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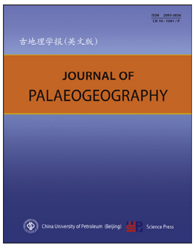

Palaeobiogeography

Earliest megafossils of scandent calamoid palms from the Deccan Intertrappean Beds of Central India and their paleobiogeographic implications

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Abstract Two well-preserved petrified palm stems from the latest Maastrichtian (Late Cretaceous) to earliest Danian (Early Paleocene) sediments of the Deccan Intertrappean Beds of Madhya Pradesh, Central India are described. Their significant anatomical characteristics include a Calamus-type general stem pattern, the presence of well-preserved fibrovascular bundles (fvbs) with two wide metaxylem vessel elements (230 μm—250 μm) and one phloem strand, uniform density of fvbs, lack of continuity between protoxylem and metaxylem vessel elements, and an absence of centrifugal differentiation of sclerenchymatous fibrous parts. These features reveal a close resemblance to those of extant genera of scandent Calamoideae. The permineralized stems are described as a new species namely, *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. The fossils represent the oldest reliable fossil records of this family, supporting their Gondwanan origin, their importance in tracing their migration pathways from India to Europe and other continents after the docking of the Indian subcontinent with Eurasia during the Paleocene, and an “Out-of-India” dispersal hypothesis. Today the subfamily Calamoideae is disjunctly occurred in Africa, Asia, Australia, Europe, and South America, but the poor deep-time fossil record of this subfamily with a small number of Cenozoic fossils makes hypotheses concerning its origin and dispersal difficult to evaluate. The present study has significant implications for the origin and migration of this subfamily and the paleoclimate.

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1. Introduction

Calamoideae (previously known as lepidocaryoid palms), the second most species-rich palm subfamily comprising about twenty-two genera with 650 accepted species (Dransfield *et al.*, 2008), is an early diverging group of palms characterized by their overlapping scale-bearing fruits and frequent spiny armature (Tomlinson *et al.*, 2011). This subfamily is divided into three tribes and nine subtribes with a disjunct distribution in Africa, Europe, South America, Australia, and Asia with the greatest diversity in the wet tropical forests of Southeast Asia (Mathew and Bhat, 1997; Tomlinson *et al.*, 2011; Baker and Dransfield, 2016; Baker and Couvreur, 2013a, 2013b).

Recent morphological and molecular phylogenetic analyses for the entire palm family strongly support the monophyletic origin of the Calamoideae (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen, 2000), but relationships within the Calamoideae are difficult to interpret because of the wide spectrum of morphological diversity. Baker *et al.* (2000) established a basic phylogenetic hypothesis for the Calamoideae that is sustained by more recent analyses of global palm phylogeny (Asmussen *et al.*, 2006; Baker *et al.*, 2009). These studies recognize three tribal clades within the subfamily, namely 1) a monogeneric Eugeissoncac sister to all other Calamoideae; 2) Lepidocaryeae, containing three subtribes (Ancistrophyllinae, Raphiinae, Mauritiinae); and 3) Calameae, containing six subtribes (Korthalsiinae, Salaccinae, Metroxylinae, Pigafettinae, Plectocomiinae, Calaminae) (Dransfield *et al.*, 2008).

The Calamoideae subfamily includes massive tree palms, undergrowth palms, and acaulescent palms; but it is best known for its climbing members: the rattans (Baker *et al.*, 2000; Dransfield *et al.*, 2008). Rattans also exhibit an extraordinary variety of growth forms, but the climbing (scandent) habit is predominant (Uhl and Dransfield, 1987; Kissling *et al.*, 2019). The scandent habit in palms has multiple origins within the family, and further, some of these lineages have fundamental differences in their stem structure (Baker *et al.*, 2000; Tomlinson *et al.*, 2001; Tomlinson and Spangler, 2002; Tomlinson and Zimmermann, 2003). This habit, generally characterized by long internodes and a narrow stem, has evolved in several unrelated groups of palms in the Calamoideae (Tomlinson and Fisher, 2000).

The climbing members of Calamoideae are ecologically diverse, mainly within forest communities, but exhibit a preference for wet conditions. Rattans can be viewed as weeds, by foresters, because they favour disturbed sites and establish best in treefall gaps. Their extreme morphological diversity illustrates their success in advancing well beyond any putative ancestral palm (Fisher and Dransfield, 1977). However, molecular evidence suggests that the Calamoideae is sister to all other palms (Asmussen and Chase, 2001; Asmussen *et al.*, 2006; Baker *et al.*, 2009; Faurby *et al.*, 2016). Baker and Couvreur (2013a, 2013b) also suggested that Calamoideae diverged from other palms at the crown node of the family in Eurasia, expanding into Africa before its crown node divergence (80 Ma; 95% highest probability density).

Calamoideae has a relatively limited megafossil record, with most fossils reported from the Cenozoic fossil floras of East Africa, Europe, New Zealand, and North America (Table 1; Stur, 1873; Jablonszky, 1914; Chandler, 1957, 1963; Dechamps and Maes, 1987; Pan *et al.*, 2006; Hartwich *et al.*, 2010; Teodoridis *et al.*, 2015). To date, there is no megafossil evidence of Calamoideae from India. Although one leaf fossil assigned to Calamoideae has been reported from the Plateau (Cherra) sandstones of Jaintia Hills, Assam, India (Barman and Daura, 1970), the identification is insecure.

In the present study, we report a new calamoid fossil palm species *Palmoxylon calamoides* sp. nov. from the latest Maastrichtian—earliest Danian sediments of the Deccan Intertrappean Beds of Madhya Pradesh, India (Table 1). This is the earliest megafossil record of Calamoid palms from India and offers valuable insights into its diversity and evolution during the latest Cretaceous—Early Paleocene time, before the first evidence of contact between greater India and Eurasia (61 Ma; An et al., 2021), and when most of India was still located south of the Equator (Molnar and

Table 1 The megafossil record of Calamoideae.

Fossil calamoid palm species	NLR (Nearest Living Relative)	Organ	Age	Locality	Reference
***Palmoxylon calamoides* Kumar, Roy et Khan sp. nov.**	**Scandent calamoid palms**	**Stem**	**Late Cretaceous to Early Paleocene**	**Deccan Intertrappean Beds, Madhya Pradesh, India**	**Present study**
Calamoides pikopiko Hartwich *et al.*	*Calamus* L.	Leaf	Late Eocene	South Island, New Zealand	Hartwich *et al.* (2010)
Lepidocaryopsis zeylanicus Hartwich *et al.*	*Calamus* L.	Fruit	Late Eocene	South Island, New Zealand	Hartwich *et al.* (2010)
Calamus daemonorops Chandler	Calamoid palm	Fruit	Oligocene	Lignite deposits, UK	Chandler (1957, 1963)
Palmoxylon daemonoropsoides Velitzelos *et al.*	*Daemonorops* Blume ex Schult. f.	Stem	Late Oligocene	Evros region, Greece	Velitzelos *et al.* (2019)
Eremospatha chilgaensis Pan *et al.*	*Eremospatha dransfieldii* Sunderl.	Leaf	Late Oligocene	Chilga Woreda, Ethiopia	Pan *et al.* (2006)
Calamus noszkyi Jablonszky	*Calamus* L.	Leaf	Early Miocene	Czech Republic	Jablonszky (1914)
Lepidocaryopsis westphaleni Stur	Calamoideae	Fruit	Miocene	Germany	Stur (1873)
Phoenicites sp. Teodoridis *et al.*	cf. *Calamus* sp.	Leaf	Miocene	Capo di Fiume site, Italy	Teodoridis *et al.* (2015)
Lepidocaryopsis sp. Berry	Calamoideae	Fruit	Miocene	Colombia	Berry (1929)
Raphia Dechamps	Raphiinae	Stem	Late Miocene	Sirt Basin, Libya	Dechamps and Maes (1987)

Stock, 2009). We review the fossil history of calamoid palms and discuss their paleobiogeographic patterns.

