

The oldest fossil of *Eucalyptus* from the Late Maastrichtian–Danian of India and the theory of its Gondwanic origin

Anumeha Shukla^{1*}, R. C. Mehrotra¹ and Antariksh Tyagi²

¹Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India

²National Botanical Research Institute, Council of Scientific and Industrial Research, Rana Pratap Marg, Lucknow 226 001, India

A fossil wood belonging to *Eucalyptus* L'Hérit of the Myrtaceae is described from the Deccan Intertrappean beds of central India, considered as Late Maastrichtian–Danian in age. Phylogenetic analysis based on the morphological data of 16 extant eucalypts and the present fossil indicates that the fossil wood belongs to the eucalypt group, closest to the *Eucalyptus* clade. The absence of authentic fossil record from Australia before the Miocene and its presence in India during the Late Cretaceous raises a question on the widely held view of Australia being the original home of *Eucalyptus*. Although *Eucalyptus* fossils are also known from other Gondwanaland continents, this fossil wood is the oldest among them and supports its Gondwanic origin.

Keywords: Deccan Intertrappean beds, Dindori District, fossil wood, Myrtaceae.

THE Deccan Traps of central and western India represent the largest volcanic event in the country since the Triassic¹. The rocks were formed as a result of the solidification of molten lava that erupted successively through fissures in the earth's crust. The sedimentary beds deposited during the quiescent intervals between two flows are called intertrappean beds. The Deccan Intertrappean flora is mostly known from central India and is unique in the sense that all the groups of the plant kingdom, ranging from algae to angiosperms, are represented in it. This flora is well known and has been enlisted by many workers^{2,3}. Angiosperms, the most dominant group in the flora are equally represented by both monocotyledonous and dicotyledonous taxa.

The age of the Deccan Traps has long been a question of debate and considerable work has been carried out on the duration and age of the Deccan volcanism⁴. It has been fairly well established that the volcanism had an extended duration of 69–61 million years, with a peak eruption between about 67 and 65 million years. However, the eruptive events in different volcanic provinces were not synchronous. The faunal assemblage as well as palynological studies advocated the Maastrichtian age for most of the intertrappean exposures⁴. Although Shukla *et*

*al.*⁵ have assigned the Deccan Traps to the Late Maastrichtian–Danian age on the basis of palaeontological, geochronological and palaeomagnetic observations, no well-defined K/T boundary could be delineated in any intertrappean section, except for one near Jhilmili in Chhindwara District, Madhya Pradesh⁶.

During the eruption of the Deccan lava, the Indian subcontinent was on its way to the north after separation from other Gondwanaland continents⁷. As a result, the Deccan Intertrappean flora includes some South American and African forms^{8–14}, which indicate ancient biogeographic links of India with these continents. The present finding of *Eucalyptus* further supports this view as its fossils have also been recorded from other Gondwanaland countries such as Australia, New Zealand and Argentina. This fossil wood finding is also significant because it is the oldest record of fossil *Eucalyptus*.

Eucalyptus is one of the largest genera, with more than 660 species, of the monophyletic group of seven genera broadly referred to as 'eucalypt'. The genus is primarily distributed in Australia, but is also represented by a few species in Indonesia, the Philippines, Timor and New Guinea. Despite being a common member of the present-day Australasian vegetation, the megafossils of *Eucalyptus* have so far not been recorded from the rocks older than the Miocene. However, a fossil resembling *Eucalyptus* has already been recorded from the early Tertiary rocks of central India¹⁵, and the present finding of the genus is from the Late Cretaceous. This raises doubt about the Australian origin of *Eucalyptus*¹⁵.

This study is based on a specimen collected from the Deccan Intertrappean beds of Dindori District, Madhya Pradesh. The fossil wood is from Ghughua (23°7'N: 83°37'E) situated at a distance of 13.5 km southwest of Shahpura (23°11'N: 80°42'E) on the Shahpura–Niwas road (Figure 1). As the locality is rich in both dicotyledonous and monocotyledonous fossil plants, especially woods, it has been declared as a national park and named the Ghughua National Fossil Park (Figure 2). The woods are generally silicified and light to dark brown in colour. The type slides are housed in the museum of the Birbal Sahni Institute of Palaeobotany, Lucknow (museum specimen no. BSIP 39904).

