophylus*, *Cubilia*, *Dimocarpus*, *Lepidopetalum*, *Lepisanthes*, *Litchi*, *Nephelium*, *Sapindus*, and *Xerospermum*. Kar et al. (2004) reported *Euphorioxylon indicum* in the Lameta Formation of India (Maastriachian). In that paper, they noted that present-day *Euphoria*, *Litchi*, and *Otonophelium* are “xylotomically indistinguishable.”

We searched InsideWood for 5p 6a 7a 8a 9a 10a 11a (diffuse porous wood with randomly arranged vessels not exclusively solitary or commonly in radial multiples of 4 or more or in clusters), 13p (simple perforation plates), 22p 24a 27a (alternate intervessel pits not minute or large), 30p (vessel-ray parenchyma pits similar to intervessel pits), 42p 47p (mean tangential diameter of vessels 100–200 μm , and 5–20 per sq. mm), 61p 69p (fibers with simple pits and thin- to thick-walled), 75p (axial parenchyma rare), 96p 104p (exclusively uniseriate rays that are composed exclusively of procumbent cells). This search returned ten genera of Sapindaceae (*Allophylus*, *Beguea*, *Blighia*, *Cubilia*, *Cupaniopsis*, *Diploglottis*, *Eriocoelum*, *Neotina*, *Schleichera*, *Tinia*) and one Solanaceae (*Solanum paludosum*). The *Solanum* differs because it has some vessel-ray parenchyma pits with reduced borders, vessels tend to be of two size classes, and fibers are very thin-walled. BSIP 35895 has a combination of features consistent with its placement in the Sapindaceae. According to Klaassen’s (1999) synoptic key to sapindaceous genera, there are differences between the fossil and four of the aforementioned extant genera: *Allophylus* – fiber dimorphism; *Blighia* and *Eriocoelum* – vessel wall thickenings; *Neotina* – intervessel pit diameter $< 4 \mu\text{m}$. This leaves the following members of subfamily Sapindoideae: *Beguea*, *Schleichera* (Tribe Schleichereae), *Cubilia* (Tribe Nephelieae), *Cupaniopsis*, *Diploglottis*, *Tinia* (Tribe Cupanieae) as sharing features with the fossil.

Euphorioxylon deccanense also occurs at Ghansor, another Deccan locality (Srivastava 2010).

Evodinium Bande & Prakash 1979 [1984]

Evodinium indicum Bande & Prakash 1979 [1984]

Current taxonomic assessment: Rutaceae? Rhamnaceae possible.

Examined: Holotype BSIP 35321; Locality: Nawargaon, Wardha District, Maharashtra. – Fig. 13 A–E

Description in IAWA Feature Numbers: 2 5 13 22 23 26 30? 31? 42 43 46 47 52 61 66 68 69 78 79 91 92 93 97 104 106v 115 136? 138?.

We were uncertain how to code the vessel ray parenchyma pits in this sample. The pits are not the type that is elongated vertically or horizontally (feature 32). Rather,

they appeared to be of nearly the same size as the intervessel pits, but it was difficult to determine whether they had distinct borders (feature 30) or reduced borders (feature 31). We chose to describe the vessel-ray parenchyma pit type as “30? 31?”, although we think 31 likely is the better descriptor. If 31 is the correct descriptor, then this wood is not related to *Evodia* or any other Rutaceae, all of which have vessel-ray parenchyma pits similar to intervessel pits.

We searched InsideWood using combinations of the other characteristics of this wood, 5p 6a 7a 8a 9a 10a (diffuse porous wood with randomly arranged vessels that are solitary and short radial multiples), 13p (simple perforation plates), 22p 24a 27a (alternate intervessel pits $> 4 \mu\text{m}$ and $\leq 27 \mu\text{m}$), 32a (vessel-ray pits not enlarged horizontally or vertically), 40a 41a 49a 50a (mean tangential diameter of vessels $> 100 \mu\text{m}$ and $< 40/\text{sq. mm}$), 61p 66p 70a (non-septate fibers with simple pits and not very thick walls), 78p 80a 83a 85a 86a (axial parenchyma scanty paratracheal and not aliform-confluent-banded), 97p 104p (rays 1–3-seriate and homocellular), 124a 125a 126a 130a (oil cells and radial canals absent). Families with species with this combination of features included the Meliaceae, Rutaceae (but not *Evodia*), Sapindaceae (Sapindales), Oleaceae (Lamiales), Rhamnaceae (Rosales). Of the aforementioned families only the Rhamnaceae has species with vessel-ray parenchyma pits with reduced borders. It is possible that this wood is a member of the Rutaceae, but affinities with Rhamnaceae cannot be excluded based on the features visible in the slides of the sample. Shete and Kulkarni (1982), while aware of the 1979 manuscript of Bande and Prakash, described another wood from Nawargaon as *Evodinium intertrappeum*; it is likely that *E. indicum* and *E. intertrappeum* are conspecific (R. Srivastava, pers. obs.).

***Garcinioxylon* Bande & Khatri 1980**

***Garcinioxylon tertiarum* Bande & Khatri 1980**

Current taxonomic assessment: family unknown.

Examined: Holotype BSIP 35212; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 13F–K

Description in IAWA Hardwood Features: 2 5 13 22 23 25 30 41 46 47 53 61? 62? 66 69 76? 77? 78 79? 93 94 98 99 102 103 107 108 110 115 130.

The holotype is a small axis with pith (Fig. 13F). We had difficulty determining the axial parenchyma distribution. In Figure 13G, the bottom 1/3 of the photo seemingly shows diffuse to diffuse-in-aggregates axial parenchyma, while in the upper 2/3, it appears as if bands of thinner-walled cells are present. In longitudinal sections, we could not confirm the occurrence of either of these features, but could only see parenchyma strands associated with the vessel elements (Fig. 13H, K).

←

Figure 13. — A–E: *Evodinium indicum*, BSIP 35321. — A: Diffuse porous, vessels solitary and occasionally in radial multiples of two, TS. — B: Fiber walls thin, narrow vasicentric parenchyma, TS. — C: Crowded alternate intervessel pits, angular in outline, simple perforation plate, vessel-ray parenchyma pits, procumbent ray cells, RLS. — D: Rays mostly 3-seriate; non-septate fibers, TLS. — E: Rays with procumbent cells, RLS. — F–K: *Garcinioxylon tertiarum*, BSIP 35212. — F: Pith, TS. — G: Diffuse porous wood, vessels solitary and in short multiples, in bottom third of photo, likely diffuse to diffuse-in-aggregates axial parenchyma, TS. — H: Simple perforation plates, and small alternate intervessel pits, RLS. — I: Wide and tall rays with idioblasts, TLS. — J: Detail of ray, idioblasts (arrows), axial parenchyma strands next to vessels, TLS. — K: Ray cellular composition, likely section of a narrow ray composed of upright and procumbent cells, vessel-ray parenchyma pitting similar to intervessel pitting, RLS. — Scale bars: 200 μm in A, F, G, I; 100 μm in B, D, E, J, K; 50 μm in C, H.

Originally we searched InsideWood using these features: 5p (wood diffuse porous), 6a 7a 8a 10a 11a (vessels randomly arranged and without radial multiples commonly 4 or more or in clusters), 13p (simple perforation plates), 22p 26a 27a (intervessel pits alternate and not medium–large), 30p (vessel-ray parenchyma pits similar to intervessel pits), 98p (rays 4–10-seriate), 102p (rays more than 1 mm high), 130p (radial canals). In InsideWood, only species of *Garcinia* have this combination of features. However, according to Metcalfe and Chalk (1950), “Secretory canals universally present in the primary cortex and pith” of Guttiferae, the family in which *Garcinia* was placed in 1950. Canals are absent from this sample’s pith. Moreover, the shape and abundance of the structures that Bande and Khatri and we initially interpreted as canals differ from canals seen in present-day species of *Garcinia*, e.g. *G. cowa*, *G. intermedia*, *G. macrophylla*, *G. madruno*. Consequently, we considered alternative interpretations of the structures, namely, that they are idioblasts or break-down areas.

Some Myrsinoideae (family Primulaceae) resemble this wood in having rays of two sizes, large rays with idioblasts (secretory cells) and break-down areas (some can look like canals), small intervessel pits and vessel-ray parenchyma pits similar in size to intervessel pits (Lens *et al.* 2005). Axial parenchyma in Myrsinoideae is scanty paratracheal to vasicentric, so if there is diffuse-in-aggregates or banded parenchyma in BSIP 35212, then this wood cannot be Myrsinoideae, and its affinities remain unresolved.

***Glochidioxylon* Ramanujam 1956**

***Glochidioxylon sahnii* Prakash 1958 [1959]**

Synonym: *Paraphyllanthoxylon sahnii* (Prakash) Mädel

Synonym: *Phyllanthinium sahnii* (Prakash) Prakash, Bande, & Lalitha 1986

Current taxonomic assessment: Malpighiales/Salicaceae-Euphorbiaceae clade.

Examined: Holotype BSIP 10363; Locality: Bharatwada, Nagpur District, Madhya Pradesh. – Fig. 14A

Description in IAWA Feature Numbers: 2 5 13 21v 22 26 31 42 48 52 56 61 65 70 75 76v 78v 98 102 103v 106v 107 108? 116.

The preservation of this sample was poor and it was only possible to obtain photographs of the transverse sections. Prakash (1958 [1959]) commented on this wood’s poor preservation and noted that its features “occur in remotely related orders and families.”

Figure 14. — A: *Glochidioxylon sahnii*, BSIP 10363. Diffuse porous wood, vessels commonly in radial multiples, thick-walled fibers, TS. — B–F: “*Gmelina*” *tertiara*, BSIP 35770. — B: Diffuse porous wood, vessels solitary and in short multiples, paratracheal parenchyma, TS. — C: Crowded alternate intervessel pits, angular in outline, TLS. — D: Vessel-ray parenchyma pits oval in outline with reduced borders, RLS. — E: Heterocellular rays often 3-seriate, short uniseriate margins, septate fibers, TLS. — F: Body ray cells procumbent, marginal row of square cells (S), RLS. — G–L: *Gomphandroxylon samnapurens*, BSIP 35313. — G, H: Diffuse porous wood, vessels exclusively solitary, diffuse and diffuse-in-aggregates axial parenchyma, TS. — I: Opposite intervessel pits, TLS. — J: Scalariform perforation plate with fewer than 20 bars, RLS. — K, L: Wide rays, commonly >10-seriate, scalariform perforation plates in side view (PP), TLS. Scale bars: 200 µm in A, B, G; 100 µm in E, F, H, K, L; 50 µm in F, I, J; 20 µm in C, D.

A search for diffuse porous (5p), simple perforation plates (13p), alternate inter-vessel pits that are $>4\ \mu\text{m}$ across (22p 24a), vessel-ray parenchyma pits with reduced borders (31p), mean vessel diameter 100–200 μm and 5–40 vessels/sq.mm (42p 46a 49a 50a), tyloses common (56p), septate fibers (65p), axial parenchyma rare (75p), rays 4–10-seriate, more than 1 mm high, and not homocellular (98p 102p 104a 105a) returned species of Achariaceae and Phyllanthaceae, but not *Glochidium*.

Mädel (1962) transferred this species to *Paraphyllanthoxylon* Bailey. However, the features of this wood as described by Prakash and our observations do not support this transfer. This Deccan species tends to have rays of two distinct sizes, fibers are very thick-walled, ray parenchyma cells are not thin-walled, and there is a marked difference between the marginal ray cells and the body ray cells. These are not features of *Paraphyllanthoxylon* Bailey (1924).

Gmelina L.

“*Gmelina*” *tertiara* Bande 1986 [1987]

Current taxonomic assessment: Lamiaceae.

Examined: Holotype BSIP 35770; Locality: Nawargaon, Wardla District, Maharashtra. – Fig. 14B–F

Description in IAWA Feature Numbers: 2 5 13 22 23 26 31 42 47 52 56 61 65 78 79 92 93 97v 98 106 107v 115.

Bande used these features – “small to large vessels with simple perforations [13p] and alternate bordered pits [20a 21a 22p], paratracheal vasicentric to aliform to aliform-confluent parenchyma [79p 80p 83p], 1–4-seriate [98p] weakly heterogeneous xylem rays [106p] and septate fibers [65p]” – to conclude that the affinities of this wood were with *Gmelina* (Lamiaceae). He considered this sample to have features unique to *Gmelina* and consequently concluded that it did not need assignment to an *-oxylon* genus. We agree that this wood has features found in *Gmelina*, but it also has features found in *Vitex* (Lamiaceae).

The features Bande 1986 [1987] listed are not enough to confirm relationship with the Lamiaceae. We searched InsideWood using the aforementioned features and some additional obvious features of the wood: diffuse porous wood (5p), vessels solitary and in short radial multiples that are not arranged in an obvious pattern (6a 7a 8a 9a 10a 11a), storied structure absent (118a 120a), oil cells absent (124a 125a 126a). This search did not return *Gmelina* or any member of the Lamiaceae, but members of 11 other families: Acanthaceae, Anacardiaceae, Bignoniaceae, Combretaceae, Fabaceae, Lauraceae, Meliaceae, Moraceae, Phyllanthaceae, Sapindaceae, and Vochysiaceae.

We observed vasicentric axial parenchyma in BSIP 35770 (Fig. 14B), but not aliform to aliform-confluent parenchyma, so subsequently we only searched for vasicentric parenchyma (79p). The literature on extant *Gmelina* wood does not indicate that aliform-confluent parenchyma is a typical feature of the genus, *e.g.*, Kribs (1968); Louppe *et al.* (2008); Soerianegara & Lemmens (1993), and this feature was not obvious in the extant material available to us for study. Also, rays commonly are 3-seriate in BSIP 35770 (Fig. 14E), so rather than search for wider rays commonly >4-seriate (feature 98), we used absence of exclusively uniseriate rays and rays >10-seriate (96a 99a), as well as absence of rays >1 mm high (102a). Bande did not describe vessel-ray parenchyma pits, but we observed vessel-ray parenchyma pits that were similar in size to the intervessel pits (Fig. 14D), but with reduced borders (31p 32a). We also used intervessel pits *not* minute–small (24a 25a) in our next search. This combination of features occurs in only two families: Anacardiaceae (Sapindales) and Lamiaceae (Lamiales). Uniseriate rays are rare and septate fibers predominate in this Deccan wood indicating similarity with

the Lamiaceae (*Vitex* and *Gmelina*), rather than the Anacardiaceae. There is overlap in the features of *Vitex* and *Gmelina*. If we had observed a few scalariform perforation plates, this would suggest affinities with *Vitex*, rather than with *Gmelina*, but we did not. This wood has features of *Gmelina*, but it also resembles some species of *Vitex*, e.g., *V. agnus-castus*, *V. cofassus*, *V. gaumeri* (images in InsideWood).