2. Geological setting

The Deccan Intertrappean Beds (within the Deccan Volcanic Province, DVP; Fig. 1) are unique as their large volume (~2.5 × 10^6 km^3), temporal proximity to the Cretaceous—Paleogene boundary (K—Pg) and the dominance of tholeiitic basaltic lava covering the western, central and southern regions of peninsular India (Kale, 2020). Geographically, the DVP is divided into three main subprovinces, namely the Malwa Lobe subprovince, the Mandla Lobe subprovince, and the Central Deccan subprovince. The present palm stem fossils studied here come from the Mandla Lobe, a 900 m-thick package of 29 flows dated as primarily belonging to Chron 29R (Pathak *et al.*, 2017). Lava poured out through numerous fissures bounding the K—Pg transition and in so doing flooded and created a range of terrestrial and lacustrine environments (Nair and Bhusari, 2001). The fissures occurred in separate episodes with intermittent quiescent periods which marked the accumulation of Intertrappean sediments comprising lacustrine shale, silt, and carbonate deposits hosting floral and faunal fossils (Khosla and Verma, 2015; Verma and Khosla, 2019).

The age of Deccan Intertrappean sediments in Madhya Pradesh is considered to be the latest Maastrichtian—earliest Danian (close to the base of Chron 29R) based on radiometric $^{40}Ar/^{39}Ar$ dating, planktonic foraminifera, and magnetostratigraphy (Venkatesan *et al.*, 1997; Khosla, 1999; Hofmann *et al.*, 2000; Sheth *et al.*, 2001; Chenet *et al.*, 2007; Keller *et al.*, 2009; Shrivastava *et al.*, 2015; Renne *et al.*, 2015; Schoene *et al.*, 2015; Smith *et al.*, 2015).

3. Material and methods

The permineralized fossil stem specimens described in the present study were collected from surface exposures of Deccan Intertrappean Beds at Umariya Ryt (22°46′26″N, 80°32′19″E, Elevation of 490 metre), a medium-sized village located in Dindori District, Madhya Pradesh, Central India (Fig. 1). The Deccan Intertrappean Beds preserved remnants of many lineages of angiosperm plant species (Srivastava *et al.*, 2014; Manchester *et al.*, 2016; Matsunaga *et al.*, 2019; Roy *et al.*, 2021; Kumar *et al.*, 2023). The intertrappean sediments of Madhya Pradesh are rich in permineralized woods (Mahabale, 1958; Lakhanpal *et al.*, 1979; Ambwani and Mehrotra, 1989; Bonde *et al.*, 2008; Khan *et al.*, 2019, 2020a, 2020b), but also yield a few leaves and seed remains (Srivastava *et al.*, 2014; Manchester *et al.*, 2016; Matsunaga *et al.*, 2019; Roy *et al.*, 2021; Kumar *et al.*, 2023).

The detailed anatomy of the fossil stems described here was revealed following the standard thin section-making method (cutting, grinding, polishing, and mounting) of Hass and Rowe (1999) for permineralized (silicate) materials. The thin sections were examined using a transmitted light compound microscope with a photographic attachment (Leica DM 2500) and images of the specimen's external morphological features were made using a digital camera (NIKON D3300) (Fig. 2). For identification, details revealed by the prepared slides were compared with those in published xylotomical databases, a palm website (http://www.infosyslab.fr/Palm—ID/Thomas, 2011) and articles (Tomlinson, 1961; Tomlinson *et al.*, 2011; Thomas and Franceschi, 2013). The holotype specimen (SKBU/PPL/U3) and additional specimen (SKBU/PPL/U4) with prepared slides (SKBU/PPL/U3/T1 and SKBU/PPL/U4/T1) are deposited at the repository in the Department

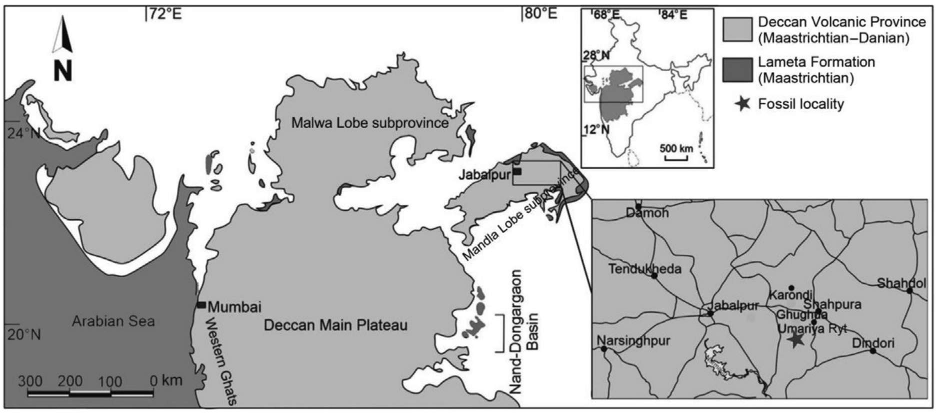

Fig. 1 Map showing the surviving extent of the Deccan Volcanic Province (DVP), and the star showing fossil locality (modified after Smith *et al.*, 2015).