For the study of xylotomical characters, the wood was cut into thin sections, viz. transverse/cross, tangential and radial longitudinal sections and slides were prepared by the usual method of grinding and polishing with carborundum powder. The thin sections were examined under a high-power light microscope. The fossil was identified after comparison with a large number of modern woods, both from thin sections and the published literature. The anatomical terms used in describing the fossil wood are those adapted by Wheeler *et al.*¹⁶ and the International Association of Wood Anatomists¹⁷.

Using a combined matrix of morphological and molecular data, phylogenetic analysis of the fossil wood

*For correspondence. (e-mail: anu_bsip@yahoo.co.in)

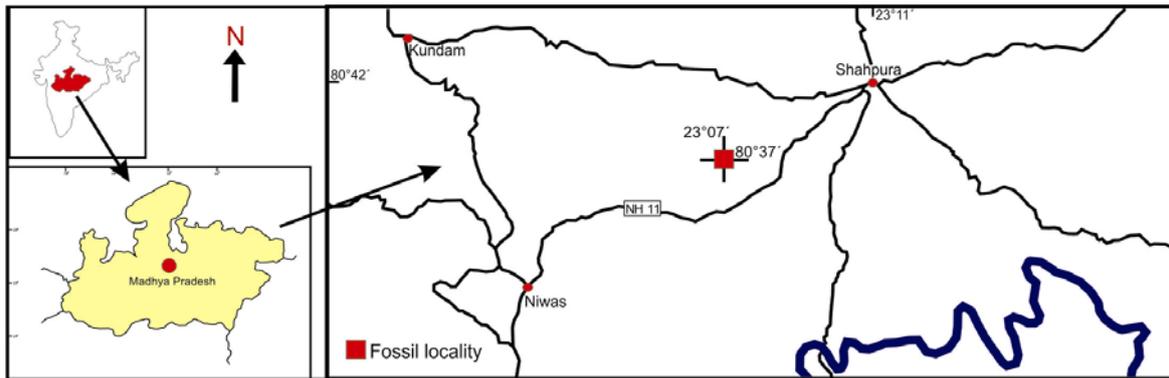


Figure 1. Map of Dindori District, Madhya Pradesh showing the fossil locality (marked by a rectangle).

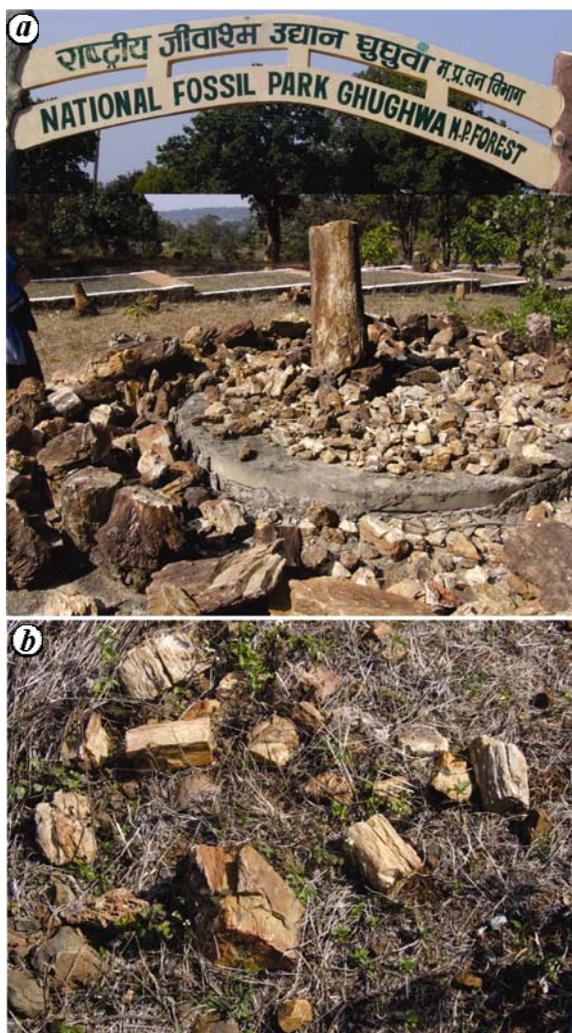


Figure 2. Photographs of the fossil locality showing scattered fossil wood on the ground.