***Gomphandroxyton* Bande & Khatri 1980**

***Gomphandroxyton samnapurens* Bande & Khatri 1980**

Current taxonomic assessment: possibly Stemonuraceae.

Examined: Holotype BSIP 35313; Locality: Samnapur, Dindori District, Madhya Pradesh – Fig. 14 G–L

Description in IAWA Feature Numbers: 2 5 9v 14 15 16 20? 21 22 30? 31? 32? 42 47 54 62 66 70 77 86v 92? 93? 94? 98 99 102 103v 108 114 115 136? 138?.

The basic combination of mostly solitary vessels randomly arranged (5p, 6a, 7a, 8a, 9p), exclusively scalariform perforation plates (13a 14p), predominantly opposite pitting (21p), thick-walled non-septate fibers with distinctly bordered pits (62p, 66p, 70p), diffuse-in-aggregates axial parenchyma (77p), wide and tall markedly heterocellular rays (99p, 102p, 108p) occurs in the Stemonuraceae, the family to which *Gomphandra* belongs. The available material of this genus shows that its parenchyma distribution and ray features are remarkably similar to this fossil. However, this general combination of features also occurs in the Cardiopteridaceae (*Citronella*) and Icacinaceae (*Cassinopsis*, *Emmotum*). Other families with that combination, but differing in having abundant uniseriate rays, include the Dilleniaceae and Sladeniaceae. Previously, the genera of the Stemonuraceae and Cardiopteridaceae were included in the Icacinaceae, but now are in separate families in the Aquifoliales. The Icacinaceae (Icacinales) is among the basal Lamiids near Garryales (Stull *et al.* 2015).

***Grewinium* (Bande & Srivastava) Srivastava & Guleria 2000**

Synonym: *Grewioxyton* Shallom *non* Schuster

***Grewinium canalisum* (Bande & Srivastava) Srivastava & Guleria 2000**

Synonym: *Grewioxyton canalisum* Bande & Srivastava 1995

Current taxonomic assessment: Malvaceae, subfamily Grewioideae.

Examined: Holotypes: BSIP 36795; Locality: Nawargaon, Wardla District, Maharashtra, and BSIP 36796; Locality: Mohgaon Kalan, Chhindwara District, Madhya Pradesh. – Fig. 15 A–F

Description in IAWA Feature Numbers: 2 5 12v 13 22 23 25 30 41 42 46 47 52 53 61 65? 66 68v 69 78 79v 92? 93? 98 99 102 103 109 111 115 130.

In the 1995 publication describing this wood type, Bande and Srivastava wrote “the woods are characterized by the presence of tile cells and radial canals. Since these two characters are never reported to occur together in the woods of extant genera or families of dicotyledons, their simultaneous occurrence in the present fossil woods is phylogenetically significant.” However, Bande and Srivastava cited Mouton and Jacquet’s (1981) paper that reported the sporadic occurrence of secretory elements in the rays (*i.e.* radial canals) of present-day *Apeiba* and *Luehea*, both New World genera belonging to the Malvaceae, subfamily Grewioideae. There are three other reports of

the combination of tile cells (111p) and radial canals (130p) in present-day *Luehea* (Kukachka & Rees 1943; Détienne & Jacquet 1983; Sonsin *et al.* 2014). The canals in *Luehea paniculata* figured by Détienne and Jacquet (1983) are not surrounded by numerous small (discolored) cells as in the Deccan woods. Although we cannot place it directly in an extant genus, this wood type can confidently be assigned to the Malvaceae, Tribe Grewioideae.

Srivastava and Guleria (2000) noted that the name *Grewioxylon* Schuster had originally been applied to a wood with features of the Dipterocarpaceae and so proposed the substitute name *Grewinium*. The name *Grewinium* was established with *Grewinium intertrappeum* (Shallom) Srivastava and Guleria as the type species. This species apparently lacks canals (Shallom 1963b) and so differs from *G. canalisum*. In addition to the occurrences that we studied, a similar wood was reported as *Grewioxylon mahurzariense* by Prakash and Dayal (1963) and later transferred to *Grewinium* by Srivastava and Guleria (2000). Although Prakash and Dayal did not mention radial canals in their description of *G. mahurzariense*, re-examination of the original slides (R.S. pers. obs.) revealed the presence of canals similar to those described for *G. canalisum*.

Whether it might be warranted to create a new genus to accommodate fossil woods with the distinctive combination of tile cells and radial canals needs consideration. Woods with this combination have been found at multiple localities in the Deccan Traps (R. Srivastava, work in progress), providing an opportunity to determine its variability and refine information on its features, e.g., number of cells per axial parenchyma strand, which we were not able to observe.

Fossil fruits of Malvaceae are known from the Deccan as well. *Harrisocarpon sahnii* Chitale and Nambudiri (1973) is a pentalocular, pentaribbed, septicidal capsule resembling that of *Abutilon*. Each locule contains two seeds arranged one above the other in a row on a central placenta. *Dabrocarpon gerhardii* Chitale and Sheikh (1971 [1973]) is a ten locular fruit with similarities to *Malvastrum* and *Sida*. Both of these fruits occur at Mohgaon Kalan where *Grewinium canalisum* occurs. Whether these fruits may have been produced by the plant that had *G. canalisum* wood is uncertain. If so, this might imply a common ancestor of Grewioideae and Malvoideae in the Deccan flora.

***Heyneoxylon* Bande & Prakash 1980**

***Heyneoxylon tertiarum* Bande & Prakash 1980**

Current taxonomic assessment: Sapindales.

Examined: Holotype BSIP 35377; Locality: Shahpura, Dindori District, Madhya Pradesh. – Fig. 15G–L

Description in IAWA Feature Numbers: 2 5 13 22 23 24 25 30 41 42v 47 52 61 65v 66 69 70 79v 80v 81v 83 85 86 91 92 98 104 106 107v 115.

This sample might have been wounded, as suggested by the abrupt change in vessel density (Fig. 15G) and somewhat disorganized rays observed in some areas.

←

Figure 15. — A–F: *Grewinium canalisum*, BSIP 36795. — A: Diffuse porous wood, vessels solitary and in short multiples, TS. — B: Crowded alternate intervessel pits, simple perforation plate in side view, TLS. — C: Vessel-ray parenchyma pits similar to intervessel pits, RLS. — D: Ray cellular composition, tile cells present, RLS. — E, F: Wide rays with large canals, TLS. — G–L: *Heyneoxylon tertiarum*, BSIP 35377. — G, H: Diffuse porous, vessels solitary and in radial multiples, variation in vessel size and spacing, TS. — I: Vessels solitary and in radial multiples, banded axial parenchyma, thick-walled fibers, TS. — J: Simple perforation plates, RLS. — K: Vessel elements with simple perforation plates, viewed from the side, minute–small alternate intervessel pits (IVP), TLS. — L: Multiseriate rays, TLS. — Scale bars: 200 µm in A, E, G, H; 100 µm in D, F, I; 50 µm in B, C, J–L.

Bande and Prakash (1980) assigned this wood to the Meliaceae on the basis of it having “mostly small vessels with simple perforations, broad bands of paratracheal parenchyma, 1–6-seriate heterocellular xylem rays and thick-walled mostly non-septate fibers.” This combination of features occurs in *Heynea*, a meliaceous genus that occurs today in India. However, the aforementioned features are not unique to the Meliaceae. We searched for those features and some others: diffuse porous wood with randomly arranged vessels that are solitary and in multiples (5p 6a 7a 8a 9a), simple perforation plates (13p), alternate intervessel pits that are minute–small (22p 26a 27a), vessel-ray parenchyma pits similar to intervessel pits (30p), vessels not wide (43a), non-septate fibers (66p), axial parenchyma confluent and in broad bands (83p 85p), rays not uni-seriate and not >10-seriate (96a 99a), aggregate rays, tile cells, storied structure, cambial variant structure all absent (101a, 111a, 118a, 119a, 120a, 133a, 134a). This expanded combination of features occurs most commonly in the Sapindales (Meliaceae, 12 records; Rutaceae, 9 records; Sapindaceae, 10 records), with additional matches for species of the Bignoniaceae, Boraginaceae, Cannabaceae, Clusiaceae, Fabaceae, Loganiaceae, Malpighiaceae, Malvaceae, Myrtaceae, Phyllanthaceae, Violaceae, and Vochysiaceae.

Including fiber wall features (69p) and ray features, absence of rays of 2 distinct sizes (103a), body of ray consisting of procumbent cells with 1 row of upright/square marginal cells (106p), absence of sheath cells (110a) leaves the Boraginaceae, Cannabaceae, Fabaceae, Meliaceae, Rutaceae, and Vochysiaceae. The appearance of the axial parenchyma bands and the vessel-ray pits in the Meliaceae and Rutaceae suggests that these two families are most similar to BSIP 35377 and we consider it probable to belong to the Sapindales.

***Homalioxylon* Prakash & Tripathi 1972 [1974]**

***Homalioxylon mandlaense* Bande 1974**

Current taxonomic assessment: family unknown, possibly Malpighiales.

Examined: Holotype BSIP 35152; Locality: Parapani, Mandla District, Madhya Pradesh. – Fig. 16A–H

Description in IAWA Feature Numbers: 2 5 13 22 23 26 31 42 47 52 61? 62? 66 69 76 78 97 106 107 115.

BSIP 35151 is a small axis with pith (Fig. 16A). Although the original diagnosis mentioned septate fibers, we were not able to confirm their presence. It is unlikely that this wood represents a record for *Homalium*-like wood.

Figure 16. — A–H: *Homalioxylon mandlaense*, BSIP 35152. — A, B: Diffuse porous wood, vessels solitary and in radial multiples, randomly arranged; pith, TS. — C: Diffuse axial parenchyma, TS. — D: Crowded alternate intervessel pits, polygonal in outline, simple perforation plates in side view, TLS. — E: Vessel-parenchyma pits with reduced borders, RLS. — F: Simple perforation plate, RLS. — G: Heterocellular rays, RLS. — H: Rays mostly 1–3-seriate, TLS. — I–L: *Hydnocarpoxylon indicum*, BSIP 35311. — I: Diffuse porous wood, vessels solitary and in radial multiples, some with >4 per multiple, TS. — J: Scalariform perforation plate, bars to left of PP, RLS. — K: Opposite (to alternate) intervessel pits, TLS. — L: Tall rays, predominantly 3-seriate, TLS. — Scale bars: 500 µm in A; 200 µm in A, B, I; 100 µm in C, G, H, L; 50 µm in D, F, J; 20 µm in E, K.

Present-day *Homalium* (Salicaceae, Malpighiales) has minute to small intervessel pits and vessel-ray parenchyma pits similar to intervessel pits (e.g., Miller 1975; Normand & Paquis 1976); these are not features of BSIP 35152. We tried different searches for this wood's features, using different combinations of presence and absence; none returned any Salicaceae. This fossil has a suite of wood anatomical features found in numerous families. If this wood is from a tree, then it is possible (probable) that the ray features

of this young stem differ from those of mature wood and it would be mature wood features that were recorded in the literature. Two examples of our searches are given here:

2p 5p 6a 7a 8a 9a 10a 13p 22p 23p 24a 27a 31p 40a 43a 46a 49a 50a 76p 77a 80a 83a 85a 86a 97p 103a 104a 105a returned Anacardiaceae, Cannabaceae, Erythroxylaceae, Euphorbiaceae, Lamiaceae, Lecythidaceae, Phyllanthaceae, Rhamnaceae;

2p 5p 6a 7a 8a 9a 13p 22p 23p 24a 27a 31p 42p 47p 76p 77a 79a 80a 83a 85a 86a 97p 103a 104a 105a returned Cannabaceae, Lecythidaceae, Phyllanthaceae.

More work is needed to determine if this wood's affinities can be ascertained. It is possible that it belongs to the Malpighiales, based on shared features with the Euphorbiaceae and Phyllanthaceae, but it is not a record of *Homalium*.

***Hydnocarpoxylon* Bande & Khatri 1980**

***Hydnocarpoxylon indicum* Bande & Khatri 1980**

Current taxonomic assessment: Achariaceae, similar to *Hydnocarpus*.

Examined: Holotype BSIP 35311; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 16 I–L

Description in IAWA Feature Numbers: 2 5 7v 10v 14 16 17 21 22 25 26 30? 31? 41 47 48 53 54 56? 61? 62? 65? 66? 75 78 97 102 107 108 116.

This is one of the few Deccan woods that has exclusively scalariform perforations (Fig. 16J). Unfortunately, we were not able to observe vessel-ray parenchyma pits or determine fiber type. The original description reported fibers as septate, but we could not confirm presence of septate fibers in the holotype. Without knowing the details of these systematically useful features, we cannot state with absolute certainty that this wood has a character set unique to *Hydnocarpus* (Achariaceae). However, *Hydnocarpus* was the only result of a search for the sample's combination of features: diffuse porous wood with radial multiples (5p 9e – required absence of exclusively solitary vessels), both opposite and alternate pitting (21p 22p), exclusively scalariform perforation plates (13a 14p), similar vessel diameter and density and vessel element lengths (43a 46a 49a 50a), rare axial parenchyma (75p), and narrow tall heterocellular rays that are >12/mm (97p 102p 104a 116p).