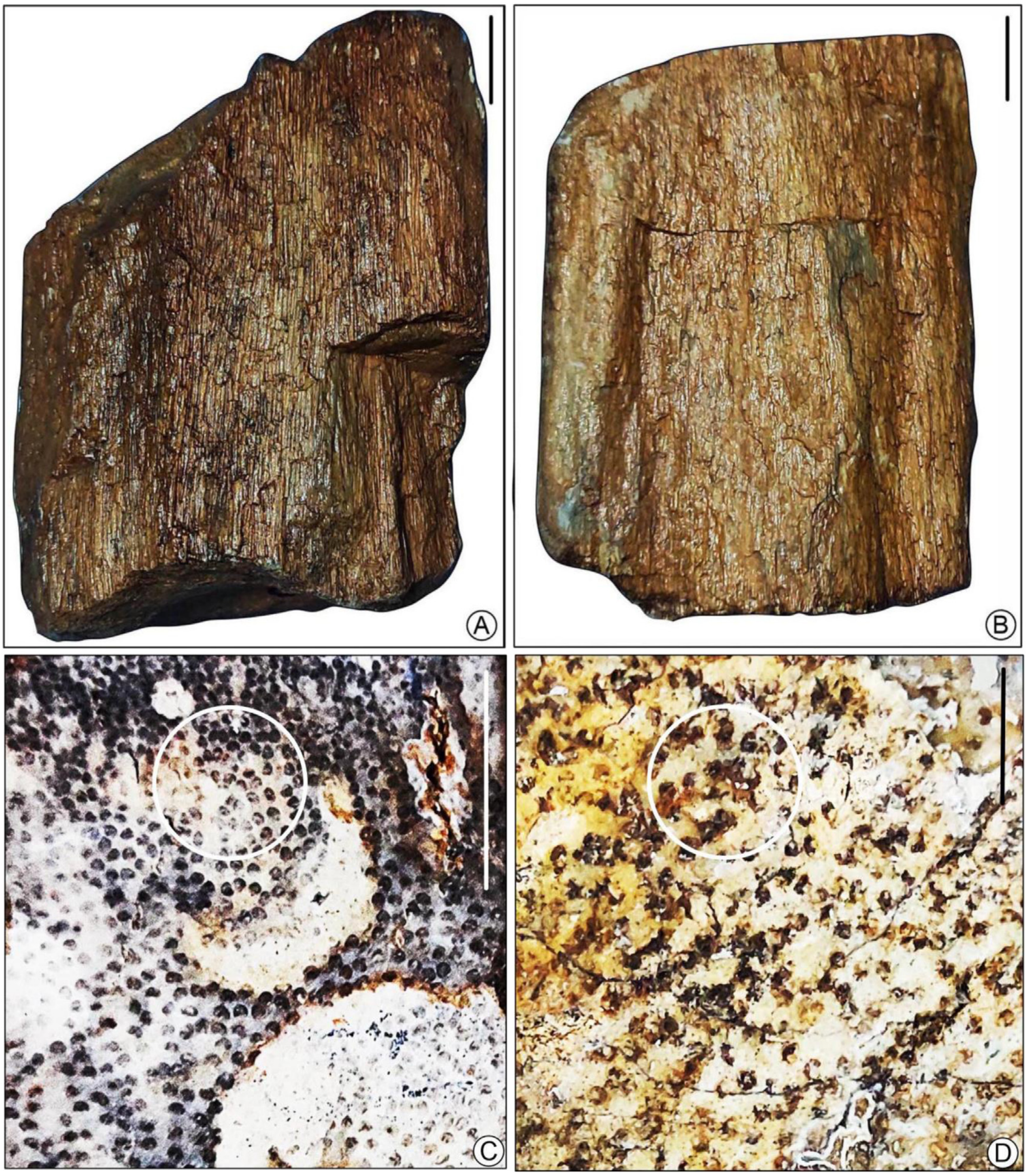

Fig. 2 Recovered fossilized palm stems in **A)** specimen SKBU/PPL/U3 and **B)** specimen SKBU/PPL/U4 (scale bar = 1 cm); **C)** The enlarged view of **A** and **D)** The enlarged view of **B** on the cross-section, white circles showing the fibrovascular bundles (scale bar = 0.5 cm).

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4. Results — Systematic description of fossil stems

Family: Arecaceae Schultz, 1832.
Subfamily: Calamoideae Beilschmied, 1833.
Genus: *Palmoxylon* Schenk, 1882.
Species: *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. (Figs. 3 and 4).

Etymology: The specific epithet "*calamoides*" recognizes similarities of our palm stem specimens with calamoid palms.

Specific diagnosis: Calamus-type general stem organization; mostly uniform density and regularly oriented fibrovascular bundles (fvbs) with two large-sized metaxylem vessels throughout the cortical and central zone, presence of gum residues within vessels; the fibrous part or dcap (the outer fibrous part of fibrovascular bundle) not pronounced; reniform-shaped (mostly) to sagittate-shaped dcap; both tabular and radiating parenchyma absent; fibrous

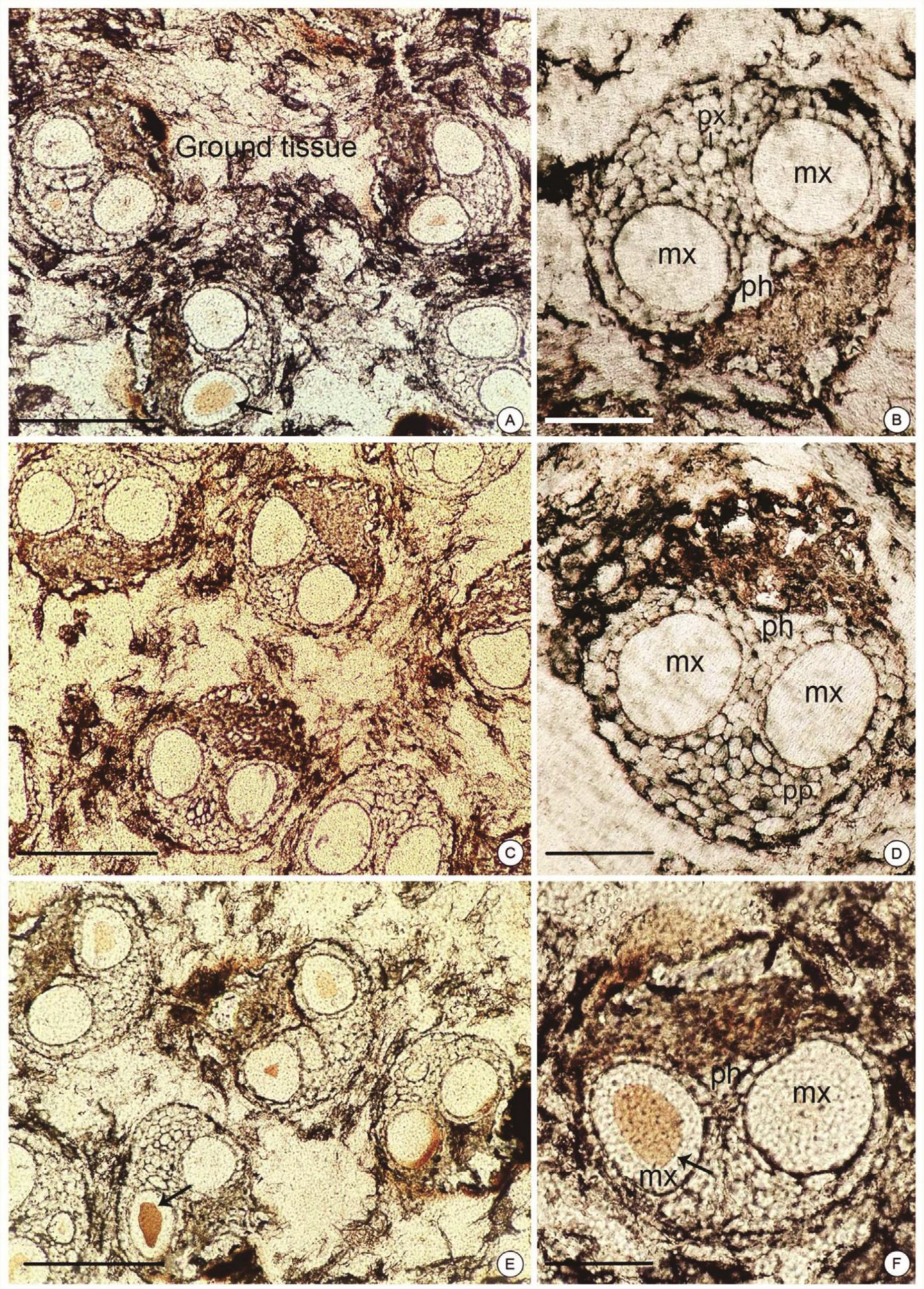

Fig. 3 Transmitted light compound microscopic images of a transverse section of the outer sub-cortical zone (SZ), the sub-dermal central zone (SD) and the inner central zone (IN) of the fossil palm stem, *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. (Specimen No. SKBU/PPL/U3). **A)** Fibrovascular bundles with wide metaxylem vessel showing gum residue (black arrow) and ground tissue in the SZ (Scale bar = 500 μm); **B)** Enlarged view of a fibrovascular bundle in the SZ (Scale bar = 200 μm); **C)** Fibrovascular bundles in the SD (Scale bar = 500 μm); **D)** Transverse section showing an enlarged view of a fibrovascular bundle with a single phloem strand and two wide vessels (Scale bar = 200 μm); **E)** Fibrovascular bundles in the IN showing gum residue (black arrow) (Scale bar = 500 μm); **F)** Fibrovascular bundles showing gum residue (black arrow) in a metaxylem vessel (Scale bar = 200 μm). Abbreviations: mx: metaxylem; px: protoxylem; ph: phloem strand.

bundles absent; no centrifugal differentiation of fibrous part of fvbs; zone of transition between sub-cortical zone (SZ) and central zone (CZ) absent.