was performed along with modern eucalypt taxa to show the possible location of our fossil in the eucalypt group. The morphological matrix was obtained from previously published data^{18,19}, whereas the molecular matrices were

produced from the sequence data of four regions of DNA, namely 5S rDNA, psbA-trnH spacer, trnL intron and trnL 39exon-trnF spacer, which were originally analysed by Ladiges *et al.*²⁰ and Udovicic and Ladiges²¹ (the sequences were downloaded from GenBank, www.ncbi.nlm.nih.gov). The morphological matrix included six characters of 18 taxa, with one terminal representing the fossil. The characters were selected to capture variations within the group of this study. Autapomorphies and invariant characters were excluded from the morphological matrix. The uninformative and ambiguously aligned characters were removed from the molecular sequence datasets as described by Udovicic and Ladiges²¹ using PAUP *4.0b (ref. 22). The combined matrix possesses 122 characters of 18 taxa (Supplementary material S1). The fossil is scored as missing for all the molecular sequences and indel characters. However, the ITS dataset was excluded owing to certain reasons as described by Gandolfo *et al.*¹⁹ and a combined dataset was recreated for the analysis.

All analyses were launched from PAUP *4.0b (ref. 22). The parsimony trees were generated using bootstrap analyses with 10,000 replicates. Bootstrap searches were heuristic with simple addition of taxa, TBR branch-swapping and MulTrees turned-off. The tree statistics (length, consistency index, retention index) was recorded as calculated in PAUP*4.0b.

Systematic description

Family Myrtaceae

Genus *Eucalyptus* L'Hérit

Eucalyptus ghughuensis Shukla *et al.*, sp. nov.

Etymology: After the fossil locality Ghughua

Holotype: Specimen no. BSIP 39904

Type locality: Ghughua (23°7'N : 83°37'E) near Shahpura on Shahpura–Niwas road, Dindori District, Madhya Pradesh.

Type horizon: Deccan Intertrappean beds.

Specific diagnosis: Wood semi-ring porous. Vessels tylosed, small to medium arranged in echelon. Vasicentric

tracheids present. Parenchyma diffuse and scanty paratracheal. Rays mostly uniseriate and homogeneous. Fibres non-septate.

Age: Late Maastrichtian–Danian.

Description. Wood semi-ring porous (Figure 3 *a* and *d*). Growth rings distinct, demarcated by large and small vessels (Figure 3 *d*). Vessels generally very small to medium in size (small to very small in the late wood, while small to medium in the early wood), t.d. 62–84 μm and r.d. 125–150 μm in the early wood, and t.d. 42–55 μm and r.d. 34–84 μm in the late wood, almost exclusively solitary, rarely in radial pairs, sometimes forming echelon (Figure 3 *b*), generally 25–45 per sq. mm (29–54 per sq. mm in the early wood, while 45–54 per sq. mm in the late wood); tyloses present, especially in the late wood (Figure 3 *d*); vessel members 170–400 μm with oblique to horizontal ends; perforations simple; intervessel pits bordered, alternate, filled with black-coloured material, 8–10 μm in diameter (Figure 4 *b*). Tracheids vasicentric

forming a thin sheath of 3–4 cells around the vessels, in vertical rows, about 4 μm in diameter (Figure 4 *c*). Axial parenchyma paratracheal and apotracheal; paratracheal parenchyma rare, apotracheal parenchyma diffuse (Figures 3 *c* and 4 *a*); parenchyma cells thin-walled, 20–60 μm in length and 12–21 μm in diameter. Rays 19–22 per mm, almost exclusively uniseriate (Figure 4 *d*), sometimes bi-celled (Figure 4 *e*), made up of procumbent cells only, 8–17 μm in width and 2–34 cells or 38–555 μm in height; ray tissue homogenous (Figure 4 *f*); ray cells thin-walled, usually filled with dark-coloured deposits, 12–21 μm in tangential height and 30–42 μm in radial length. Fibres aligned in radial rows between the xylem rays, semi-libriform to libriform, angular in cross-section, non-septate, 8–17 μm in diameter and 385–725 μm in length. Apart from above characters, the bark is also preserved (Figure 3 *a*).