In addition to the original occurrence at Parapani (Bande & Khatri 1980), Guleria and Srivastava (2001) later described this species from another Deccan Intertrappean locality far to the northwest, Kachchh District, Gujarat. The specimen they examined was better preserved than the holotype. Given that the occurrence of septate fibers was confirmed in this better preserved Gujarat specimen, this indicates that there are indeed *Hydnocarpus*-like woods in the Deccan Traps.

Figure 17. — A–G: *Lanneoxylon grandiosum*, BSIP 39100. — A: Diffuse porous wood, vessels solitary and in short radial multiples, TS. — B: Vessels solitary and in radial pairs; thick-walled fibers; scanty paratracheal parenchyma, TS. — C: Crowded alternate intervessel pits, TLS. — D: Vessel-ray parenchyma pits, RLS. — E: Rays mostly 2–3-seriate, gum canal (arrow), tyloses, TLS. — F: Ray with gum canal, TLS. — G: Body of ray composed of procumbent cells, marginal row of square cells, RLS. — H–J: *Laurinoxylon deccanense*, BSIP 35378. — H: Scattered solitary vessels, TS. — I: Procumbent body cells and square marginal cells, simple perforation plates, RLS. — J: Rays 1–3(–4)-seriate, simple perforation plates, TLS. — Scale bars: 200 µm in A, H; 100 µm in B, E, I, J; 50 µm in C, D, F, G, J.

Lanneoxylon Prakash & Tripathi 1967

Lanneoxylon grandiosum Prakash & Tripathi 1967 [Holotype from Oligocene/Miocene]

Current taxonomic assessment: Sapindales, probably Anacardiaceae, Burseraceae also possible.

Examined: BSIP 39100 [not holotype]; Locality: Betul District, Madhya Pradesh. – Fig. 17A–G

Description in IAWA Feature Numbers: 2 5 13 22 23 27 31 32 42 47 56 61 65 69 70 78 97 106 107v 115 130p.

We examined the sample described by Srivastava and Guleria (2004), not the holotype, which is much younger. BSIP 39100 was assigned to *Lanneoxylon* because it was compared to present-day Indian woods belonging to the Anacardiaceae and Burseraceae and the criteria of Chauhan and Dayal (1990) were used to determine it was most similar to *Lannea*.

We searched InsideWood for the features Srivastava and Guleria mentioned as important for determining its relationships: indistinct growth rings (2p), vessels solitary and in radial multiples (9a 10a 11a), abundant tyloses (56p), scanty paratracheal parenchyma (78p), 1–3-seriate heterocellular rays (97p 104a), thick-walled septate fibers (65p 68a), radial canals (130p), but also included simple perforation plates (13p), large alternate intervessel pits (22p 27p), and vessel-ray parenchyma pits not similar to intervessel pits (30a). We did not use any quantitative vessel features or the presence of silica bodies and crystals in the rays because we could not confirm their presence. This combination of features was found in the Anacardiaceae (17 genera including *Lannea*) and Burseraceae (5 genera). While this wood is similar to *Lannea*, this broader comparison to woods from other continents indicates that it is also similar to other anacardiaceous genera, including some from Malaysia, Africa, and South America, and to some South American Burseraceae. Based on our current understanding we cannot suggest affinities with a single genus or small group of genera, but consider this sample to be, more generally, a sapindalean wood belonging to the Anacardiaceae/Burseraceae clade.

Laurinoxylon Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala, & De Franceschi 2008

Laurinoxylon deccanense Bande & Prakash 1980

Current taxonomic assessment: family unknown, not Lauraceae.

Examined: Holotype BSIP 35378; Locality: Ghughua, Dindori District, Madhya Pradesh. – Fig. 17H–J

Description in IAWA Feature Numbers: 2 5 7v 9 13 20? 21? 22? 24? 27? 30? 31? 32? 42 47 52? 53? 54? 62 66 69 78? 79? 91 92 97 98v 106 107 108 115.

Mehrotra (1989) remarked that this wood was not Lauraceae and suggested that it was close to *Callistemonoxylon deccanense*. The exclusively solitary vessels with a slight tendency to a radial/diagonal arrangement (Fig. 17H) and fibers with distinctly bordered pits are not features of the Lauraceae (Metcalf & Chalk 1950). These features occur in the Myrtaceae (Myrtales) as well as in other families, *e.g.*, Calophyllaceae, Chrysobalanaceae, Goupiaceae (Malpighiales). However, the preservation of this wood is poor and neither intervessel pits, albeit expected to be rare in a wood with solitary vessels, nor vessel-ray parenchyma pits were seen. These features are needed to determine its affinities with confidence.

Leeoxylon Prakash & Dayal 1963 [1964]

Leeoxylon multiseriatum Prakash & Dayal 1963 [1964]

Current taxonomic assessment: Vitaceae, similar to *Leea*.

Examined: Holotype BSIP 10392; Locality: Mahurzari, Nagpur District, Maharashtra.

Fig. 18A–D

Description in IAWA feature numbers: 2 5 13 20 21v 30? 31? 32? 41 47 53 56 61? 62? 65? 66? 75 78 99 102 105 109 110v 114.

The features that could be observed in this wood, especially scalariform pits (Fig. 18C) and tall, wide rays (Fig. 18B), with intermixed procumbent and square/upright cells, are consistent with features seen in present-day *Leea* as suggested by Prakash and Dayal (1963 [1964]).

The preservation of this wood sample is such that vessel-ray parenchyma pitting type, fiber pitting, and fiber type could not be observed. A search using the features:

Figure 18. — A–D: *Leeoxylon multiseriatum*, BSIP 10392. — A: Vessels in radial multiples, wood diffuse porous, TS. — B: Wide (>10-seriate) and tall (>1 mm) rays, TLS. — C: Scalariform intervessel pits, TLS. — D: Simple perforation plates, RLS. — E–I: *Lophopetalumoxylon indicum*, BSIP 35535. — E, F: Diffuse porous wood, vessels solitary and in radial multiples, often >4 vessels per multiple; banded axial parenchyma, TS. — G: Center of the stem, narrow vessels near pith, TS. — H: Small alternate intervessel pits, TLS. — I: Rays 1–2-seriate, mostly uniseriate, TLS. — Scale bars: 500 μ m in A, B, G; 200 μ m in E, I; 100 μ m in F; 50 μ m in C, D, H.

5p (diffuse porous wood), 9a (vessels not exclusively solitary), 13p (simple perforation plates), 20p (scalariform intervessel pits), 80a 83a 85a 86a (axial parenchyma not abundant), 99p 102p (wide and tall rays) with intermixed procumbent, square, and upright cells (109p) returns *Cereus* (Cactaceae), which lacks frequent radial multiples and has alternate and opposite pits in addition to scalariform ones; *Macropiper*, which has storied structure and has only wide and tall rays, and *Leea* – the only compelling look-alike of this fossil.

Vitaceous seeds, *Indovitis chitaleyae*, are also known from the Mahurzari site, and several other Deccan locations. The seeds correspond to the clades of *Vitis-Ampelocissus* or *Ampelopsis* and are morphologically quite distinct from those of extant *Leea* (Manchester *et al.* 2013). We do not have sufficient data to know whether *Indovitis* seeds were borne by a lianescent wood with anatomy comparable to that of *Vitis*, *Ampelocissus* or *Ampelopsis*, or perhaps was borne by the same arborescent plant that is known by its stem anatomy as *Leeoxylon*.

Lophopetalumoxylon Mehrotra, Prakash, & Bande 1983 [1984]

Lophopetalumoxylon indicum Mehrotra, Prakash, & Bande 1983 [1984]

Current taxonomic assessment: possibly Sapindales, unlikely Celastraceae.

Examined: Holotype BSIP 35535; Locality: Ghughua near Shahpura, Dindori District, Madhya Pradesh. – Fig. 18E–I

Description in IAWA Feature Numbers: 2 5 10v 13 22 24v 25 30? 31? 32? 42 46 47 52 53 61 63? 66 69 70v 78 79v 85 92 93 96v 97 106 107 109? 115 116v.

BSIP 35535 is a small axis with a pith. Preservation of this sample is poor, so we are not sure of the vessel-parenchyma pitting. We think it is probably similar to intervessel pitting because there were some faintly preserved regions in the radial section suggesting that they were similar.

According to Mehrotra *et al.* (1983 [1984]), “Important anatomical characters of the fossil wood, namely small to medium-sized vessels, apotracheal bands of parenchyma, fine homogeneous rays, and non-septate fibers strongly indicate its affinities with the family Celastraceae.” We did not observe rays composed exclusively of one cell type, but rather rays with procumbent and upright/square cells. We searched InsideWood for the aforementioned features, aside from ray cellular composition, by coding for absence of wide vessels, all axial parenchyma features except for banded parenchyma, and wide rays, and presence of non-septate fibers. These features occur in many more families than the Celastraceae, so we included these features: diffuse porous wood with vessels in multiples and randomly arranged (5p 6a 7a 8a 9a), simple perforation plates (13p), alternate intervessel pits that are not large (22p 27a), parenchyma not rare (75a), absence of canals, tubes, and cambial variants (127–130a, 132–133a). With the addition of these features, the list was narrowed, but still quite long. Families in the resulting list that we believe easily can be excluded are Annonaceae (axial parenchyma bands regularly spaced), Ebenaceae (axial parenchyma bands consistently narrower and regularly spaced), Euphorbiaceae (bands consistently narrower), Gentianaceae (rays composed of all upright cells), Himantandraceae (straight bands more widely spaced). This left representatives of the families Celastraceae (including *Lophopetalum*),

Irvingiaceae, Ixonanthaceae, Lecythidaceae, Fabaceae, Meliaceae, Ochnaceae, Picrodendraceae, Rubiaceae, Rutaceae, Sapindaceae, and Sapotaceae.

If we are correct in interpreting the vessel-parenchyma pits as similar to vessel-ray parenchyma pits (30p 31a 32a 33a) then Ixonanthaceae, Lecythidaceae, and Sapotaceae can be excluded. Although we do not think the rays are homocellular, adding that feature to the search still leaves Ochnaceae (Malpighiales), Fabaceae (Rosales), Meliaceae, Rutaceae, Sapindaceae (Sapindales) as well as Celastraceae (Celastrales).

Features of BSIP 35535 do indeed occur in *Lophopetalum* (Celastraceae), but are not unique to it. Parenchyma bands in Celastraceae generally are straighter and more consistent in thickness than in this Deccan wood. Mehrotra *et al.* (1983 [1984]) noted that the features of BSIP 35535 are seen in the Sapindaceae, as well as in the Celastraceae. Based on a review of images of the aforementioned families in InsideWood and in Illic's (1991) CSIRO atlas, we think it most probable that this wood belongs to the Sapindales.

Mallotoxylon Lakhanpal & Dayal 1962 [1964]

Mallotoxylon kerienne Lakhanpal & Dayal 1962 [1964]

Current taxonomic assessment: Euphorbiaceae, features of *Croton* and *Mallotus*.

Examined: Holotype BSIP 32735; Locality: Keria, Chhindwara District, Madhya Pradesh – Fig. 19A–F

Description in IAWA Feature Numbers: 2 5 13 22 23 26 27 30 31 41 47 53 61 66 69 76 77 78 97 102 105 108 115 116.

We concur with Lakhanpal and Dayal (1962 [1964]) that BSIP 32735 belongs to the Euphorbiaceae, but do not think it is a record for *Mallotus* (Acalyphoideae) because it has more features in common with *Croton* (Crotonoideae).

BSIP 32735 is a small axis with a pith. Preservation quality was variable, and in spite of our best efforts, we were unable to obtain photos that clearly show the diffuse to diffuse-in-aggregates axial parenchyma that we observed. Figure 19D shows vessel-ray parenchyma pits resembling intervessel pits, but there were some areas (not illustrated) with vessel-ray parenchyma pits with obviously reduced borders (IAWA feature 31). Procumbent ray cells are rare and some rays are composed exclusively of upright/square cells (Fig. 19E).

Initially, we searched for diffuse porous wood with randomly arranged vessels that are solitary and in short radial multiples (5p 6a 7a 8a 9a 11a), simple perforation plates (13p), alternate intervessel pits that are polygonal in outline and medium-large (22p 23p 24a 25a), vessel-ray parenchyma pits that are not horizontally or vertically elongated (32a), vessels not > 200 µm in diameter and not less than 5 per sq. mm or more than 40 per sq. mm (43a 46a 49a 50a), non-septate fibers with simple pits (61p 66p), axial parenchyma diffuse-in-aggregates and scanty paratracheal, not vasicentric or aliform or confluent or in broad bands (77p 78p 79a 80a 83a 85a), rays 1–3 cells wide and with more than 4 marginal rows of upright cells (97p 108p). This search returned only *Croton* (Euphorbiaceae). A less restrictive search (5p 6a 7a 8a 9a 11a 13p 22p 24a 25a 32a 43a 46a 49a 50a 61p 66p 77p 78p 79a 80a 83a 85a 101a 108p) returned *Croton* and two other genera of Euphorbiaceae (*Fahrenheitia*, *Sebastiania*)

and *Luehea* (Malvaceae), although the latter is easily excluded because it has storied structure and canals in its rays. Variations on the above searches gave results that also included *Croton* and *Mallotus*.

Mallotus has a higher proportion of uniseriate rays than BSIP 32735; many *Mallotus* species have exclusively uniseriate rays. Crystals can be of variable occurrence, but crystals in chambered upright ray cells appear to be a consistent feature of *Mallotus*.

We did not observe evidence of chambered ray cells in the fossil, however. Some Old World species of *Croton* (Crotonoideae) lack crystals (Ogata & Kalat 1997; Jangid & Gupta 2015). *Croton* is a large genus with more than 1300 species. New World species are more abundant and have received more attention than the 400–450 Old World species, of which ~150 are native to Madagascar (*e.g.*, Berry *et al.* 2005; Riina *et al.* 2010; Van Ee *et al.* 2011). Both *Mallotus* and *Croton* have species that act as pioneer species in disturbed tropical forests.

Oleoxylon deccanense Srivastava, Wheeler, Manchester, & Baas 2015 *ex* Trivedi & Srivastava 1981

Current taxonomic assessment: Oleaceae.

Examined: Holotype BSIP 40570; Locality: Jheria, near Mohgaon Kalan, Chhindwara District, Madhya Pradesh.