Description: Two permineralized stems are brownish and well-preserved; both are anatomically divisible into an outermost cortical zone (CT), an outer sub-cortical zone (SZ), and a central zone (CZ), and exhibit a Calamus-type general stem organization. Fibrovascular bundles (fvbs) are uniformly distributed; a zone of transition (TZ) is absent between the SZ and

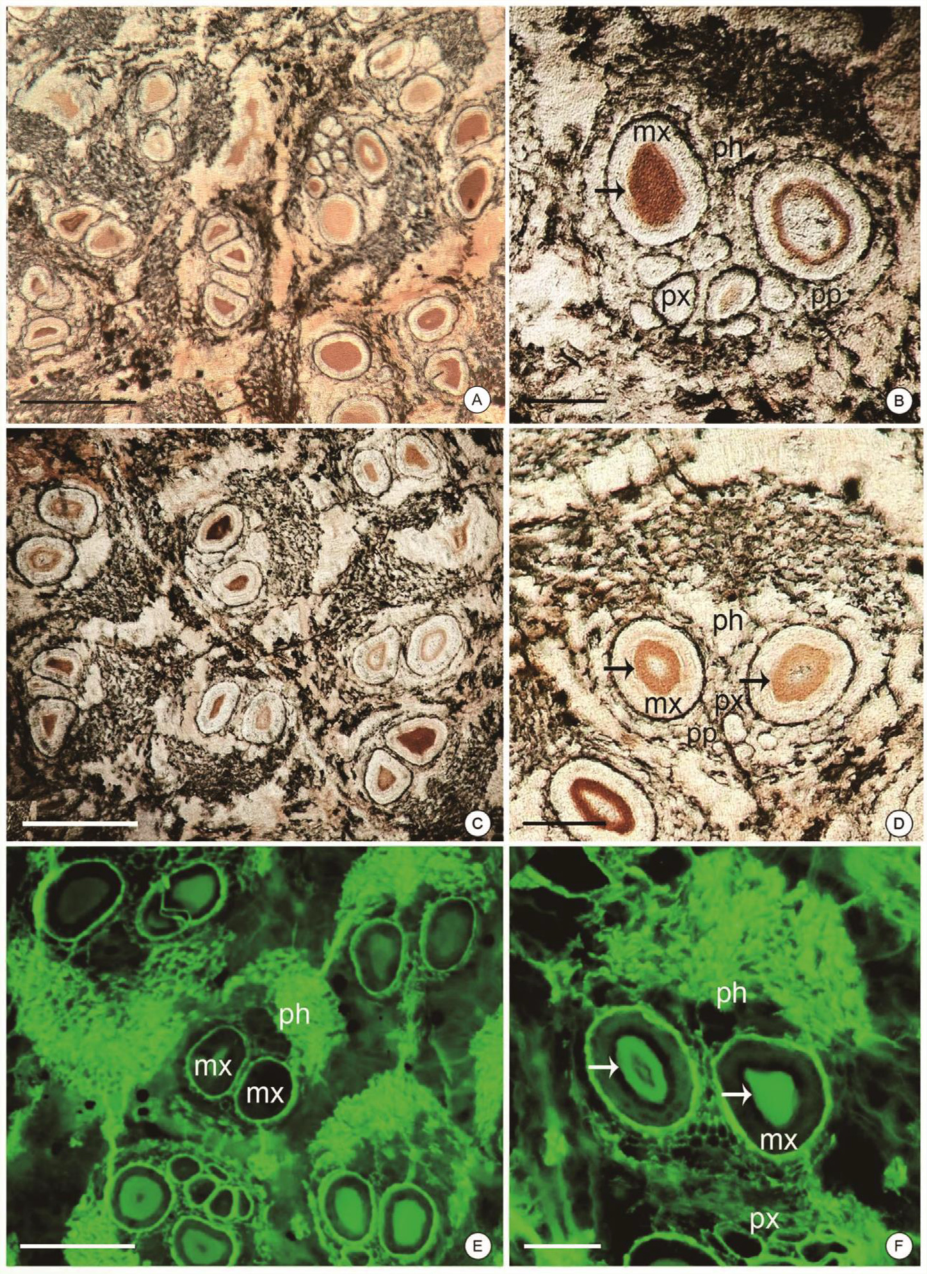

Fig. 4 Transmitted light compound microscopic images of a transverse section of the outermost cortical zone (CT), the outer sub-cortical zone (SZ) and the sub-dermal central zone (SD) of the fossil palm stem, *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. (Specimen No. SKBU/PPL/U4). **A)** Fibrovascular bundles with wide metaxylem vessels in the CT (Scale bar = 500 μm); **B)** Enlarged view of a fibrovascular bundle in the SD with gum residue (black arrow) in the metaxylem vessel and several protoxylem vessels (Scale bar = 200 μm); **C)** Fibrovascular bundles in the SD (Scale bar = 500 μm); **D)** Transverse section showing an enlarged view of a fibrovascular bundle with gum residue (black arrows) (Scale bar = 200 μm); **E)** An inverted fluorescence microscope image showing a transverse section of the SZ (Scale bar = 500 μm); **F)** Enlarged inverted fluorescence microscope image of a single fibrovascular bundle showing gum residue (white arrows) (Scale bar = 200 μm). Abbreviations: mx: metaxylem; px: protoxylem; ph: phloem strand; pp: paravascular parenchyma.

the CZ; the fibrous part of fvbs has no centrifugal differentiation and is not pronounced. Based on the orientation, the distribution of fvbs, and the nature of the ground tissue, the CZ is divided into three subzones termed dermal (D) central zone, sub-dermal (SD) central zone, and inner (IN) central zone. In D, SD as well as IN central zones, fvbs are more or less similar in size ranging from 600 × 500 μm to 750 × 650 μm, and similar in shape as oval, and uniformly distributed (Figs. 3 and 4). A more or less

Table 2 Comparative anatomical chart of modern calamoid taxa with *Palmoxylon calamoides* sp. nov. (Based on Thomas and Franceschi, 2013).

Calamoideae	Stem anatomical characters									
	Von Mohl-type classification	Shape of the fibrous part in TS	Developed cortex	Fibrous bundles in central cylinder	Auricular sinus	Number of vessel elements/fibrovascular bundles	Number of phloem strands	Radiating parenchyma	Tabular parenchyma	Centrifugal differentiation of fibrous parts
Metroxylon or *Pigafetta* (Calameae)	Mauritia-type	Sagittata and Reniforma	Absent	Absent	Angular and absent in central zone	1	1	Absent	Absent	Present
Eugeissona (Eugeissoneae)	Mauritia-type	Reniforma	Absent	Present	Angular and absent in central zone	[1(2)]	1	Absent	Absent	Present
Raphia or *Mauritia* or *Mauritiella* (Lepidocaryeae)	Mauritia-type	Sagittata and Reniforma	Absent	Absent	Angular and absent in central zone	[1(2)]	1	Absent	Absent	Present
Lepidocaryum (Lepidocaryeae)	Mauritia-type	Reniforma	Absent	Absent	Angular and absent in central zone	1	1	Absent	Absent	Present
Scandent Calamoideae	Calamus-type	—	Absent	Present or Absent	—	1	1 and 2	Absent	Absent	Absent
Palmoxylon calamoides sp. nov.	Calamus-type	Sagittata and Reniforma	Absent	Absent	Seemingly angular	2	1	Absent	Absent	Absent