Affinities: The characteristic xylotomical features of the fossil such as solitary vessels plugged with tyloses and arranged in echelon, scanty paratracheal as well as diffuse apotracheal parenchyma, vasicentric tracheids, fine rays and non-septate fibres indicate its morphological

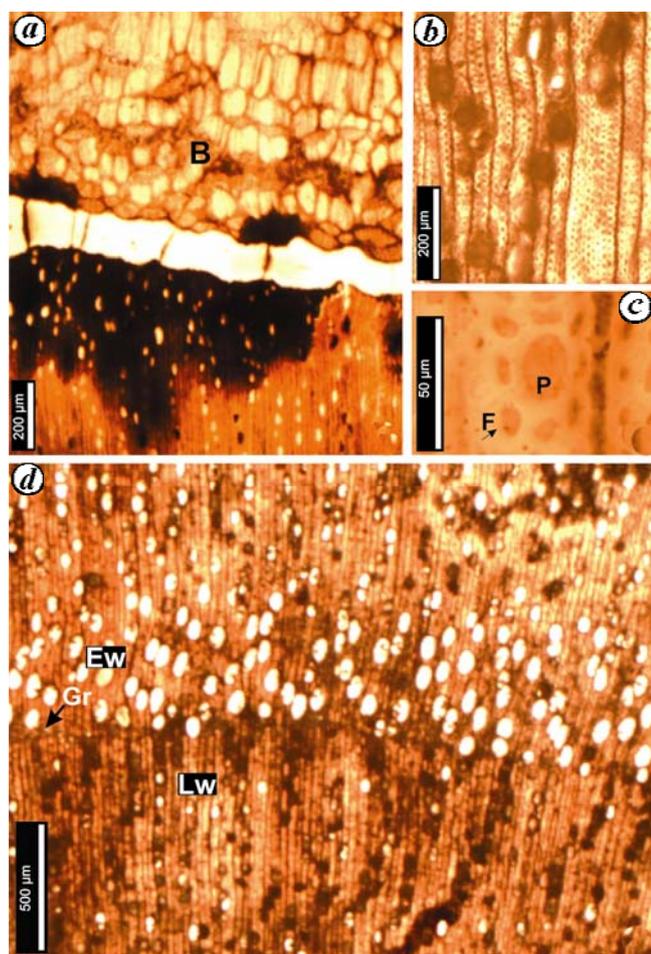


Figure 3. *Eucalyptus ghughuensis* Shukla *et al.*, sp. nov. *a*, Cross-section of the fossil wood showing bark portion (B) attached to the wood. *b*, Cross-section of the fossil showing tylosed vessels arranged in echelon. *c*, Cross-section of the fossil showing diffuse parenchyma (P) Fibre. *d*, Another cross-section showing semi-ring porosity. Gr, Growth ring; Ew, Early wood; Lw, Late wood.