Description in IAWA Feature Numbers: 2 5 10 13 22 23v 26 30 41 42 48 49 60v 61 66 69 78 79 89? 92 97 106 107 115.

Because Trivedi and Srivastava (1981) did not validly publish this name, we recently did so (Srivastava *et al.* 2015).

Polyalthioxylon Bande 1973 emend. Mehrotra 1990 [1991]

Polyalthioxylon parapaniense Bande 1973

Current taxonomic assessment: Annonaceae, but generic affinities uncertain.

Examined: Holotype BSIP 36524; Locality: Parapani, Dindori District, Madhya Pradesh. – Fig. 19G–L

Description in IAWA Feature Numbers: 2 5 13 22 24 25 30 41v 42 47 52 53 61 66 68? 69 78 85v 86 88 93 98 102 104 106v 115 124.

The combination of minute–small intervessel pits (Fig. 19K), vessel-ray parenchyma pits similar to intervessel pits, regularly spaced narrow bands of axial parenchyma (Fig. 19G,H), tall rays often more than 4-seriate and tending to homocellular and with oil cells (Fig. 19J,K) is unique to the Annonaceae.

We further searched InsideWood for this combination of features: diffuse porous wood (5p), vessels not exclusively solitary, not in radial multiples of > 4 or in clusters (9a 10a 11a), simple perforation plates (13p), alternate intervessel pits that are < 7 µm across (equivalent to minute–small) (22p 26a 27a), vessel-ray parenchyma similar

←

Figure 19. — A–F: *Mallotoxylon keriense*, BSIP 32735. — A, B: Diffuse porous wood, vessels solitary and in short radial multiples, randomly arranged. — C: Crowded alternate intervessel pits, polygonal in outline, simple perforation plates in side view, TLS. — D: Vessel-ray parenchyma pits similar to intervessel pits, RLS. — E: Rays composed predominantly of upright and square cells, RLS. — F: Rays 1–3-seriate, multiseriate rays with uniseriate margins of > 4 cells, RLS. — G–L: *Polyalthioxylon parapaniense*, BSIP 36524. — G, H: Vessels solitary and in short radial multiples, axial parenchyma in narrow bands, wood diffuse porous, TS. — I: Simple perforation plates, RLS. — J: Rays predominantly > 6-seriate, ray cells with dark contents (oil or mucilage cells) common, TLS. — K: Detail of rays, small alternate intervessel pits, TLS. — L: Procumbent ray cells, RLS. — Scale bars: 200 µm in A, G, J; 100 µm in B, E, F, H, K; 50 µm in C, I, L; 20 µm in D.

to intervessel pits (30p), vessels averaging more than 50 μm in diameter with 5–20/sq.mm (40a 47p), fibers with simple pits and non-septate (61p 66p), axial parenchyma in narrow regularly spaced lines (86p 88p), rays more than 4-seriate, commonly >1 mm high and some homocellular rays (98p 102p 104p), oil cells in rays (124p).

Eight genera of Annonaceae had this combination of features, all Old World species, representing 3 of the 4 subfamilies and 3 of the 14 tribes of Chatrou *et al.* (2012) suggested. They are listed below grouped by the subfamilial and tribal classification of Chatrou *et al.* (2012), who acknowledged that additional work is needed to resolve relationships within the family.

Subfamily Ambavioideae: *Cyathocalyx*;

Subfamily Annonoideae: Tribe Duguetieae – *Duguetia*; Tribe Monodoreae – *Mono-dora*;

Subfamily Malmeoideae: Tribe Miliuseae – *Alphonsea*, *Meiogyne*, *Orophea*, *Polyalthia*, *Sageraea*.

We concur that this wood belongs to the Annonaceae, but additional work is needed to determine if its features are unique to any one subfamily or tribe or genus. Many genera in the Annonaceae have similar anatomy (*e.g.*, Ingle & Dadswell 1953; Koek-Noorman & Westra 2012), so it may not be possible to do other than say it has features unique to the Annonaceae. The family is also known from the locality of Nawargaon, based on a seed with characteristic ruminations (Bonde 1993).

***Sapindoxylon* Kräusel 1922 [Tertiary of Sumatra]**

***Sapindoxylon schleicheroides* Dayal 1964 [1965]**

Current taxonomic assessment: Sapindaceae.

Examined: Holotype BSIP 8224; Locality: Keria, near Mohgaon Kalan, Chhindwara, District, Madhya Pradesh. – Fig. 20 A–D

Description in IAWA Feature Numbers: 2 5 13 22 23 24 25 30 42 47 52 61 65 66 68 69 78 79v 96v 97 104 106 115 116.

We concur that this wood belongs to the Sapindaceae. It has features suggesting affinities with subfamily Sapindoideae, tribe Cupanieae. We searched for 5p 6a 7a 8a 9a 10a 11a (diffuse porous wood with randomly arranged vessels that are solitary and in short radial multiples), 13p (simple perforation plates), 22p 26a 27a (alternate intervessel pits that are <7 μm), 30p (vessel-ray parenchyma pits similar to intervessel pits), 42p 47p (mean tangential diameter between 100–200 μm , 5–20 vessels/sq.mm.), 61p 66p (non-septate fibers with simple pits), 78p 80a 83a 85a 86 (axial parenchyma

Figure 20. — A–D: *Sapindoxylon schleicheroides*, BSIP 8224. — A: Vessels solitary and in radial multiples; axial parenchyma rare, TS. — B: Crowded alternate intervessel pits, TLS. — C: Simple perforation plates, vessel-ray parenchyma pits similar to intervessel pits, procumbent ray cells, TLS. — D: Predominantly uniseriate rays, TLS. — E–J: *Simarouboxylon indicum*, BSIP 5585. — E, F: Diffuse porous wood, vessels solitary and in radial multiples of 2, winged aliform-confluent axial parenchyma, forming narrow bands, TS. — G: Crowded alternate intervessel pits, polygonal in outline, TLS. — H: Vessel-axial parenchyma pits (arrows), RLS. — I: Rays mostly 3–4-seriate, ray cells polygonal outline and uniform in size and shape, TLS. — J: Septate fibers, TLS. — Scale bars: 200 μm in A, E; 100 μm in D, F, I, J; 50 μm in C, H; 20 μm in B, G.

scanty paratracheal and not aliform to confluent or in bands), 98a 99a (rays less than 4-seriate), 104p 116p 111a (homocellular rays >12/mm, tile cells absent). In some regions rays appeared partially biseriata, but that may have been because the tangential section was slightly oblique. We observed mostly non-septate fibers in BSIP 8224; there are some septate fibers as well (Fig. 20B,D) and Dayal (1964 [1965]) described the fibers as septate.

This combination of features returned 20 genera of the Sapindaceae, but not *Schleichera*, a genus occurring today in Central South Asia and Indochina. The specific epithet dates to a time when it was expected that the Deccan woods would have affinities with present-day Indian plants. Data available on *Schleichera* indicate it differs from this fossil in having larger intervessel pits; also, it has prismatic crystals in chambered axial parenchyma cells (Détienne, unpublished data for Indochinese woods from InsideWood; Pearson & Brown 1932). Of those 20 genera, one belongs to subfamily Dodonaeoideae (*Erythrophysa*) which differs in having marginal parenchyma and crystals; the rest to the subfamily Sapindoideae and to five of its tribes as recognized by Muller and Leenhouts (1976): 1) Tribe Lepisantheae (*Glennia*, *Placodiscus*), both differ in having marginal parenchyma; 2) Tribe Sapindeae (*Toulisia*), differing in not having predominantly uniseriate rays, and having diffuse and marginal parenchyma; 3) Tribe Schleichereae (*Begonia*, *Camptolepis*, *Tinopsis*), a strictly African group, noted as having wood anatomy resembling the Tribe Cupanieae; 4) Tribe Cupanieae (*Blighia*, *Cupania*, *Cupaniopsis*, *Elatostachys*, *Guioa*, *Jagera*, *Matayba*, *Mischocarpus*, *Neotina*, *Paviesia*, *Tina*, *Vouarana*), Klaassen (1999, p.165) noted that this tribe was wood anatomically fairly homogeneous, and that “most of the genera cannot be distinguished from one another”; 5) Tribe Nephelieae (*Dimocarpus*, *Litchi*, *Xerospermum*); these three genera are “wood anatomically almost identical” and they differ from BSIP 8224 in having many crystals and very thick-walled fibers. It is possible that this wood has affinities with Tribe Cupanieae.

***Simarouboxylon* Shallom 1960b**

cf. *Simarouboxylon indicum* Shallom 1960b; revised by Prakash 1962 [1964]

Current taxonomic assessment: possibly Simaroubaceae.

Examined: BSIP 5585 (not holotype), sample with pith; Locality: Mohgaon Kalan, Chhindwara District, Madhya Pradesh – Fig. 20 E–J

Description in IAWA Feature Numbers: 2 5 13 22 23 26 31 32v 42 47 52 56v 61 65? 66 68 69 80 82 83 86 93 97 98v 104 115.

The sample we examined is one that Prakash (1962 [1964]) assigned to *Simarouboxylon* Shallom. The distinctive features of the sample – winged aliform parenchyma, with the wings being narrow and greatly extended tangentially, sometimes confluent and forming narrow tangential bands (Fig. 20 E,F); few vessel multiples; homocellular rays with the cells polygonal in outline as viewed in tangential section (Fig. 20 I,J); uniseriate rays rare, thin-walled fibers – are features of *Simarouboxylon* and *Simarouba*. However, we observed vessel-parenchyma pits with reduced borders (Fig. 20 H). Thus, this sample presents the same problems as did sample BSIP 5568 of *Ailanthoxylon indicum*. Namely, its combination of vessel, ray, and axial parenchyma patterns is distinctive and similar to Simaroubaceae, but its vessel-parenchyma pits differ from those of present-day *Simarouba* and the Simaroubaceae.

Shallom's (1960b) description mentioned “vessel ray pitting is similar to intervessel pitting” and so we consider her sample to have a combination of features unique to Simaroubaceae.

***Sonneratioxylon* Hofmann 1952 [Oligocene of Austria]**

The first use of the name *Sonneratioxylon* was for an Oligocene wood from Austria (Hofmann 1952). No generic diagnosis was explicitly provided, but a specific diagnosis for *Sonneratioxylon prambachense*. The specific diagnosis was brief, mentioning diffuse porous wood, vessels in short multiples, simple perforation plates, vessel walls covered with pits, rare axial parenchyma, homocellular uniseriate rays, and very thick-walled fibers. Hofmann's description fits members of the Sapindaceae better than *Sonneratia* because very thick-walled fibers are not a characteristic of *Sonneratia*, but are of many Sapindaceae with the aforementioned features of Hofmann's diagnosis. Subsequently, Kramer (1974) provided a generic diagnosis of *Sonneratioxylon*, but this diagnosis seems to have been done without reference to Hofmann's sample and was done to accommodate the Tertiary Southeast Asian woods Kramer was studying and that he thought resembled *Sonneratia*.

Deccan woods described as *Sonneratioxylon* include:

Sonneratioxylon caeseolarioides Shete & Kulkarni 1982

Sonneratioxylon duabangoides Shallom 1963a emend. Chitaley 1977 [1978]

Sonneratioxylon intertrappeum Biradar & Mahabale 1973 [1975]

Sonneratioxylon nawargaoensis Bande & Prakash 1979 [1984]

Sonneratioxylon preapetalum Awasthi 1968 [1969], holotype from the Mio-Pliocene Cuddalore Series.

When Mehrotra (1988) described an occurrence of *S. preapetalum* from Ghughua, he compared that wood to *S. intertrappeum* Biradar & Mahabale (1973 [1975]) from Mohgaon Kalan, Chhindwara District, Madhya Pradesh, and to *S. caseolarioides* Shete & Kulkarni (1982) and *S. nawargaoense* Bande & Prakash (1979 [1984]), which are both from the Deccan Intertrappean beds of Nawargaon, Wardla District, Maharashtra. He concluded that these four species were "quite similar to each other and differ only in some minor characters" and all should be considered as *Sonneratioxylon preapetalum*. We were only able to examine two samples of Deccan *Sonneratioxylon*. It is understandable why these samples were considered related to extant *Sonneratia* (Sonneratiaceae / Lythraceae) because they have rare axial parenchyma and uniseriate rays. Investigators were also influenced by the co-occurrence of this wood type with fruits of *Enigmocarpon* and flowers of *Sahnianthus* at Mohgaon Kalan, which were already considered to have lythraceous affinities somewhat close to *Sonneratia* (e.g., Shallom 1963a; Chitaley 1977 [1978]). However, the details we observed in the specimens BSIP 5930 and BSIP 35941 from Nawargaon and Ghughua, respectively, indicate that neither can be considered a reliable record of *Sonneratia* (see discussion below).

BSIP 5930 – Locality: Nawargaon, Wardha District, Maharashtra, described by Bande & Prakash 1979 [1984] as ***Sonneratioxylon nawargaoense***. – Fig. 21 A–C

Current taxonomic assessment: family unknown.

Description of BSIP 5930 in IAWA Feature Numbers: 2 5 13 22 23 26 30? 31? 32? 42 46 47 52 53 61 66 68 69 75 78 93 96 97v 104? 105? 109? 106? 115.

The preservation of this specimen is poor. We were not able to observe vessel-ray parenchyma pits or be sure of ray cellular composition. The combination of diffuse

porosity, simple perforation plates, alternate intervessel pits, mean vessel diameter 100–200 μm and vessel density less than 40/sq.mm, rare axial parenchyma and narrow rays, mostly uniseriate, is not unique to *Sonneratia* (Lythraceae), but also occurs in the Salicaceae and Sapindaceae. Vessels are wider and fewer, and vessel multiples are less common in this sample than they are in BSIP 35941 (Fig. 21A vs Fig. 21D). It is possible that such differences between these samples might be due to ontogeny. Nonetheless, we think that the information available is insufficient to state that *S. nawargaoense* is synonymous with *S. preapetalum*.