constant density of fvbs also occurs throughout the central cylinder. The vascular part of each fvb has two wide prominent metaxylem vessels, and characteristically one phloem strand, with three to six narrow, small protoxylem vessels observed in some fvbs. Gum residues are prominently in the wide metaxylem vessels (Figs. 3F, 4B, 4D). Diminutive fvbs, as well as fibrous bundles, are absent. The fvbs have the following mean dimensions: Hmax (maximal height of the fvb) = 650 μm; Lmax (maximal width of the fvb) = 500 μm; Hvasc (height of the vascular part) = 500 μm; Lvasc (width of the vascular part at the auricular sinus level) = 150 μm; and, vessel mean diameter = 230—250 μm. A reniform- to sagittate-shaped dcap is present adjacent to the single phloem strand. The dcap has thick-walled, sclerenchymatous type cells (Figs. 3 and 4). A very narrow ventral fibrous sclerenchymatous part (vcap) is adjacent to the xylem of some fvbs. The median sinus is not clear and the auricular sinus is seemingly angular, without stegmata or radiating and tabular parenchyma. In the D central zone, the fvbs are somewhat sparsely placed and their frequency is slightly more than those in SD and IN central zones. The frequency of fvbs in the D central zone varies from 40 per cm^2 to 50 per cm^2. In the SD central zone, the fvbs are slightly larger, more sparsely placed, and their frequency is less than those in the D central zone. The frequency of fvbs in the SD central zone varies from 35 per cm^2 to 45 per cm^2. The ground tissue is not well-preserved, and in the central zone, some round to oval parenchymatous cells with diameters of 50 μm—80 μm are present (Fig. 3A).

Materials: Two well-preserved fossil stems.

Holotype: SKBU/PPL/U3.

Paratype: SKBU/PPL/U4.

Type horizon and age: Deccan Intertrappean Beds; latest Maastrichtian (Late Cretaceous)—earliest Danian (early Paleocene).

Type locality: Umariya Ryt village (location: 22°46′26″N, 80°32′19″E, elevation of 1607.61 ft a.m.s.l) in Dindori District, Madhya Pradesh, Central India.

Repository: Department of Botany, Sidho-Kanho-Birsha University, West Bengal, India.

5. Discussion

5.1. *Comparison*

For the taxonomic placement of the fossil specimens reported here, we follow the scheme of stem anatomical descriptors for modern palms compiled by Thomas and Franceschi (2013) and the book entitled "*The Anatomy of Palms*" by Tomlinson *et al.* (2011). The major anatomical characteristics of the present Deccan fossil specimens are as follows: a Calamus-type general stem pattern; the presence of well-preserved fvbs with two wide metaxylem vessel elements (230 μm—250 μm) and one phloem strand; lack of continuity between protoxylem and metaxylem vessel elements; and an absence of centrifugal differentiation in sclerenchymatous fibrous parts. The diagnostic stem anatomical features of climbing calamoid palms are as follows: a Calamus-type general stem pattern; a uniform density of their fvbs and disproportionately wide metaxylem vessels up to 400 μm as compared to other palms; one or two large metaxylem vessels in the central axial portion of each vascular bundle; and a lack of continuity between protoxylem and metaxylem vessel elements and central fvbs with one or two phloem strands (Tomlinson and Fisher, 2000; Fisher, 2002; Tomlinson *et al.*, 2011). However, non-scandent calamoid palms (*Metroxylon* Rottb. of Calameae, *Eugeissona* Griff. of Eugeissoneae, *Raphia* P. Beauv. and *Lepidocaryum* Mart. of Lepidocaryeae) generally exhibit Mauritia-type general stem patterns, showing the centrifugal differentiation of fibrous parts of fvbs (Thomas and Franceschi, 2013). Based on the Calamus-type general stem organization with no centrifugal differentiation of fibrous parts, combined with the structure of the fvbs (reniform- to sagittata-shaped dcap), the number of fvbs (mostly 2) and wide metaxylem vessel elements (230 μm—250 μm) in each fvb with one phloem strand, our Deccan fossil stem specimens are most similar in terms of stem anatomy to modern scandent calamoid palm genera, and are distinct from non-scandent calamoid palms (Table 2).

The number of metaxylem vessel elements per fvb is an important anatomical character at the subfamily level (Thomas and Boura, 2015). An affinity to arecoid palms can be ruled out because they mostly have one metaxylem vessel (rarely two), highly lacunose ground tissue, and well-developed massive fibrous parts. However, our specimens do possess relatively poorly developed fibrous parts. Coryphoid palms have one, two, or more metaxylem elements per fvb (Couvreur *et al.*, 2011) and these metaxylem vessels are smaller in comparison to those of our specimens. In addition, members of the Coryphoideae generally exhibit a Cocos-type stem pattern (fvbs are uniformly distributed throughout the cross-section) or Corypha-type stem pattern (a progressive decrease of the fibrous parts of fvbs). In some members of coryphoid palms, tabular parenchyma (around the vcap of the fvb) and radiating parenchyma (around the dcap of the fvb) are present. Thus, an affinity to our palm

Fig. 5 Fibrovascular bundles (fvbs) of different extant genera of Calamoideae (Scale bar = 200 μm). **A)** *Plectocomia* Mart. ex-Blume; **B)** *Daemonorops* Blume ex Schult. f.; **C)** *Calamus* L.; **D)** *Laccosperma* (G. Mann & H. Wendl.) Drude; **E)** *Korthalsia* Blume; **F)** *Oncocalamus* (G. Mann & H. Wendl.) H. Wendl.; **G)** *Eremospatha* (G. Mann & H. Wendl.) Schaedtler; **H)** *Raphia* P. Beauv.; **I)** *Mauritia* L. f.; **J)** *Plectocomiopsis* Becc.; **K)** *Myrialepis* Becc.; **L)** *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. Abbreviations: dcap: the outer fibrous part of the fibrovascular bundle; mx: metaxylem; px: protoxylem; ph: phloem strand; pp: paravascular parenchyma.

specimens can be ruled out because they lack both tabular and radiating parenchyma like in the members of the Calamoideae. Ceroxyloideae members differ in having a Mauritia-type general stem pattern and exhibiting an abrupt decrease of the fibrous part from the periphery to the centre. However, in our specimens, no gradual differentiation occurs within the fibrous part of the fvbs from the periphery toward the centre. In addition, Ceroxyloideae has 2, 3, or ≥4 metaxylem vessels per fvb. However, the monotypic subfamily Nypoideae, represented by *Nypa fruticans* Wurmb, is distinguishable from our palm stem specimens because *Nypa* has diffusely arranged fvbs and very narrow metaxylem vessels. Therefore, based on the above anatomical characteristics, we regard Calamoideae as the most closely related extant subfamily to our fossil specimens.

To determine the generic affinity of these fossil specimens, we compared them with different modern genera of scandent calamoid palms such as *Korthalsia* Blume, *Calamus* L., *Oncocalamus* (G. Mann & H. Wendl.) H. Wendl., *Eremospatha* (G. Mann & H. Wendl.) Schaedtler, *Myrialepis* Becc., *Plectocomiopsis* Becc., *Laccosperma* (G. Mann & H. Wendl.) Drude, and *Plectocomia* Mart. ex-Blume (Fig. 5). Two calamoid palm genera, *Korthalsia* and *Calamus*, can be ruled out because they have central fvbs with two phloem strands and one wide metaxylem vessel. *Laccosperma*, *Plectocomiopsis*, and *Plectocomia* differ in having one wide metaxylem vessel in their central fvbs. Our specimens show the most anatomical similarity to the Southeast Asian calamoid palm genus, *Myrialepis*, and the Western African genera *Oncocalamus* and *Eremospatha*. This is based on the nature of fvbs (central fvbs with one phloem strand and two wide metaxylem vessels), the nature of the ground tissue, and the presence of gum residue in the metaxylem vessel (Tomlinson *et al.*, 2011).