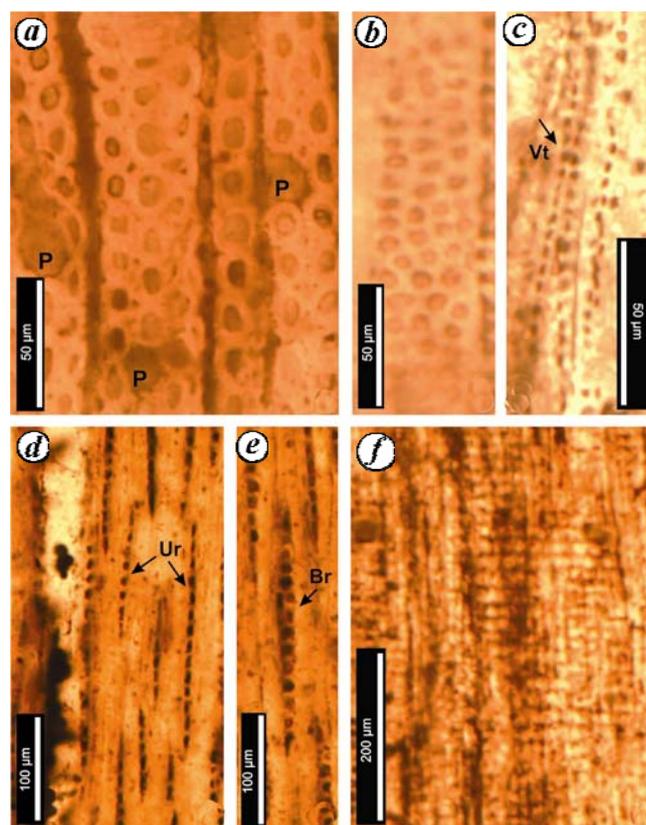


Figure 4. *E. ghughuensis* Shukla *et al.*, sp. nov. *a*, Cross-section of the fossil wood showing diffuse parenchyma (P). *b*, Tangential, longitudinal section of the fossil showing bordered intervessel pits. *c*, Another tangential, longitudinal section showing vesicentric tracheids (Vt, marked by an arrow). *d*, Tangential section showing predominantly uniseriate rays (Ur, marked by arrows). *e*, Tangential section showing a bi-celled ray (Br, marked by an arrow). *f*, Radial, longitudinal section of the fossil showing homogeneous ray tissue.

Table 1. Character-by-character comparison of the fossil with closely allied taxa of the family Myrtaceae

Characters	Fossil species (<i>Eucalyptus ghughuensis</i> Shukla <i>et al.</i> , sp. nov.)	Extant <i>Eucalyptus</i>	Extant <i>Tristania</i>	Extant <i>Xanthostemon</i>
Wood	Semi-ring porous	Mainly diffuse porous, but in some cases ring/semi-ring porosity present	Diffuse porous	Diffuse porous
Vessels	Exclusively solitary and arranged in echelon pattern	Solitary and arranged in oblique manner (echelon)	Solitary, but without any distinctive pattern	Solitary and arranged in oblique manner
Tyloses	Present	Present	Present	Present
Perforation plate	Simple	Simple	Simple	Simple
Intervessel pits	Bordered, alternate	Alternate	Alternate	Alternate
Vasicentric tracheids	Present	Present	Present	Present
Parenchyma	Scanty paratracheal and diffuse	Scanty paratracheal and diffuse to diffuse-in-aggregate	Mainly apotracheal	Scanty paratracheal to vasicentric
Rays	Exclusively uniseriate, rarely bicelled	Exclusively uniseriate, rarely bi-triseriate	Uniseriate to bi-triseriate	Uniseriate
Ray tissue	Homogeneous	Homogeneous or heterogeneous	Homogeneous	Heterogeneous
Fibres	Non-septate	Non-septate, rarely septate	Non-septate	Non-septate