BSIP 35941 – Locality: Ghughua, near Shahpura, Dindori District described by Mehrotra (1988) as *Sonneratioxylon preapetalum*. – Fig. 21D–I

Figure 21. — A–C: *Sonneratioxylon nawargaoense*, BSIP 5930. — A: Diffuse porous wood, vessels solitary and occasionally in short multiples, TS. — B: Simple perforation plates, crowded alternate intervessel pits, TLS. — C: Uniseriate rays, TLS. — D–I: *Sonneratioxylon preapetalum*, BSIP 35941. — D: Diffuse porous wood, vessels solitary and in radial multiples, TS. — E: Crowded alternate intervessel pits, TLS. — F: Simple perforation plates, vessel-ray parenchyma pits, RLS. — G: Uniseriate rays, simple perforation plates, TLS. — H, I: Ray cellular composition. — H: Procumbent, square, and upright cells, RLS. — I: Mostly upright and square cells, RLS. — Scale bars: 200 μm in A, D; 100 μm in C, G, H; 50 μm in B, E, F, I.

Current taxonomic assessment: family unknown.

Description of BSIP 35941 in IAWA Feature Numbers: 2 5 13 21? 22? 25v 26 30 31 32 33 41 47 53 61 63? 66 69 75 78 93 96 105 109 115.

The type of this species is Mio-Pliocene (Awasthi 1968 [1969]), and we did not study its holotype. BSIP 35941 is a narrow axis with pith. The pith did not have the internal phloem characteristic of Myrtalean families. The vessel-ray parenchyma pits of extant *Sonneratia alba*, *S. apetala*, *S. caseolaris* are much larger than the intervessel pits and have much reduced borders, differing from BSIP 35941 (Fig. 21F). The rays in extant *Sonneratia* are composed predominantly of procumbent cells, unlike this fossil with its predominantly square/upright cells. The Mio-Pliocene holotype may represent *Sonneratia*, but this sample does not. Its combination of wood anatomical features occurs in some Melastomataceae, another myrtalean family with internal phloem. Again, this leaves the affinities of this sample unresolved. Affinities of the wood treated as *Sonneratioxylon duabangoides* Shallom 1963a emend. Chitale 1977 [1978] from Mohgaon Kalan, need to be reconsidered in light of these findings. We did not have access to its holotype.

Sterculinium Guleria 1982 [1983]

Sterculinium deccanensis (Lakhanpal, Prakash, & Bande) Guleria 1982 [1983]

Synonym: *Sterculioxylon deccanense* Lakhanpal, Prakash, & Bande 1976 [1978]

Conservative taxonomic assessment: Malvaceae, probably Sterculioideae.

Examined: Holotype BSIP 1505; Locality: Mohgaon, Mandla District, Madhya Pradesh. – Fig. 22A–F

Description in IAWA Feature Numbers: 2 5 13 22 25 30 42 47 52 53 61 66 76 77 79 98 99v 102 103v 106 107 108v 110 115 120v.

Lakhanpal *et al.* (1976 [1978]) used the features “diffuse to diffuse-in-aggregates parenchyma with a tendency towards storied structure, broad xylem rays separated by a number of narrow rays with sheath cells and thick-walled non-septate fibers” to conclude that BSIP 1505 had affinities with the extant genus *Sterculia*. We searched InsideWood for those features (76p, 77p, 120p - coded for presence of storied axial parenchyma, 98p, 103p - rays of two distinct sizes, 110p, 66p, 69p) as well as diffuse porous wood with randomly arranged vessels that are solitary and in short multiples (5p 6a 7a 8a 9a), simple perforation plates (13p), and alternate intervessel pits that are not >10 µm across (22p 27a). This particular combination of characters returned only Malvaceae, including one record for *Sterculia*, as well as *Chiranthodendron* (Bombacaceae), *Dombeya* (Dombeyoideae), *Apeiba*, *Goethalsia*, *Grewia* (Grewioideae), *Brachychiton*, and *Tarrietia* (Sterculioideae). However, present-day *Sterculia* species do not appear to be a good match for this wood because they have more axial parenchyma, storied structure and two distinct size classes of rays are both considerably better developed, and usually there are vessel-parenchyma pits with reduced borders—a feature we did not observe. We also performed a search without 120p because there is only a tendency to storied parenchyma and added in vessel-parenchyma pits similar to intervessel pits (30p), simple fiber pits (61p 62a), and absence of tile cells (111a). This search also yielded only Malvaceae, including *Commersonia* (Byttnerioideae), *Dombeya* (Dombeyoideae), *Apeiba* (unlikely because of the broad bands of unlignified

parenchyma), *Glyphaea*, *Goethalsia*, *Grewia* (Grewioideae), *Brachychiton*, *Tarrietia* (Sterculioideae), but not *Sterculia*.

Hence, the combination of features that occurs in BSIP 1505 indicates placement somewhere in the Malvaceae, but does not confirm close affinities with the genus *Sterculia*. Based on comparisons with samples and images of *Brachychiton* and *Tarrietia*, it is probable that this sample represents Sterculioideae because of similarities in vessel and axial parenchyma characteristics with some species in those genera.

Sterculinium shahpurensis (Bande & Prakash 1980) Guleria 1982 [1983]

Synonym: *Sterculioxylon shahpurens* Bande & Prakash 1980

Current taxonomic assessment: Malvaceae, Sterculioideae; generic placement uncertain.

Examined: Holotype BSIP 35368; Locality: Ghughua, near Shahpura, Dindori District. – Fig. 22 G–L

Description in IAWA Feature Numbers: 2 5 10v 13 22 26 30 31? 42 43 46 47 52? 53? 54? 61? 65? 66 69 70 76 77 78 79 86 92 93 99 102 103 107 108 110 114.

The first combination of features we used to search InsideWood yielded only species of *Sterculia*. However, present-day *Sterculia* differs in having storied axial parenchyma, although not always well-defined, and a higher proportion of solitary vessels. The criteria used in that first search were: 5p 6a 7a 8a 9a (diffuse porous wood without any distinctive vessel patterns and not exclusively solitary vessels), 13p 14a (exclusively simple perforation plates), 22p 27a (alternate intervessel pits that are < 10 µm across), 30p (vessel-ray parenchyma pits similar to intervessel pits), 66p 68a (non-septate fibers not very thin-walled), 77p 79p 85a (axial parenchyma diffuse-in-aggregates, vasicentric, and not in bands > 3 cells wide), 92p (axial parenchyma strands of 3–4 cells), 99p 102p 110p 114p (rays commonly > 10-seriate and > 1 mm high with sheath cells, and fewer than 4/mm).

Another search was for 5p 9a (diffuse porous wood without exclusively solitary vessels), 13p (simple perforation plates), 22p 24a 27a (alternate intervessel pit not minute or large), 30p (vessel-ray parenchyma pits similar to intervessel pits), 40a 49a 50a (mean tangential diameter of vessels > 50 µm and fewer than 40 vessels per sq. mm), 66p (non-septate fibers), 77p (diffuse -in-aggregates axial parenchyma), 99p 102p 103p 110p (rays commonly > 10-seriate and > 1 mm high, of two distinct sizes, and with sheath cells). This search yielded Anisophylleaceae (*Anisophyllea*, *Combretocarpus*), Malvaceae / Sterculioideae (*Brachychiton*, *Pterocymbium*, *Scaphium*), and Rhizophoraceae (*Carallia*). *Carallia* can be eliminated because, in addition to vessel-ray parenchyma pits similar to intervessel pits, it has some pits with reduced borders and some unilaterally compound ones. The genera of Rhizophoraceae and Anisophyllaceae retrieved in our search have fibers with distinctly bordered pits and obvious parenchyma bands that are typically > 3 cells broad. The genera of Malvaceae recovered from this search also have storied structure, unlike this fossil.

←

Figure 22. — A–F: *Sterculinium deccanensis*, BSIP 1505. — A: Diffuse porous wood, vessels solitary and in short multiples, axial parenchyma diffuse, diffuse-in-aggregates, and vasicentric, TS. — B: Small alternate intervessel pits, TLS. — C: Vessel-axial parenchyma pits similar to intervessel pits, RLS. — D: Ray cellular composition, simple perforation plate (arrow). — E: Rays tending to two size classes, TLS. — F: Wide rays with sheath cells, series of vessel elements with simple perforation plates, TLS. — G–L: *Sterculinium shahpurensis*, BSIP 35368. — G: Vessels solitary and in radial multiples, often with > 4 vessels; axial parenchyma diffuse-in-aggregates to narrow lines; thick-walled fibers; wood diffuse porous, TS. — H: Vessel-axial parenchyma pits similar to intervessel pits, TLS. — I: Crowded alternate intervessel pits, sheath cells at edge of ray, TLS. — J: Rays of two size classes, TLS. — K: Simple perforation plates in side view, wide ray with cells of variable sizes, sheath cells, TLS. — L: Procumbent ray cells, RLS. — Scale bars: 200 µm in A, E, G, J; 100 µm in D, F, K, L; 50 µm in H, I; 20 µm in B, C.

Thus, this wood's features suggest affinities with the pantropical Sterculioideae, and at 67–64 Ma old, it is considerably older than the ages suggested for the Sterculioideae node of the Malvaceae phylogeny, *e.g.*, (34–)31, 28(–25) Ma (Wikström *et al.* 2001) or (36–)29, 27(–20) Ma (Stevens 2001-onwards).

Tetrameleoxylon Lakhanpal & Verma 1965 [1966]

Tetrameleoxylon prenudiflora Lakhanpal & Verma 1965 [1966]

Current taxonomic assessment: possibly *Tetrameles*, but also similar to Hernandiaceae.

Examined: Holotype BSIP 33076; Locality: Mohgaon Kalan, Chhindwara District,

Madhya Pradesh. – Fig. 23 A–G

Description in IAWA Feature Numbers: 2 5 13 22 23 26 27 31 43 46 52 61 66 68 69 79 80? 82? 83? 86? 91 92 93 98 104 106v 114.

Because of the thin-walled fibers, it is difficult to determine with certainty the axial parenchyma distribution in transverse section (Fig. 23 A,B). Longitudinal sections indicate paratracheal parenchyma is present (Fig. 23 C–E). Uniseriate rays are absent (not a feature of the IAWA Hardwood List) and there is a tendency for the imperforate elements to be storied (Fig. 23 C,D). Initially we searched using: 5p (diffuse porous wood), 6a 7a 8a 9a 10a 11a (randomly arranged vessels that are solitary and in short radial multiples), 13p (simple perforation plates), 22p 24a 25a (alternate pits that are >7 µm across), 30a (vessel-ray parenchyma pits different from intervessel pits), 40a 41a 48a 49a 50a (vessels not narrow and not numerous), 61p 70a (fibers with simple pits and not thick-walled), 79p (axial parenchyma vasicentric), 98p 103a 108a 109a 111a (multiseriate rays 4–10 cells wide, not of two size classes, not markedly heterocellular and lacking tile cells), 116a 118a 119a (rays not more than 12/mm and non-storied), 124a 125a 126a 127a 128a 129a 130a 133a 134a 135a (oil cells, canals, and cambial variants absent).

This search returned Cannabaceae, Hernandiaceae, Lauraceae, Lecythidaceae, Moraceae, Myrtaceae, Tetramelaceae, and Urticaceae. A review of images of tangential sections of these families in InsideWood and in Illic's (1991) CSIRO atlas indicates that Myrtaceae always have some uniseriate rays, while in the other families there are some species with rare to absent uniseriate rays. We conducted other searches by adding these features: thin-walled fibers (68p), which yielded Hernandiaceae, Lauraceae,

→

Figure 23. — A–G: *Tetrameleoxylon prenudiflora*, BSIP 33076. — A, B: Diffuse porous wood, solitary vessels and occasional radial multiples of two, thin-walled fibers, TS. — C: Multiseriate rays, imperforate elements tending to storied structure, series of vessel elements with simple perforations and alternate intervessel pits, TLS. — D: Crowded alternate intervessel pits, polygonal in outline, TLS. — E: Vessel-parenchyma pits with reduced borders, RLS. — F: Simple perforation plate, ray cellular structure, RLS. — G: Wider rays to 6-seriate, uniseriate rays absent. — H–M: "*Tristania confertoides*", BSIP 35883. — H: Diffuse porous wood, vessels exclusively solitary, TS. — I: Simple perforation plates in side view, oblique section. — J: Vessel-ray parenchyma pits with reduced borders, circular in outline, RLS. — K: Vessel-vasicentric tracheid pits, TLS. — L: Uniseriate rays, TLS. — M: Possible chambered crystalliferous axial parenchyma cells to right of CCs, RLS. — Scale bars: 200 µm in A, G, H; 100 µm in B, C, F, I; 50 µm in K, L, M; 20 µm in D, E, J.

Moraceae, Tetramelaceae, and Urticaceae; rays fewer than 4/mm (114p), which yielded Hernandiaceae, Moraceae, and Tetramelaceae.

A comparison of BSIP 33076 with the above-listed families indicated greatest similarities of *Tetrameleoxylon prenudiflora* with some species of *Hernandia* and *Gyrocarpus* (Hernandiaceae, order Laurales) and with *Tetrameles* (Tetramelaceae, order Cucurbitales). The vessel-ray pitting in Tetramelaceae is more elongated horizontally or vertically than the pitting in BSIP 33076. However, the ray sizes and ray

spacing of BSIP 33076 resemble *Tetrameles* more than the Hernandiaceae. In general, vessel-parenchyma pitting is considered of greater systematic value than ray size and spacing, which are features known to vary. We did not observe any oil cells in BSIP 33076, a feature that would confirm affinities with the Hernandiaceae, but oil cells are not present in all samples of *Gyrocarpus* and *Hernandia*. Stevens (2011- onwards) cited molecular based age estimates for crown-group Hernandiaceae as 120–64.4 Ma, none was given for the crown-group of Tetramelaceae, but an estimate of (33–)26(–19) Ma was given for divergence of the two genera in Tetramelaceae.

“*Tristania*” *confertoides* Bande, Mehrotra, & Prakash 1986 [1987]

Current taxonomic assessment: Myrtaceae, subfamily Myrtoideae.