We compare our fossil specimens with earlier reported reliable Indian fossil species of *Palmoxylon* (Table 3). Our specimens differ from ten Indian *Palmoxylon* species (*Palmoxylon mohgaonensis*, *Palmoxylon penchense*, *Palmoxylon parapaniensis*, *Palmoxylon mandlaensis*, *Palmoxylon livistonoides*, *Palmoxylon arviensis*, *Palmoxylon dilacunosum*, *Palmoxylon phytelephantoides*, *Palmoxylon dindoriensis* and *Palmoxylon coryphaoides*) in the absence of fibrous bundles. However, the above-mentioned Indian species have characteristic fibrous bundles in the central zone. *Palmoxylon mohgaonensis*, *P. mandlaensis*, *P. livistonoides*, *P. arviensis*, *P. siltherensis*, *P. phytelephantoides*, *P. bhisiensis*, *P. lametaei*, *P. deoriensis*, and *P. dindoriensis* exhibit tabular parenchyma around fibrous parts of fvbs. Radiating parenchyma around vascular parts of fvbs are prominent in *Palmoxylon livistonoides*, *P. kamalam*, *P. deoriensis*, and *P. phytelephantoides*. However, the current fossil specimens lack both tabular and radiating parenchyma as in *Palmoxylon penchense*, *P. parapaniensis*, *P. shahpuraensis*, *P. dilacunosum*, *P. ceroxyloides* and *P. coryphaoides*. Some earlier reported species differ in their stem pattern. Five species namely, *Palmoxylon parapaniensis*, *P. livistonoides*, *P. lametaei*, *P. deoriensis*, and *P. dindoriensis* are distinct from the current specimens within the presence of Cocos-type general stem organization. The Corypha-type is noticed in *P. mandlaensis* and *P. coryphaoides* while the Mautitia-type is found in *P. ceroxyloides*. However, the present specimens show Calamus-type general stem organization.

To date, only one calamoid palm stem species *Palmoxylon daemonoropsoides* has been reported from the late Oligocene sediments of the Evros region, Greece, Europe (Table 1; Velitzelos *et al.*, 2019). Our specimens are different from the Greek Oligocene species because they possess much larger metaxylem vessels (230 µm—250 µm) than those of Greek species (50 µm—100 µm). Thus, given the distinction of the present Deccan fossil palm specimens from the hitherto recorded species of palm stem, it is preferred to describe it as a new palm species *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov.

5.2. *Paleobiogeographic implications*

The origin and immigration of the Calamoideae remain a mystery because of its very limited fossil record (Table 1). The discovery of our Deccan fossils, together with phylogenetic and paleobiogeographic analyses calibrated using earlier fossil records, supports a Gondwanan origin for Calamoideae.

Reliable megafossils with features similar to those of the Calamoideae have been recovered from late Eocene sediments of New Zealand, the Oligocene sediments of Europe and Africa, and the Miocene sediments of Europe and South America (Table 1; Fig. 6). They are mainly reported in the form of leaves (Pan *et al.*, 2006; Teodoridis *et al.*, 2015), fruits (Stur, 1873; Berry, 1929; Hartwich *et al.*, 2010) and stems (Dechamps and Maes, 1987; Velitzelos *et al.*, 2019). Our megafossils of scandent calamoid palm stems from the Deccan Intertrappean Beds of Central India, dated as the latest Maastrichtian—earliest Danian, are the oldest so far, confirming the Gondwanan presence of calamoid palms. They also indicate that this palm subfamily had already presented in India during the Late Cretaceous (Maastrichtian), about 4 million years before the collision between India and Eurasia. Earlier

Table 3 Comparative anatomical details of earlier reported reliable fossil species of *Palmoxylon* with *Palmoxylon calamoides* sp. nov.

Fossil species of *Palmoxylon*	Stem anatomical characters									
	Von Mohl-type classification	Shape of the fibrous part in TS	Developed cortex	Fibrous bundles in central cylinder	Number of vessel elements/ fibrovascular bundles	Number of phloem strands	Radiating parenchyma	Tabular parenchyma	Centrifugal differentiation of fibrous parts	References
Palmoxylon mohgaonensis Trivedi and Surange	—	Cordata	Present	Present	2—3	Poorly developed	—	Present	Absent	Trivedi and Surange (1970)
P. penchense Trivedi and Verma	—	Reniforma	Present	Present	1—2	1	Absent	Absent	Absent	Trivedi and Verma (1972)
P. parapaniensis Lakhanpal *et al.*	Cocos-type	Reniforma to Lunata	—	Present	2, 3—4	—	Absent	Absent	—	Lakhanpal *et al.* (1979)
P. mandlaensis Lakhanpal *et al.*	Corypha-type	Reniforma to Cordate	—	Present	1—2, 2—3	?	Absent	Present	—	Lakhanpal *et al.* (1979)
P. livistonoides Prakash and Ambwani	Cocos-type	Reniforma	Present	Present	1—2	1	Present	Present	Absent	Prakash and Ambwani (1980)
P. arviensis Ambwani	—	Cordata to Reniforma	—	Present	1, rarely 2	—	Absent	Present	Absent	Ambwani (1981)
P. shahpuraensis Ambwani	—	Reniforma to Cordata	—	Absent	1—2, 3	—	Absent	Absent	—	Ambwani (1983)
P. dilacunosum Ambwani	—	Reniforma	Present	Present	1—2	—	Absent	Absent	Absent	Ambwani (1984a)
P. siltherensis Ambwani	—	Reniforma	Present	Absent	1	—	Absent	Present	Absent	Ambwani (1984b)
P. kamalam Datar and Patil	—	Complanata	Present	Absent	2	—	Present	—	—	Datar and Patil (2002)
P. phytelephantoides Chate *et al.*	—	Reniforma	Present	Present	Many xylem elements devoid of vessels	—	Present	Present	Absent	Chate *et al.* (2019)
P. bhisiensis Dutta *et al.*	—	Reniforma to Cordata	Present	Absent	2	1	Absent	Present	Absent	Dutta *et al.* (2007)
P. lametaei Dutta *et al.*	Cocos-type	Lunata and Vaginata	Present	Absent	2	1	Absent	Present	Absent	Dutta *et al.* (2011)
P. deoriensis Khan *et al.*	Cocos-type	Reniforma	Present	Absent	1—2	—	Present	Present	Absent	Khan *et al.* (2019)
P. dindoriensis Khan *et al.*	Cocos-type	Reniforma	Present	Present	2	1	Absent	Present	Absent	Khan *et al.* (2020a)
P. ceroxyloides Khan *et al.*	Mauritia-type	Reniforma	Absent	Absent	>4	1	Absent	Absent	Present	Khan *et al.* (2020b)

P. coryphaoides Ali *et al.*	Corypha-type	Vaginata to Lunata	Present	Present	1, 2, >4	1	Absent	Absent	Absent	Ali *et al.* (2023)
***Palmoxylon calamoides* Kumar, Roy et Khan sp. nov.**	**Calamus-type**	**Sagittata and Reniforma**	**Absent**	**Absent**	**2**	**1**	**Absent**	**Absent**	**Absent**	**Present study**

fossil pollen records of Calamoideae from the Late Cretaceous sediments also favour a Gondwanan origin (Van Hoeken-Klinkenberg, 1964; Salard-Cheboldaeff, 1981; Schrank, 1994; Baker *et al.*, 2000; Harley and Baker, 2001).

Fossil Calamoideae has been reported from the Oligocene and Miocene sediments of Europe (Table 1; Fig. 6; Stur, 1873; Jablonszky, 1914; Teodoridis *et al.*, 2015; Velitzelos *et al.*, 2019), our findings from the Late Cretaceous—Early Paleocene of India suggest this palm subfamily arrived in Europe via the "raft" of India. It may have migrated to Europe after the suturing of India and Eurasia following the formation of the initial connection around 61 Ma (An *et al.*, 2021), and possibly via the West Siberian Sea and Turgai Strait (Akhmetiev and Beniamovski, 2009).