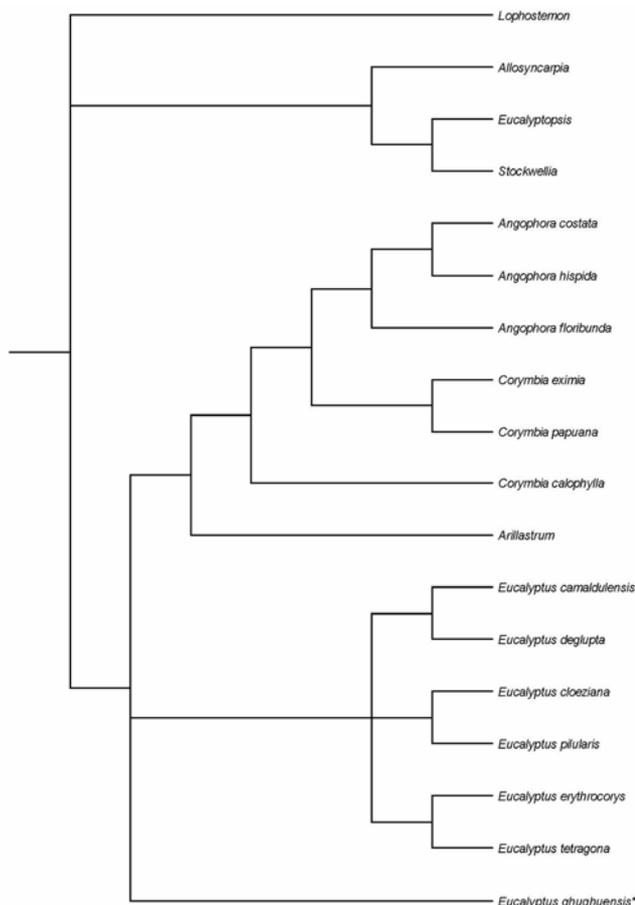


Figure 5. Fifty per cent majority-rule consensus tree showing the position of fossil (marked by *) with the other eucalypts. Bootstrap 50% majority-rule consensus of 10,000 trees (using tree weights) found during analysis of combined molecular and morphological matrix. Tree length = 380; consistency index (CI) = 0.6591, retention index (RI) = 0.7573.

similarity with the families Fagaceae and Myrtaceae. A detailed comparison of the fossil with the help of available literature^{23–27} and modern wood slides has been

made with various genera of both the families. In the family Fagaceae, the genus *Castanopsis* (D. Don) Spach. shows similarities with the fossil in having solitary vessels arranged in echelon, vasicentric tracheids and thin rays, but can be separated out due to the presence of abundant apotracheal parenchyma and aggregate rays. A few genera of the Myrtaceae²³, namely *Angophora* Cav., *Calycorectes* D. Legrand, *Campomanesia* Ruiz and Pav., *Eucalyptus* L'Hérit, *Kjellbergiodendron* Burret., *Lophospermum* D. Don ex R. Taylor, *Marlierea* Cambess., *Melaleuca* L. Nom. Cons. and *Xanthostemon* F. Muell. possess echelon arrangement of the vessels, which is the most characteristic feature of the fossil. However, among these genera, *Eucalyptus*, *Melaleuca* and *Xanthostemon* possess uniseriate rays like the fossil and hence, the possible affinity with the other genera can be ruled out. The genus *Melaleuca* can also be separated out in having aliform to confluent parenchyma against the scanty paratracheal parenchyma present in the fossil. Although the genus *Tristania* R. Br. of the Myrtaceae does not possess echelon arrangement, it is similar to the fossil in all other characters. *Xanthostemon* F. Muell. also shows some similarities with the fossil, but it can easily be excluded in having diffuse porous wood and heterocellular rays. A detailed comparison of the fossil with *Eucalyptus*, *Tristania* and *Xanthostemon* has also been shown in Table 1. This indicates that the fossil is identical to *Eucalyptus*. Thin sections as well as the published literature^{23–27} of various species of the genus were consulted to further confirm this identification. Generally, diffuse porous woods are found in *Eucalyptus*, but two of its species, namely *E. delegatensis* R.T. Baker (syn. *E. gigantea* Hook. F.) and *E. globulus* Labill. show ring/semi-ring porosity. In *E. delegatensis*²⁸ the rays are almost similar to those of the fossil, but the vessel frequency is comparatively less than that of the fossil²⁷, while in *E. globulus*²⁹, the rays are 1–2 seriate and parenchyma is mostly