Examined: Holotype BSIP 35883; Locality: Umaria near Ghughua, Dindori District, Madhya Pradesh. – Fig. 23 H–M

Description in IAWA Feature Numbers: 2 5 7v 9 13 22 23 27 31 42 46 47 53 56 60 61? 62? 76 96 104 115 136? 142?.

This sample’s features are consistent with its assignment to the Myrtaceae. A tendency for the vessels to be arranged in a radial-diagonal pattern as is seen in BSIP 35882 (Fig. 23 H) is reported for species of *Eucalyptus* and *Lophostemon*. Crystal-liferous chambered axial parenchyma (Fig. 23 M) has not been reported for present-day *Lophostemon* (syn. *Tristania*), but has been for *Eucalyptus*. BSIP 35883 has a combination of features unique to the Myrtaceae, but is not a perfect match for either of these Australian genera.

We searched InsideWood using: diffuse porous (5p), vessels exclusively solitary (9p), alternate intervessel pitting not small–minute (22p 24a 25a), vessel-ray parenchyma pits with reduced borders and circular (31p), vessels with mean tangential diameter 100–200 µm and with fewer than 20 vessels per sq. mm (42p 48a 49a), vasicentric tracheids (60p), axial parenchyma diffuse and not abundant paratracheal or banded (76p 79a 80a 81a 82a 83a 85a 86a), uniseriate rays homocellular (96p 104p). This search returned only *Eucalyptus* species and *Lophostemon confertus* (synonym *Tristania conferta*).

“*Turraeanthus*” *deccanensis* Awasthi, Mehrotra, & Srivastava 1995 [1996]

Current taxonomic assessment: family and order uncertain, but not Meliaceae.

Examined: Holotype BSIP 36710; Locality: Ghughua, near Shahpura, Dindori District, Madhya Pradesh. – Fig. 24 A–D

Description in IAWA Feature Numbers: 2 5 13 22 23 26 27v 31 42 46 47 52? 53? 61? 65? 66 69 75? 78? 92? 93? 97 104 106 114 115.

BSIP 36710 appears to have vessel-ray parenchyma pits with reduced borders, a feature that does not occur in the Meliaceae. Moreover, the intervessel pits are larger (medium–large) than is typical of the Meliaceae (minute–small). The preservation of this sample is not good and whether additional work will allow establishing its relationship is questionable. We searched for the features we observed: diffuse porous wood with randomly arranged vessels that are solitary and in short multiples (5p 6a 7a 8a 9a), simple perforation plates (13p), medium-sized alternate intervessel pits (22p 26p), vessel-ray parenchyma pits with reduced borders (31p), fewer than 20 vessels/sq. mm

Figure 24. — A–D: *“Turraeanthus” deccanensis*, BSIP 36710. — A: Diffuse porous wood, vessels solitary and in radial multiples of 2–3. TS. — B: Crowded alternate intervessel pits, TLS. — C: Vessel elements with simple perforation plates, procumbent ray cells, RLS. — D: Rays mostly 2–3-seriate, RLS. — E–I: *“Walsura” deccanensis*, BSIP 35939. — E, F: Diffuse porous, vessels solitary and in radial multiples, banded axial parenchyma, thick-walled fibers, TS. — G: Rays mostly 2-seriate, TLS. — H: Simple perforation plates, RLS. — I: Vessel-ray parenchyma pits similar to intervessel pits, RLS. — Scale bars: 500 µm in A; 200 µm in C, D, E; 100 µm in F, G; 50 µm in B, H, I.

(48a 49a 50a), rays 1–3-seriate without a high proportion of upright cells (97p 105a 108a). This combination of features occurs in over 250 records, including members of the Anacardiaceae, Burseraceae (Sapindales), Cannabaceae, Moraceae (Rosales), Lamiaceae, Verbenaceae (Lamiales).

“Walsura” deccanensis Mehrotra 1989

Current taxonomic assessment: possibly Meliaceae.

Examined: Holotype BSIP 35939; Locality: Ghughua, Dindori District, Madhya Pradesh. — Fig. 24E–I

Description in IAWA Feature Numbers: 2 5 13 22 23 24 25 30 42 47 52 61 66 69 70 78 79 85 86v 92 93 97 104v 106v 116.

This sample shares features with *Walsura* and other meliaceous genera, but its combination of features also occurs in caesalpinoid legumes. There are no convincing reports of legumes from the Deccan Intertrappean Beds; we determined that *Aeschynomene tertiara*, which Prakash (1962 [1963]) reported from Mahurzari, is not a legume (this article; Baas *et al.* in prep.).

We searched for 5p (diffuse porous wood), 6a 7a 8a 9a 10a 11a (vessels randomly arranged and solitary and in short radial multiples), 13p 14a (perforation plates exclusively simple), 22p 26a 27a (alternate intervessel pits that are minute to small), 30p (vessel-ray parenchyma pits similar to intervessel pits), 42p 47p (mean vessel diameter 100–200 μm and 5–20 vessels/sq. mm), 54a (vessel elements less than 800 μm long), 61p 66p 69p (non-septate fibers with simple to minutely bordered pits that are thick-walled), 85p (axial parenchyma bands > 3 cells wide), 90a 94a (fusiform parenchyma and parenchyma strands of 8 or more both absent), 97p 105a 108a 109a 116p (rays 1–3-seriate, not composed of all upright/square cells, with fewer than 4 rows of marginal ray cells, procumbent/upright/square cells not intermixed throughout the rays, ≥ 12 rays/mm), 118a 119a 120a (rays and parenchyma non-storied). Families having species with this combination of features are: Fabaceae (5 genera of Caesalpinioideae, *Neochevalierodendron*, *Plagiosiphon*, *Scorodophloeus*, *Storckia*, *Zenkerella*), Meliaceae (*Dysoxylum*, *Guarea*, *Walsura*), Oleaceae (*Chionanthus*, parenchyma bands not as abundant and often < 3-seriate, marginal ray cells markedly different from the body cells), Sapindaceae (*Majidea*, with predominantly uniseriate rays).

DISCUSSION

We begin this discussion by summarizing our findings on the affinities of the Deccan woods we examined and whether their anatomical features are consistent with the names originally assigned to them. We use the APG-IV classification for this summary. Within this classification, we list and discuss: 1) woods with anatomy that occurs in the genus, family or order originally assigned, and 2) woods whose affinities are unresolved or ambiguous. Finally, we analyze certain functional wood anatomical traits in the Deccan woods and compare their incidences with those of other fossil and modern woody assemblages. We briefly reflect on the status of wood anatomical evolution on the Indian plate during the latest Cretaceous–earliest Paleocene, and attempt to contribute to the reconstruction of Deccan paleoecology on the basis of current ecological trends in wood anatomy.

Comments on affinities

Deccan woods with features consistent with assigned name (genus, family, or order)

Magnoliids

Magnoliales

Annonaceae – *Polyalthioxylon parapaniense*. Pollen, seeds, and a flower indicate that Annonaceae were present in the Late Cretaceous of Africa, Asia, and South America (Friis *et al.* 2011). This Deccan wood extends the Cretaceous record for the family to another Gondwanan region.

Rosids

Vitales

Vitaceae – *Leeoxylon multiseriatum* represents the Leeoideae. Seeds of *Indovitis chitaleyae* occur at several Deccan locations and represent the Vitoideae, particularly the *Vitis-Ampelocissus* or *Ampelopsis* clades (Manchester et al. 2013). Estimates of the age of crown group Leeoideae are (86.2–)72.1(–65.0) Ma years; estimates of the age of crown group Vitoideae are 87 Ma to 91 Ma (summaries in Stevens 2001-onwards).

Malpighiales

Achariaceae – *Hydnocarpoxylon indicum*.

Phyllanthaceae – *Bischofinium deccanii*, similar to *Bridelia*.

Euphorbiaceae – *Mallotoxylon keriense*, features seen in *Mallotus* and *Croton*.

According to Friis et al. (2011), flowers of *Paleoclusia* (Clusiaceae) are the only secure Cretaceous record of the order. The features of these three species of Deccan woods are unique to the Malpighiales and represent additional Cretaceous-Paleocene records for the order. Stevens (2001-onwards) remarked that the Malpighiales can be divided into three main clades. These woods represent clade 1, the Salicaceae-Euphorbiaceae, while the Cretaceous *Paleoclusia* flowers represent clade 2, the Rhizophoraceae-Clusiaceae.

In addition to the woods listed above that we consider to have features unique to a single malpighialean family, there are other woods that have features found in more than one malpighialean family. These are:

Bridelioxylon krausellii – features of Achariaceae and Phyllanthaceae.

Glochidioxylon sahnii – features of Achariaceae and Phyllanthaceae.

Homalioxylon mandalense – features of Euphorbiaceae and Phyllanthaceae.

Rosales

Moraceae – *Artocarpoxylon deccanense*, tribe Castilleae.

Over the years, many fossil leaves have been assigned to the Moraceae, particularly to *Ficus*. Closer examination of most of those leaves has shown that they are not Moraceae. However, Friis et al. (2011) suggest that, although they have not been restudied since they were first described by Nathorst in 1890, leaves and reproductive structures from the Late Cretaceous of Greenland “appear to be correctly assigned” to the Moraceae. The combination of features of *Artocarpoxylon* is unique to the Moraceae, providing independent evidence for the Late Cretaceous/Paleocene occurrence of this family and most probably the tribe Castilleae, not the tribe Artocarpeae of Zerega et al. (2005) as suggested by the generic name. These two geographically distant earliest occurrences of the family raise additional questions about where, when, and how the Moraceae diversified.

Malvids, Eurosids II

Myrtales

Myrtaceae, subfamily Myrtoideae – Three species of Deccan woods have features unique to the Myrtaceae: *Calistemonoxylon deccanense* with features found in

Eucalyptus, *Lophostemon*, *Syncarpia*, and *Tristania*; “*Eucalyptus*” *dharmendra* with features found in *Eucalyptus* and *Lophostemon*; “*Tristania*” *confertoides* with features found in *Eucalyptus* and *Lophostemon*.

Berger *et al.* (2016) suggested that the Myrtales originated in west Gondwana (South America, Africa), rather than in east Gondwana (Antarctica, Australia, India, Madagascar). Moreover, their analyses supported a “K-Pg boundary origin ~67 Mya for subfamily Myrtoideae in the part of Gondwana that broke off to form Australia.” The occurrence of Indian fossil woods with characteristics of the Myrtoideae suggests that this scenario might need modification. Thornhill and Macphail (2012) reviewed the record of fossil myrtaceous pollen assigned to *Myrtaceidites* and noted the Late Cretaceous occurrence of *Myrtaceidites* from localities on Antarctica, Australia, India, and South America. These Deccan woods are noteworthy as the oldest known macrofossils of the family. Bande *et al.* (1988) and Mehrotra (2003) noted that the occurrence of Australian taxa in the Maastrichtian–Danian of India raises questions about an out-of-India origin for these taxa.

Sapindales

We consider three Deccan woods to belong to the Sapindales, although their features are not unique to a single family.

Burseroxylon preserratum – features seen in Anacardiaceae, Burseraceae, Kirkiaceae.

Heyneoxylon tertiarum – features seen in Meliaceae and Rutaceae.

Lanneoxylon grandiosum – features seen in Anacardiaceae and Burseraceae.

Anacardiaceae – *Anacardioxylon semecarpoides* (features seen in 7 anacardiaceous genera, including *Semecarpus*); *Dracontomeloxylon palaeomangiferum* (features seen in 4 genera, including *Dracontomelon*).

Friis *et al.* (2011) commented that the Cretaceous record for Sapindales is relatively sparse. The Anacardiaceae has an extensive Early Tertiary record, but all Cretaceous leaf and pollen records are uncertain and need reevaluation (Collinson *et al.* 1993). These two Deccan woods with combinations of features found in the Anacardiaceae represent the oldest known occurrences of woods with features diagnostic of the family and subfamily Anacardiaceae. Intrafamilial relationships are said to need additional work (Stevens 2001-onwards). Estimates of the ages of crown-group Anacardiaceae range from 54.8 Ma to 97 Ma (summarized in Stevens 2001-onwards).

Simaroubaceae – There are two simaroubaceous genera, *Ailanthoxylon* and *Simarouboxylon*. *Ailanthoxylon indicum* is similar to *Ailanthus* in all features except vessel-ray parenchyma pitting. Although we were not able to examine slides of it, the description and illustrations of *Ailanthoxylon mahurzarii* Shallom (1959a [1961]), also a Deccan wood, show that its combination of features, including vessel-ray parenchyma pit type, is unique to *Ailanthus*. The sample of *Simarouboxylon indicum* we examined also had vessel-parenchyma pits different from the Simaroubaceae. However, Shallom (1959b) described the holotype as having vessel-ray parenchyma pits similar to intervessel pits as characterizes present-day *Simarouba*.

Usually the type of vessel-ray parenchyma is uniform throughout a genus, but there are some asterid genera with variation in this feature, with some species having vessel-ray parenchyma pits similar to intervessel pits and other species with vessel-ray pits that are enlarged and with reduced borders, *e.g.* *Symplocos*, *Aesculus*. The Deccan *Ailanthoxylon* and *Simarouboxylon* might be other examples of this phenomenon. No leaves or fruits/seeds of this family are known from the Cretaceous, so these Deccan woods apparently are the earliest record of the family. Clayton *et al.* (2009) suggested that crown-group Simaroubaceae dated to the K-Pg boundary.

Sapindaceae – *Euphorioxylon deccanense* and *Sapindoxylon schleicheroides* have combinations of features found in the pantropical subfamily Sapindoideae; both with features found in the tribe Cupanieae.

Friis *et al.* (2011) cited *Sapindoxylon schleicheroides* as among the earliest records of the family. The other Cretaceous occurrences they recognized were seeds of *Sapindospermum* from the Late Turonian–Maastrichtian of Europe. Age estimates for the crown-group Sapindaceae range from 36 Ma to 116 Ma (Stevens 2001-onwards).

Malvales

Malvaceae, Tribe Grewioideae – *Grewinium canalisum*.

Malvaceae, Tribe Sterculioideae – *Sterculinium deccanense*.

Malvaceae, Tribe Sterculioideae – *Sterculinium shahpurens*.