Additional fossil evidence of Calamoideae from the late Oligocene sediments of Ethiopia (Pan *et al.*, 2006) and the Miocene sediments of the Sirt Basin of Libya, Africa (Dechamps and Maes, 1987) mark its dispersal from India to Africa. Various researchers (e.g., Briggs, 1989, 2003; Case, 2002; Rage, 2003; Chatterjee and Scotese, 2010; Clementz *et al.*, 2011) have suggested that the floral and faunal exchange between India and Africa could have been via Greater Somalia towards the end of the Cretaceous. Additionally, the Kohistan Ladakh Arc, which existed during the Late Cretaceous (Chatterjee *et al.*, 2013), may have facilitated the migration of Calamoid palms from India to Africa.

Evidence of Calamoid palms from the Eocene sediments of South Island, New Zealand (Hartwich *et al.*, 2010) suggests long-distance trans-oceanic dispersal (LDD), possibly abiotically by ocean currents (Carlquist, 1967, 1983), and biotically by mammals or birds (Winkworth *et al.*, 2002). Various animals may act as important LDD agents of calamoid fruits and seeds (Zona and Henderson, 1989). The spread of some scandent calamoid species of *Laccosperma*, *Eremospatha*, *Calamus*, and *Plectocomia* was likely facilitated by mammals, excluding bats because the scaly fruits and spiny infructescences of the Calamoideae may preclude bats as dispersers (Bartels, 1964; Dubost, 1984; Lahm, 1986), but several bird species such as *Anthracoceros convexus*, *Ducula spilorrhoa*, and *Casuarius* may have played a key role in the long-distance seed dispersal of some members of Calamoideae (Crome, 1975, 1976; Dransfield, 1981; Stocker and Irvine, 1983). If this is the case then it explains the arrival of calamoid palms in South America by the Miocene (Morley, 1998, 2003), but does not explain why they did not transfer to Europe preceding the docking of India at around 60 Ma.

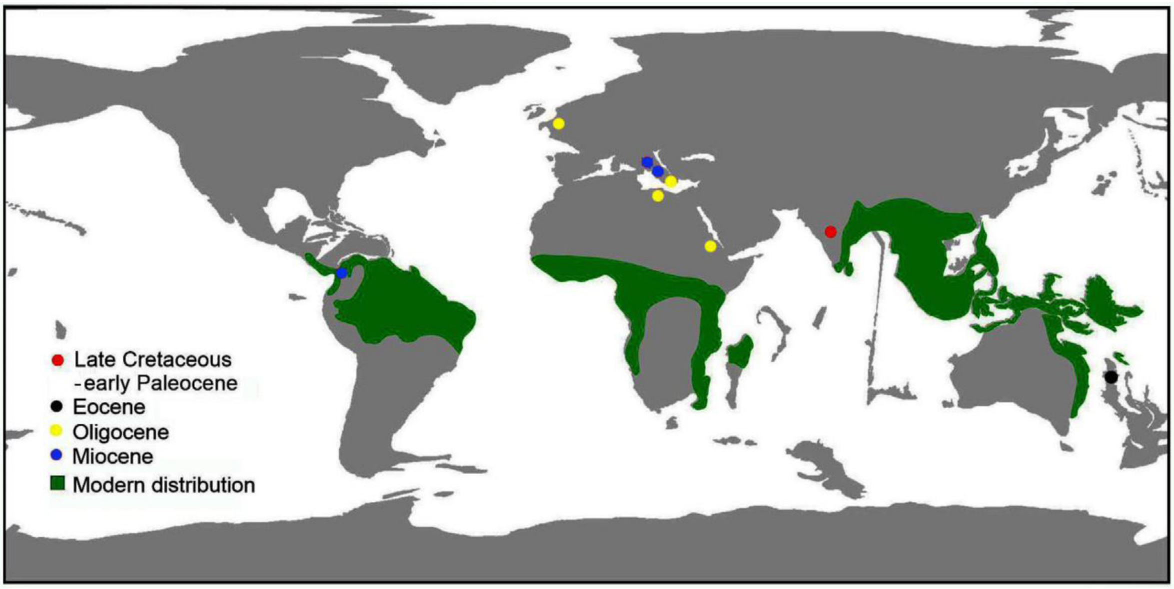

Fig. 6 Extant fossil distribution of Calamoideae (Modified base maps from https://www.odsn.de/odsn/services/paleomap/paleomap.html).

Further fossil evidence is needed for the origin and dispersal routes of the Calamoideae.

5.3. *Paleoclimatic implications*

Calamoid palms generally grow in high-rainfall tropical or subtropical areas with average annual temperatures mostly >15 °C (Xu *et al.*, 2000; McClatchey *et al.*, 2006). The presence of Calamoideae palm stems from the latest Maastrichtian—earliest Danian sediments of the Deccan Intertrappean Beds of Madhya Pradesh indicates that the temperature was warm enough to allow tropical or subtropical plants to grow during the time of deposition. This inference is also consistent with earlier reported qualitative (Prasad *et al.*, 2013; Srivastava *et al.*, 2014; Manchester *et al.*, 2016; Baas *et al.*, 2017; Kapgate *et al.*, 2017; Khan *et al.*, 2019; Smith *et al.*, 2021) and quantitative (Bhatia *et al.*, 2021) climate data (Climate Leaf Analysis Multivariate Program) based on plant megafossils recovered from the same locality.

6. Conclusions

This study presents a new species of *Palmoxylon calamoides* Kumar, Roy et Khan sp. nov. from the latest Maastrichtian (Late Cretaceous) to earliest Danian (early Paleocene) (Chron 29R) sediments of the Deccan Intertrappean Beds of Central India. This is the earliest megafossil record of scandent calamoid palms from India. The presence of scandent Calamoideae in India at the very beginning of the Cenozoic suggests they were likely an important immigrant that went on to become a characteristic component of the wet tropical forests of Southeast Asia. For a better understanding of the calamoid palm biogeography, further fossil discoveries in deep time are required.

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Availability of data and materials

Data supporting the findings of this research are available upon request from the corresponding author.

Authors' contributions

Sanchita Kumar: Data curation, Methodology, Writing — original draft, Writing — review & editing. **Kaustav Roy:** Data curation, Resources. **Robert A.**

Spicer: Conceptualization, Methodology, Writing — review & editing. **Mahasin Ali Khan:** Supervision, Writing — review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Akhmetiev, M.A., Beniamovski, V.N., 2009. Paleogene floral assemblages around epicontinental seas and straits in Northern Central Eurasia: Proxies for climatic and paleogeographic evolution. *Geológica Acta*, 7(1), 297—309.

Ali, A., Roy, K., Mukherjee, B., Bera, S., Khan, M.A., 2023. A new permineralized corypha-type coryphoid palm stem from K—Pg of India: Anatomy, systematics, saprophytic fungi, and paleoecology. *Turkish Journal of Botany*, 48(2), 105—119.

Ambwani, K., 1981. *Palmoxylon arviensis* sp. nov. from Deccan Intertrappean Beds of Nawargaon, Wardha District, Maharashtra. *Journal of Palaeosciences*, 27(1—3), 132—137.

Ambwani, K., 1983. *Palmoxylon shahpuraensis* sp. nov. resembling *Licuala* from the Deccan Intertrappean Beds of Mandla District. *Madhya Pradesh Palaeobotanist*, 31, 52—59.

Ambwani, K., 1984a. *Palmoxylon dilacunosum* sp. nov., from the Deccan Intertrappean Beds of Mandla District, Madhya Pradesh. *Palaeobotanist*, 32, 211—216.

Ambwani, K., 1984b. *Palmoxylon siltherensis* sp. nov., from the Deccan Intertrappean Beds of Mandla District, Madhya Pradesh. *Palaeobotanist*, 31, 213—217.