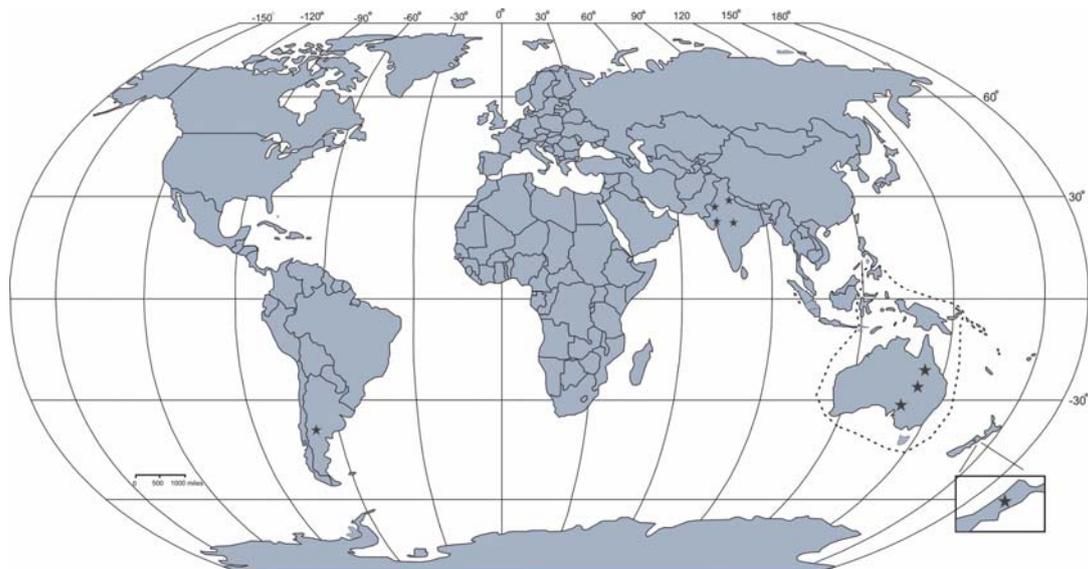


Figure 6. Map showing present (encircled by dotted line) and past distribution (marked with star) of *Eucalyptus*.

Table 2. Fossil records of *Eucalyptus*

Fossil	Country	Age
<i>Eucalyptus bugaldiensis</i> (fruits) ³⁰	Australia	Middle Miocene
<i>Eucalyptus pluti</i> ³¹	Australia	Pliocene
<i>Eucalyptus?</i> (leaves) ^{32,33,50}	Australia	Middle Miocene
Myrtaceous wood ⁵¹	Australia	Middle Miocene
<i>Myrtacidites eucalyptoides</i> (Myrtaceae) ^{34,36} ; <i>M. tunis</i> ⁵²	Australia	Plio–Pleistocene or up to Palaeocene–Eocene
<i>Eucalyptus spathulata</i> (pollen) ³⁵	Australia	Plio–Pleistocene
Eucalypt-like leaves/fructification ³⁷	New Zealand	Early Miocene?
Tentatively recorded pollen ⁵³	New Zealand	Mio–Pliocene
<i>Eucalyptus patagonicus</i> (fruit) ³⁸	Argentina	Miocene?
<i>Eucalyptus</i> macrofossils (leaves, buds, flowers) ¹⁹	Argentina	Early Eocene
<i>Eucalyptophyllum raoi</i> (leaf) ³⁹	India	Late Mio–Pliocene
<i>Eucalyptus dharmendrae</i> (wood) ¹⁵	India	Early Tertiary

vasicentric²⁷, in contrast to predominantly uniseriate rays and diffuse parenchyma in the fossil wood.

The only previously known fossil wood of *Eucalyptus* is *E. dharmendrae* described from the similar Deccan Intertrappeans¹⁵. The fossil wood presented here can be differentiated from it by the presence of semi-ring porosity, high vessel frequency and non-septate fibres. As the present fossil is distinct from the previously published fossil wood, it is described under a new species, *Eucalyptus ghughuensis* Shukla *et al.*, sp. nov.; the specific name is after the fossil locality.

The consensus tree based on cladistic analysis indicates the position of our fossil within the eucalypt group, closer to all *Eucalyptus* species (Figure 5); it further supports our NLR (nearest living relative) result. Although taxonomically we are sure about the affinity of the fossil with *Eucalyptus*, phylogenetically the fossil acquired an unresolved position, closer to the *Eucalyptus* clade. This might be either because of its older age (Late Maas-

trichtian–Danian) or due to only wood characters as the morphological matrix.

The genus *Eucalyptus* is mainly distributed today in Australia, but a few species are also found in the adjacent areas, growing in a wide range of habitats from evergreen to desert. In contrast, it had a vast spatial distribution in different areas of Gondwanaland (Figure 6) in the deep time ranging from the uppermost Cretaceous to Plio–Pleistocene (Table 2). The genus is known by its fruits³⁰, leaves^{31–33} and pollen^{34–36} from the Neogene of Australia (Figure 6), while the *Eucalyptus*-like leaves and fructification have been reported³⁷ from the Miocene sediments of New Zealand. *Eucalyptus* leaves, buds as well as flowers were described from the Miocene³⁸ and the Eocene¹⁹ of South America. From India, a Miocene leaf³⁹ and an early Tertiary wood¹⁵ are known. Despite its rich diversity and economic significance today, the early evolution of *Eucalyptus* is not well known because of its incomplete fossil record.