Friis *et al.* (2011), in their review of Malvaceae occurrences in the Cretaceous, only referred to the questionably named *Hibiscoxylon* from Egypt (Kräusel 1939) and implied that the family is not reliably known until the Early Cenozoic. However, these three Indian woods and malvaceous woods from the Campanian and Maastrichtian of Texas and Mexico (Wheeler *et al.* 1994; Estrada-Ruiz *et al.* 2007, 2010), and the Maastrichtian of Peru (Mourier *et al.* 1988) document that by the Maastrichtian, Malvaceae were present on three continents. Further, the Deccan malvaceous fruits have features of the Malvoideae. This suggests substantial diversification within the family by the K-Pg boundary, with three subfamilies present. Richardson *et al.*'s (2015) estimate of the age of the crown-group Malvaceae (70.7 Ma) used Paleocene leaves of Malvoideae as a calibration point. Others estimated considerably younger ages, *e.g.* (47–)44, 31(–27) Ma (Wikström *et al.* 2001).

Asterids

Ericales

Lecythidaceae, subfamily Planchoidae – *Barringtonioxylon deccanense*, *Barringtonioxylon eopterocarpum*, with *Barringtonioxylon mandlaense*, similar to both *Petersianthus* and *Barringtonia*.

There are some Late Cretaceous reproductive structures recognized as being ericalean, but neither Friis *et al.* (2011) nor Collinson *et al.* (1993) mention any fossils referable to Lecythidaceae. Estimates for the diversification of crown-group Lecythidaceae range from 46 Ma to 84 Ma (Stevens 2001-onwards).

Lamiales

Lamiaceae, subfamily Viticoideae – “*Gmelina*” *tertiara* – features found in *Gmelina* and *Vitex*.

This wood extends the record for the order, family and subfamily Viticoideae considerably back in time. According to Friis *et al.* (2011) “There are no Cretaceous fossils that can be assigned to Lamiales” and they mention that the earliest Lamiaceae are Eocene. Subsequently, Manchester *et al.* (2015) remarked that the fossil record of the Lamiaceae was not good and that the features of Eocene pollen attributed to the Lamiaceae did not allow it to be confidently placed in the family.

There is a considerable range in estimates of the age of crown-group Lamiales – 61.5 Ma (Tank *et al.* 2015); 77 Ma (Magallón *et al.* 2015); 97 Ma (Bremer *et al.* 2004); 100.6–97.5 Ma (Nylinder *et al.* 2012: suppl.), and (96–)87(–77) Ma (Wikström *et al.* 2015). According to Wikström *et al.* (2001) the age of the Viticoideae clade is (30–)28, 17(–15) Ma.

Family not known, features occur in family or order suggested by assigned name, but also occur in other families or orders

Elaeocarpoxydon antiquum – possible Elaeocarpaceae (Oxalidales), but features also shared with Achariaceae, Phyllanthaceae, and Salicaceae (Malpighiales).

Evodinium indicum – possible Rutaceae (Sapindales) as suggested, but also possible Meliaceae, Sapindaceae (Sapindales), Rhamnaceae (Rosales).

Garcinioxydon tertiarum – many features shared with *Garcinia* (Clusiaceae), but the identification rested largely on radial canals that could not be confirmed. Affinities with Myrsinaceae (Primulaceae, Ericales) should be considered.

Lophopetalumoxydon indicum – possible Celastraceae (Celastrales), but features also shared with Meliaceae, Rutaceae, Sapindaceae (Sapindales), Ochnaceae (Malpighiales), and Fabales (Rosales).

Sonneratioxydon nawargaoense – preservation poor, features observed occur in *Sonneratia* (Lythraceae), but also in Sapindaceae (Sapindales) and Salicaceae (Malpighiales).

Sonneratioxydon preapetalum – some features in common with *Sonneratia* (Lythraceae, Myrtales), but also similar to Melastomataceae (Myrtales), fossil lacks internal phloem of Myrtales.

Tetrameleoxydon prenudiflora – many features shared with Tetramelaceae (Cucurbitales), but also similarities with Hernandiaceae (Laurales).

“*Walsura*” *deccanense* – features occur in *Walsura*, *Dysoxylum*, *Guarea* (Meliaceae), but also in Fabaceae/Caesalpinioideae (Fabales).

Features not consistent with assigned name – Other affinities inferred

Amooroxydon deccanense – not Meliaceae, probably Urticales.

Calophylloxydon dharmendrae – not Calophyllaceae, in Myrtaceae (Myrtales).

Unknown

Aeschynomenoxydon malwaense – not Fabaceae.

Aeschynomenoxydon tertiara – not Fabaceae.

Elaeocarpoxydon ghughuense – not Elaeocarpaceae.

Elaeocarpoxydon mandlaense – not Elaeocarpaceae.

Laurinoxydon deccanense – not Lauraceae, possibly Myrtaceae (Myrtales) or Calophyllaceae, or ? Chrysobalanaceae (Malpighiales).

“*Turraeanthus*” *deccanensis* – not Meliaceae.

Some of the original identifications of Deccan woods are rejected herein. However, others are supported at various taxonomic levels, *i.e.*, some woods have a combination of features that occurs in the order, family, subfamily, tribe, or genus to which they were initially identified. These Deccan woods are significant in being among the oldest, if not the oldest, record for many clades. However, they have rarely been used in analyses inferring the ages or reconstructing the biogeographic history of a family or order. We were able to only examine about half of the reported Deccan woods (see Appendix 1 for a complete list of species); those other woods need renewed study so as to resolve their relationships. Unfortunately, with the exception of samples and slides stored at the Birbal Sahni Institute of Palaeobotany, we were unable to relocate most relevant samples and slides, many of which appear to have been lost. Equally important would be studying other low paleolatitude assemblages, especially the Late Cretaceous woods of Madagascar, about which little is known (Loubière 1939).

Some functional traits of the Deccan woods and remarks on paleoecology

The Deccan woody flora is a species-rich assemblage from a crucial period in the evolution of angiosperms at or around the K-Pg boundary (Smith *et al.* 2015), and, as such, invites an analysis of its functional wood anatomical traits and a comparison with late Cretaceous–Paleocene wood assemblages from other geographic regions, and with Recent floras (Table 1). Vessel diameter and vessel frequency are important functional traits, but they vary with cambial age and distance from the pith (*e.g.* Panshin & DeZeeuw 1980), *i.e.*, juvenile wood generally has narrower and more frequent vessels. It is unusual to find Deccan dicot axes more than 10 cm diameter, although bigger trunks of palm stems are frequently found (field observations by D. Kapgate, R. Srivastava, S. Manchester). Also, 20% of the samples we examined had pith or widely diverging rays, indicating wood from near the center of a stem or branch, *i.e.*, juvenile wood. This compromises using the hydraulic features of the Deccan woods for inferring paleoecology because comparative data for the modern flora are mostly for mature trees.

Here we only consider the incidences of distinct growth ring boundaries, scalariform perforation plates (in major angiosperm clades an ancestral state), exclusively solitary vessels, and incidence of abundant or elaborate axial parenchyma because past and present global trends and/or functionality of these attributes are reasonably well understood and they are less variable or dependent on cambial age than are quantitative vessel features (Baas *et al.* 2004; Rozendaal & Zuidema 2011; Morris *et al.* 2016; Brien *et al.* 2016).

Table 1. Percent occurrence of selected features. Data taken from InsideWood.

	Distinct growth rings	Scalariform perforation plates	Exclusively solitary vessels	Elaborate* axial parenchyma
Deccan Traps, n = 79**	19	3	5	25
India Miocene, n = 259	25	1	14	60
India Modern***, n = 555	44	9	14	40
Recent Paleotropics excluding India, n = 2679	8–13	8	17	35
Maastrichtian, Calif, n = 54	16	57	41	2
Maastrichtian- N. Hemisphere, n = 80	13	56	43	1
Maastrichtian- Campanian, S. Hemisphere, n = 22	0	32	23	9
Maastrichtian, Temp. S. America, n = 21	33	53	29	5
Danian, N. Hemisphere, n = 19	15	32	16	5
Recent North Temperate, n = 1022	85	24	22	15

* Elaborate axial parenchyma = aliform or confluent or bands >3 cells wide.
** Includes data from the literature and recorded on InsideWood as well as the woods discussed in this paper.
*** Excluded Himalayan woods.

Distinct growth rings are not only a feature of high latitude temperate to boreal floras, but are also of common occurrence in tropical regions (Brienen *et al.* 2016; Tarelkin *et al.* 2016): absence of growth ring boundaries characterizes so-called “everwet” rain-forest conditions, while presence of distinct growth rings indicates either seasonally dry periods, floodplain forests, or mangroves subjected to strong seasonal fluctuations in salinity. Groenendijk *et al.* (2014) even found a significant proportion of tree species in a wet tropical forest from Central Africa to have distinct growth rings. The Deccan woods show a low percentage of taxa (19%) with distinct growth rings, suggesting tropical, probably everwet conditions, much lower than in the modern Indian flora (44%) which includes dry seasonal (monsoonal) forests. The paucity of distinct growth rings in the Deccan flora agrees with evidence indicating that monsoonal conditions in India were definitely post-Deccan time (*e.g.*, An *et al.* 2001; Gupta *et al.* 2015).

In the incidence of vessel perforation types there is a striking difference between the Deccan woods and Maastrichtian–Danian woods from the rest of the world. The Deccan woods are surprisingly “modern” in aspect because of the low percentage of scalariform perforation plates (3%), lower even than in present-day India (9% - excluding the Himalayas) or the Paleotropics (8%). The incidence of scalariform perforation plates in woods from the Maastrichtian of California (57%) and in the rest of the Northern Hemisphere (56%) is considerably higher than that of the Deccan woods.

Scalariform perforations are an ancestral feature in the Baileyan transformation series, from vesselless gymnosperms and early angiosperms via scalariformly perforated vessel elements to simply perforated vessel elements (Bailey & Tupper 1918; Wheeler & Baas 1991; Lens *et al.* 2016). In the modern flora, scalariform perforations are most common in cool to boreal or alpine frost-prone vegetations, and rare to absent in lowland tropical and (seasonally) dry conditions (Baas 1976; Jansen *et al.* 2004; Wheeler *et al.* 2007) where hydraulic efficiency is considered important (Jansen *et al.* 2004; Feild *et al.* 2009; Christman & Sperry 2010; Jansen & Nardini 2014). Analyses of the incidence of scalariform perforations in the fossil record revealed that they are very common in Cretaceous and early Tertiary angiosperms. This high incidence has been interpreted in support of the Baileyan trends in xylem evolution (Wheeler & Baas 1991, 1993). The Deccan woods have less than 3% (2 out of 80) of taxa with scalariform perforations. This extremely low incidence of scalariform perforations is only mirrored in modern floras from dry tropical lowland forests and savannas (Baas 1976; Jansen *et al.* 2004), and remarkably enough in the Miocene fossil woods from India (Table 1). Everwet rain forests usually have 5–8% of genera with scalariform perforations, mainly small trees and shrubs from the lower story (Baas 1976). Tropical monsoon forests with 1–5% of genera with scalariform perforations perfectly match the Deccan fossil woods assemblage.

Exclusively solitary vessels are also a “primitive” feature in the Baileyan sense. The derived condition, high degrees of vessel grouping, has been associated with increased cavitation resistance (Carlquist 1984, 2001; Lens *et al.* 2011), presumably adaptive in dry ecosystems. Again, Cretaceous assemblages show a higher incidence of solitary vessels (Wheeler & Baas 1991) than do modern floras. There are, however, no very obvious ecological trends for exclusively solitary vessels or high degrees of vessel grouping (long radial multiples) when analyzed on a global scale (Wheeler *et al.* 2007), although in local and regional analysis increased vessel grouping correlates with increasing drought (Carlquist 2001). The very low incidence of exclusively solitary vessels (5%) is unique when compared with contemporary or earlier fossil wood floras (Table 1) but also when compared with modern world floras (Wheeler *et al.* 2007), where the Mediterranean flora from Europe and North Africa ranks lowest (9%) and the Australian flora, dominated by Myrtaceae with solitary vessels, ranks highest (37%) - paradoxically both floras dominated by drought-tolerant forests.

Abundant or elaborate axial parenchyma in the form of paratracheal (aliform to confluent) or wide parenchyma bands are considered derived features (Kribs 1937; Carlquist 2001), and increase in incidence through time in the global fossil record

(Wheeler & Baas 1991). However, total tissue percentages of axial and ray parenchyma may be very high in some Cretaceous woods (Wheeler & Lehman 2009). Xylem parenchyma serves multiple functions in a living tree, from storage and mobilization of carbohydrates to refilling of embolised conduits and defense against pathogens (Morris *et al.* 2016). In modern floras, abundant paratracheal and/or banded parenchyma are much more common in tropical floras than in temperate ones (Baas 1982, 1986; Baas *et al.* 2004; Wheeler *et al.* 2007; Spicer 2014; Morris *et al.* 2016), but on a global scale the total amount of parenchyma (radial and axial) seems independent of mean annual precipitation (Morris *et al.* 2016). Elaborate axial parenchyma occurs in 25% of the Deccan woods – a percentage more or less intermediate between that for the modern Indian Flora (40%) and late Cretaceous or early Paleocene fossil floras (5–9%), and also intermediate between modern tropical and temperate floras (Baas 1982; Wheeler *et al.* 2007, table 1).

Taking the four analyzed features together, we cannot draw any straightforward paleoecological conclusions. Data on the incidence of distinct growth ring boundaries and scalariform perforations both indicate tropical conditions – consistent with the relatively low paleo-latitude of the Deccan woods at the time of their fossilization. However, the rarity of scalariform perforations suggests xeric conditions, while the low percentage of woods with distinct growth rings suggests mesic rainforest conditions. The incidences of exclusively solitary vessels or elaborate parenchyma patterns are not informative for either a mesic or xeric alternative. One non-anatomical parameter pleading for the xeric option is the small stature of Deccan trees. In the tropics, dry forests typically have trees of much smaller size than rainforests (*e.g.*, Ewel 1977; Holbrook *et al.* 1995).

In their incidences of wood anatomical features, the Deccan woods have more in common with Recent Indian and other Paleotropical woods from Asia and Africa than with the Maastrichtian and Paleocene woods from the rest of the world (Table 1). There is also a fairly high similarity of the Deccan woods with the Miocene fossil woods of India, except for the much higher incidence of elaborate parenchyma patterns in the Miocene flora. The scarcity of the two “primitive” features – scalariform perforations and exclusively solitary vessels – in the Deccan wood assemblage is remarkable for such an ancient flora, because an earlier analysis of Cretaceous/lower Tertiary woody floras found much higher incidences of primitive features in the Baileyan sense (Wheeler & Baas 1991). However, that analysis used a database consisting mainly of fossil woods from relatively high paleolatitudes in the Northern Hemisphere, along with some high latitude Southern Hemisphere Cretaceous floras (see also Table 1). The Deccan woods so far constitute the most species-rich K-Pg assemblage from such a low paleolatitude. That these woods show such “modern” incidences of these primitive features suggests that hot tropical conditions may have accelerated adaptive xylem evolution to fit the high demands for hydraulic efficiency typical for the tropical lowland (Baas *et al.* 2004). The above very tentative conclusions should be tested in a broader analysis of more functional traits (*cf.* Beeckman 2016), which is beyond the scope of this paper.

CONCLUSIONS

Our re-examination of nearly half of the previously reported Deccan wood taxa has led to many changes in their taxonomic assignment, understandably so, because originally the search for closest relatives concentrated on the extant Indian flora. Broader comparisons, across all woody families and most geographic regions, facilitated by the InsideWood database and its associated multiple entry key, enabled us to reconsider the taxonomic affinities. The Deccan wood assemblage contains a diversity of angiosperm orders, families and genera from most major (supra-ordinal) clades of the angiosperms, magnoliids (one Annonaceae) and core Eudicots – rosids I and II, and asterids (but not asterid I). The Malpighiales, Malvales, and Sapindales are especially well represented. Some Deccan woods represent the earliest fossil record of an order, family, or genus, and provide valuable reference points for phylogenetic and biogeographic analyses. The very “modern” aspect of the Deccan wood flora raises questions of whether xylem evolution was accelerated at low paleolatitudes near the end of the Cretaceous.

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APPENDIX

Alphabetical list of dicotyledonous woods described from the Deccan Intertrappean beds. Species reviewed and illustrated herein indicated in bold. Additional species listed with localities, references, comments on affinities, vrp? = type of vessel-ray parenchyma pits unknown and information on this feature is needed to confirm relationships. For author and locality information on taxa in bold, see text.

Aeschynomenoxydon malwaense, not Fabaceae, affinities unknown.

Aeschynomenoxydon nawargaoense Shete & Kulkarni 1982; Nawargaon or Jhargad; affinities with Fabaceae questionable according to Awasthi 1992.

Aeschynomenoxydon tertiarum, not Fabaceae, affinities unknown.

Aesculoxydon deccanense Trivedi & R. Srivastava 1982a; Mohgaon Kalan, vrp?, affinities questionable, vasicentric/vascular tracheids reported, which is not a feature of *Aesculus*.

Aglaioxydon mandlaense Trivedi & K. Srivastava 1982b; Parapani, vrp?.

Ailanthoxydon ghiarensis (Saksena) Prakash, Verma, & Dayal 1967; Ghiar; similar to *Ailanthus* according to Saksena 1962 [1963].

Ailanthoxydon indicum, similar to *Ailanthus*.

Ailanthoxydon mahurzarii Shallom 1959 [1961]; Mahurzari, Ghiar, Sidhi; similar to *Ailanthus* according to Prakash, Verma, & Dayal 1967.

Amooroxylon deccanense, Nawargaon; not Meliaceae, Baas *et al.* 2015, affinities unknown.

Anacardioxydon semecarpoides, Anacardiaceae, subfamily Anacardioidae.

Anamirta pfeifferi Bonde 1997; Nawargaon; affinities with Menispermaceae questioned, also similar to Lardizabalaceae (Smith *et al.* 2013).

Ardisioxydon indicum Shete & Kulkarni 1982; Nawargaon, vrp not described, but likely Primulaceae/Myrsinoideae because of combination of pith canals, only multiseriate rays and IAWA features 13, 22, 105.

Aristolochioxydon prakashii Kulkarni & Patil 1977; Nawargaon; description/illustrations not sufficient to establish affinities (Smith *et al.* 2013).

Artocarpoxylon deccanense, Moraceae, tribe Castilleae.

Atalantioxydon indicum, Sapindales/Rutaceae, Sapindaceae, or Meliaceae.

Baphioxydon palaeonitidoides Trivedi & K. Srivastava 1986; Ghugua, vrp?.

Barringtonioxydon deccanense, Lecythydaceae.

Barringtonioxydon eopterocarpum, Lecythydaceae.

Barringtonioxydon mandlaense, Lecythydaceae/subfamily Planchoidae.

“*Bischofia*” *palaeojavanica* Awasthi 1988 [1989]; Anjar, vrp?.

Bischofinium deccanii, Phyllanthaceae, similar to *Bridelia*.

Boswellioxydon indicum Dayal 1964 [1966]; Keri; Sapindales/Burseraceae or Anacardiaceae.

Bridelioxydon keriense (Dayal) Thayne & Tidwell 1984 [Syn.: *Paraphyllanthoxydon keriense* Dayal 1967 [1968], *Phyllanthinium keriense* (Dayal) Prakash, Bande, & Lalitha 1986]; Keri; probably Malpighiales/Phyllanthaceae, Salicaceae-Euphorbiaceae clade.

Bridelioxylon krauseli, Malpighiales/Salicaceae-Euphorbiaceae clade.

Bridelioxylon mohgaoense Upadhye & Patil 1978; Mohgaon Kalan; diagnosis mentions aliform-confluent parenchyma, not a feature of *Bridelia* or the Phyllanthaceae, affinities unknown.

Bridelioxylon sagarens (Mahabale & Deshpande) Koeniguer 1966 [1967] (Syn.: *Euphorbioxylon sagarens* Sagar, Mahabale, & Deshpande 1963).

Burseraceoxylon baradense Sheikh 2011, Mahurzari, not Burseraceae, family unknown.

Burseroxylon preserratum, Sapindales/Burseraceae or Anacardiaceae.

Callistemonoxylon deccanense, Myrtaceae, but probably not *Callistemon*.

Calophylloxylon dharmendrae, not *Calophyllum* or in Clusiaceae, likely Myrtaceae. *Canarioxylon shahpuraensis* Trivedi & K Srivastava 1985; Shapura, Nawargaon; Khare *et al.* 2000, vrp?.

Connaroxylon dimorphum Baas, Manchester, Wheeler, & Srivastava 2017; Dhagaon; Connaraceae.

Dombeyoxylon mahabalei Biradar 1975; Mohgaon Kalan; affinities uncertain, possibly Malvaceae.

Dracontomeloxylon palaeomangiferum, Anacardiaceae.

Dryoxylon intertrappea Trivedi 1976, Mahurzari, affinities unknown.

Dryoxylon mahurzarii Trivedi 1976, Mahurzari, affinities unknown.

Dryoxylon mohgaoense Rode 1936; Mahurzari, Mohgaon Kalan; Verma 1950; Prakash 1956; Shallom 1963a; affinities unknown.

Dryoxylon tiliaceoides Trivedi 1976, Mahurzari, Malvaceae.

Ebenoxylon deccanense Trivedi & R Srivastava 1982b, Mohgaon Kalan, vrp?.

Ebenoxylon mohgaonense Chitale & Patil 1972; Mohgaon Kalan; Müller-Stoll & Mädler-Angeliowa 1984 and Süss 1987 said not Ebenaceae, affinities unknown.

Elaeocarpoxyylon antiquum, possibly Elaeocarpaceae, but also possibly malpighiale families Achariaceae, Phyllanthaceae, Salicaceae.

Elaeocarpoxyylon ghughuense, not Elaeocarpaceae, family unknown.

Elaeocarpoxyylon mandlaense, not Elaeocarpaceae, family unknown.

Elaeocarpoxyylon mohgaoense Trivedi & R Srivastava 1980; Mahurzari, vrp?.

Elaeocarpoxyylon nawargaonense Khare, Prasad, & Awasthi 2000; Nawargaon, vrp?.

“*Elaeocarpus*” *chitaleyi* Nambudiri & Tidwell 1975; Mohgaon Kalan, not Elaeocarpaceae, family unknown.

Erythroxyylon mahurzarii Kapgate 2007; Mahurzari; not Erythroxyllaceae, family unknown.

“***Eucalyptus*” dharmendrae**, Myrtaceae, subfamily Myrtoideae.

“*Eucalyptus*” *ghughuensis* Shukla, Mehrotra, & Tyagi 2012; Ghughua; Myrtaceae, features of *Eucalyptus* and *Lophostemon*, vrp?.

Euphorioxylon deccanense, Sapindaceae, subfamily Sapindoideae.

Evodinium indicum, possibly Rutaceae, Rhamnaceae also possible.

Evodinium intertrappeum Shete & Kulkarni 1982; Nawargaon; possibly Rutaceae.

Garcinioxylon tertiarum, family unknown, possibly Primulaceae/Myrsinoideae.

Glochidioxylon sahnii, Malpighiales/Salicaceae-Euphorbiaceae clade.

- Gmelina tertiara***, Lamiaceae, similar to *Gmelina* and *Vitex*.
Gomphandroxyton samnapurens, possibly Stemonuraceae.
Grewinium canalisum, Malvaceae/Grewioideae.
Grewinium intertrappeum (Shallom) Srivastava & Guleria 2000; Mahurzari, Malvaceae/Grewioideae.
Grewinium mahurzariense (Prakash & Dayal) Srivastava & Guleria 2000; Mahurzari; Prakash & Dayal 1963; Malvaceae/Grewioideae.
Heterophragmoxyton indicum Shete & Kulkarni 1982; Nawargaon, features not unique to Bignoniaceae.
Heyneoxylon intertrappeum Trivedi & Srivastava 1988; Parapani; affinities questionable, vrp? and species described as having vasicentric/vascular tracheids.
Heyneoxylon tertiarum, features of Meliaceae and Rutaceae.
Hibiscoxyton intertrappeum Trivedi & Ambwani 1971; Mahurzari; described as having tile cells, a feature of Malvaceae.
Homalioxyton mandlaense, family unknown, possibly Malpighiales.
Hydnocarpoxylon indicum, Achariaceae, similar to *Hydnocarpus*.
Lanneoxylon grandiosum, Sapindales/Anacardiaceae or Burseraceae.
Laurinoxyton deccanense, family unknown, not Lauraceae.
Leeoxylon multiseriatum, Vitaceae, similar to *Leea*.
Leptospermatoxyton indicum Trivedi & Verma 1973; Mohgaon Kalan, vrp?.
Lophopetalumoxylon indicum, possibly Sapindales, unlikely Celastraceae.
Lythreoxylon jabalpurii Meshram & Borkar 2014, Jabalpur, vrp?.
Mallotoxyton kerienne, Euphorbiaceae, features of *Croton* and *Mallotus*.
Moringaceoxylon baradii Narkhede, Bhowal, & Yadav 2011; Mahurzari; vrp? family unknown.
Oleoxylon deccanense Trivedi & Srivastava 1981 ex Srivastava, Wheeler, Manchester, Baas 2015, Jheria, Oleaceae.
Oleoxylon mahurzarii Puranik & Sakundarwar 2011; Mahurzari; features not unique to Oleaceae.
Pangioxyton mohgaonsense Trivedi & K Srivastava 1982c; Mohgaon Kalan, vrp?.
Polyalthioxyton parapaniense, Annonaceae, generic affinities uncertain.
Rhamnoxyton intertrappea Chitaley & Kate 1972; Parapani; Prakash 1974 suggested unlikely Rhamnaceae.
Rutaceoxylon mahurzarii Chitaley & Khubalkar 1974, Mahurzari, vrp?.
Sapindoxylon chhindwarensense Chitaley & Shallom 1969; Mohgaon Kalan, probably Sapindaceae.
Sapindoxylon schleicheroides, Sapindaceae, subfam. Sapindoideae, tribe Cupanieae.
Schreberoxyton mohgaonsense Trivedi & K Srivastava 1982d; Mohgaon Kalan, vrp?.
Simaroubinium mahurzari (Shallom) Jain 1959 [Syn.: *Simarubaceoxylon mahurzarii* Shallom 1959]; Mahurzari, vrp?.
Simarouboxylon indicum, similar to *Simarouba*.
Sonneratioxyton caeseolarioides Shete & Kulkarni 1982; Nawargaon, vrp?.
Sonneratioxyton duabangoides Shallom 1963a emend. Chitaley 1977 [1978]; Mohgaon Kalan, vrp?.

Sonneratioxylon intertrappeum Biradar & Mahabale 1973 [1975]; Mohgaon Kalan or Keria, vrp?.

Sonneratioxylon nawargaoense, not *Sonneratia*, family unknown.

Sonneratioxylon preapetalum, not *Sonneratia*, family unknown.

Sterculinium deccanensis, Malvaceae, probably Sterculioideae.

Sterculinium shahpurensis, Malvaceae, Sterculioideae; generic placement uncertain.

Syzygioxylon chhindwarens Nambudiri & Tidwell 1977; Mohgaon Kalan, affinities uncertain.

Syzygioxylon mandlaense Ingle 1973; Samnapur; affinities uncertain.

Syzygioxylon mohgaoense Patil & Singh 1974; Mohgaon Kalan; affinities uncertain.

Tetrameleoxylon prenudiflora, possibly *Tetrameles*, but also similar to *Hernandia*-ceae.

“Tristania” confertoides, Myrtaceae, subfamily Myrtoideae, similar to *Eucalyptus* and *Lophostemon*.

“Turraeanthus” deccanensis, family and order uncertain, not Meliaceae.

“Walsura” deccanensis, possibly Meliaceae.

Zizyphoxylon mandlaensis Trivedi & K Srivastava 1982a; Parapani; according to Guleria 1990 [1992] not *Zizyphus*; vrp?.