Phytogeographically, the eucalypt group is considered to be of ancient Australian origin (70–65 Ma)^{40–45} and the family Myrtaceae to which this group belongs also has a southern Gondwanic distribution⁴⁶. Following this and considering the wide distribution of *Eucalyptus* in different Gondwanaland continents, it can be concluded that the genus had a Gondwanic origin as all these continents had geographic links by which they might have shared a common ancestral stock during the Early Cretaceous. The above view supports the theory that the origin of the eucalypt group must predate the Late Cretaceous^{19,46,47}. Though it is difficult to pinpoint the place, time of the origin and early evolution of *Eucalyptus* or the eucalypt group because of its incomplete fossil record, *Eucalyptus ghughuensis* adds a new dimension to the ideas based on the wide distribution of *Eucalyptus* ranging from the Late Cretaceous to Plio–Pleistocene in widely divergent Gondwanic countries. In fact, we can safely conclude that Australia may not be the best choice as a place of the origin of *Eucalyptus*.

Looking through wood remains of angiosperms during the Cretaceous, there is no good record of the evolution of growth rings in porous woods. The earliest known fossil dicotyledonous wood with semi-ring porosity has been recorded from the Eocene of France⁴⁸. Distinct growth rings are not known until the Eocene and are more common throughout the Late Tertiary and modern times in Laurasia than in the tropics and the Southern Hemisphere⁴⁹. As the present authors are not aware of any record of ring/semi-ring porosity from the Late Cretaceous and Palaeogene sediments of India, *E. ghughuensis* represents the oldest record of a semi-ring porous wood in fossil angiosperms.

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Erosional vulnerability and spatio-temporal variability of the Barak River, NE India

Anwarul Alam Laskar¹ and Parag Phukon^{2,*}

¹Indian Statistical Institute, North-East Centre, Tezpur 784 028, India

²Department of Geological Sciences, Gauhati University, Guwahati 781 014, India

The alluvial segment of the Barak River within Assam has been studied for a period of 85 years (1918–2003) based on temporal satellite data and Survey of India topomaps. Ten representative reaches with distinctive planform geometry have been delineated in this segment. Overlay analysis of six temporal spatial datasets (1918, 1965, 1975, 1988, 1999 and 2003) reveals that two segments of the river are highly vulnerable to channel migration through the processes of cut-off and bank erosion predominantly effected by toe-cutting and shear failure. Migratory activity index shows cyclic variation for all the representative reaches. Quantitative assessment shows an increasing trend of both erosion and deposition. However, the quantum of deposition is more than erosion over the 85-year period of study.

Keywords: Bank erosion and deposition, Barak River, channel migration, overlay analysis, quantitative assessment.

THE Barak valley in NE India is a distinct entity vis-à-vis the Brahmaputra valley. The Barak river and its tributaries drain a significant part (about 39,390 sq. km) of the summer monsoon-dominated SE Asia, spread over Myanmar, India and Bangladesh. It forms the second largest river system in NE India next to Brahmaputra. Shillong Plateau and the Barail range form a major drainage divide between the two rivers. The alluvial segment of Barak River is well developed in the Cachar and Karimganj districts of Assam and further downstream in Bangladesh. Across its floodplain the river shows different degrees of spatio-temporal variability. However, quantitative assessment of the river variability in space and time in the Barak Valley is almost non-existent, although some snapshots of such a study are available in the Brahmaputra Valley^{1–4}. The present study addresses this information gap with emphasis on understanding the river dynamics within the 150 km segment of the Barak River between the Assam–Manipur border and Assam–Bangladesh border (Figure 1). Taking advantage of developments in the field of high-resolution satellite remote sensing and Geographical Information System (GIS), overlay analysis of six temporal datasets spanning 85 years has been carried out. All the datasets were brought

*For correspondence. (e-mail: p_phukon@rediffmail.com)