Ambwani, K., Mehrotra, R.C., 1989. A new fossil palm wood from the Deccan Intertrappean Beds of Shahpura, Mandla District, Madhya Pradesh. *Geophytology*, 19, 70—75.

An, W., Hu, X., Garzanti, E., Wang, J.G., Liu, Q., 2021. New precise dating of the India—Asia collision in the Tibetan Himalaya at 61 Ma. *Geophysical Research Letters*, 48(3), e2020GL090641. https://doi.org/10.1029/2020GL090641.

Asmussen, C.B., 2000. Phylogeny of the palm family (Arecaceae) based on rps16 intron and *trn*L—*trn*F plastid DNA sequences. In: Wilson, K.L., Morrison, D.A. (Eds.), *Monocotyledons: Systematics and Evolution*. CSIRO Publishing, Melbourne, Australia, pp. 525—535.

Asmussen, C.B., Chase, M.W., 2001. Coding and noncoding plastid DNA in palm systematics. *American Journal of Botany*, 88(6), 1103—1117.

Asmussen, C.B., Dransfield, J., Deickmann, V., Barfod, A.S., Pintaud, J.C., Baker, W.J., 2006. A new subfamily classification of the palm family (Arecaceae): Evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society*, 151(1), 15—38.

Baas, P., Manchester, S.R., Wheeler, E.A., Srivastava, R., 2017. Fossil wood with dimorphic fibers from the Deccan Intertrappean Beds of India — The oldest fossil Connaraceae? *IAWA Journal*, 38(1), 124—133.

Baker, W.J., Asmussen, C.B., Barrow, S.C., Dransfield, J., Hedderson, T.A., 1999. A phylogenetic study of the palm family (Palmae) based on chloroplast DNA sequences from the *trn*L—*trn*F region. *Plant Systematics and Evolution*, 219, 111—126.

Baker, W.J., Dransfield, J., Hedderson, T.A., 2000. Phylogeny, character evolution, and a new classification of the calamoid palms. *Systematic Botany*, 25, 297—322.

Baker, W.J., Dransfield, J., 2016. Beyond *Genera Palmarum*: Progress and prospects in palm systematics. *Botanical Journal of the Linnean Society*, 182, 207—233.

Baker, W.J., Savolainen, V., Asmussen-Lange, C.B., Chase, M.W., Dransfield, J., Forest, F., Harley, M.M., Uhl, N.W., Wilkinson, M., 2009. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology*, 58, 240—256.

Baker, W.J., Couvreur, T.L.P., 2013a. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography*, 40, 274—285.

Baker, W.J., Couvreur, T.L.P., 2013b. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. *Journal of Biogeography*, 40, 286—298.

Barman, G., Daura, B.K., 1970. *Zalaccites jaintiensis* gen. et sp. nov. from the Plateau (Cherra) sandstones of Jaintia Hills, United Khasi and Jaintia Hills District, Assam, India. *Science and Culture*, 36, 63—64.

Bartels, E., 1964. On *Paradoxurus hermaphroditus javanicus* (Horsfield, 1824). The common palm civet or tody cat in western Java. Notes on its food and feeding habits. Its ecological importance for wood and rural biotopes. *Beaufortia*, 10(124), 193—201.

Beilschmied, C.T., 1833. J. Lindley's characters distinctive oder Hauptkennzeicher der naturlichen Pflanzenfamilien. *Flora*, 16, 49—111.

Berry, E.W., 1929. Tertiary fossils from Colombia, South America. *Proceedings of the US National Museum*, 75, 1—12.

Bhatia, H., Khan, M.A., Srivastava, G., Hazra, T., Spicer, R.A., Hazra, M., Mehrotra, R.C., Spicer, T.E.V., Bera, S., Roy, K., 2021. Late Cretaceous—Paleogene Indian monsoon climate vis-à-vis movement of the Indian Plate, and the birth of the South Asian Monsoon. *Gondwana Research*, 93, 89—100.

Bonde, S.D., Chate, S.V., Gamre, P.G., Nipunage, D.S., 2008. A dichotomously branched fossil palm stem from the Deccan Intertrappean Beds of India. *Current Science*, 94(2), 182—183.

Briggs, J.C., 1989. The historical biogeography of India: Isolation or contact. *Systematic Zoology*, 38, 322—332.

Briggs, J.C., 2003. The biogeographic and tectonic history of India. *Journal of Biogeography*, 30, 381—388.

Carlquist, S., 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club*, 94(3), 129—162.

Carlquist, S., 1983. Intercontinental dispersal. In: Kubitzki, K. (Ed.), *Dispersal and Distribution*. *Paul Parey*. Germany, Hamburg, pp. 37—47.

Case, J.A., 2002. A new biogeographic model for dispersal of Late Cretaceous vertebrates into Madagascar and India. *Journal of Vertebrate Paleontology*, 22, 42A.

Chandler, M.E.J., 1957. The Oligocene Flora of the Bovey Tracey Lake Basin, Devonshire. *Bulletin of the British Museum, Natural History (Geology)*, 3, 71—123.

Chandler, M.E.J., 1963. *The Lower Tertiary Floras of Southern England, Vol. 3. Flora of the Bournemouth Beds; the Boscombe, and the Highcliff Sands*. British Museum (Natural History), London.

Chate, S.V., Bonde, S.D., Gamre, P.G., 2019. *Palmoxylon phytelephantoides* sp. nov. A New Fossil Palm from the Deccan Intertrappean Beds of Umaria, Madhya Pradesh, India. *International Journal of Advanced Scientific Research and Management*, 4(6), 189—193.

Chatterjee, S., Goswami, A., Scotese, C.R., 2013. The longest voyage: Tectonic, magmatic, and paleoclimatic evolution of the Indian Plate during its northward flight from Gondwana to Asia. *Gondwana Research*, 23(1), 238—267.

Chatterjee, S., Scotese, C., 2010. The wandering Indian Plate and its changing biogeography during the Late Cretaceous—Early Tertiary period. *New Aspects of Mesozoic Biodiversity. Lecture Notes in Earth Sciences*. Springer, Berlin, Heidelberg, pp. 105—126.

Chenet, A.L., Quidelleur, X., Fluteau, F., Courtillot, V., Bajpai, S., 2007. ^{40}K—^{39}Ar dating of the main Deccan Large Igneous Province: Further evidence of KTB age and short duration. *Earth and Planetary Science Letters*, 263(1—2), 1—15.

Clementz, M., Bajpai, S., Ravikant, V., Thewissen, J.G.M., Saravanan, N., Singh, I.B., Prasad, V., 2011. Early Eocene warming events and the timing of terrestrial faunal exchange between India and Asia. *Geology*, 39(1), 15—18.

Couvreur, T.L., Forest, F., Baker, W.J., 2011. Origin and global diversification patterns of tropical rain forests: Inferences from a complete genus-level phylogeny of palms. *BMC Biology*, 9(1), 44.

Crome, F.H.J., 1975. Breeding, feeding and status of the Torres Strait Pigeon at Low Isles, north-eastern Queensland. *Emu-Austral Ornithology*, 75(4), 189—198.

Crome, F.H.J., 1976. Some observations on the biology of the Cassowary in northern Queensland. *Emu-Austral Ornithology*, 76(1), 8—14.

Datar, K., Patil, K.S., 2002. *Palmoxylon kamalam* Rode from Wardha District, Maharashtra. *Journal of Palaeosciences*, 51(1—3), 161—164.

Dechamps, R., Maes, F., 1987. Paleoclimatic interpretation of fossil wood from the Sahabi Formation. In: Boaz, N.T., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., Boaz, D.D. (Eds.), *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss Inc, New York, pp. 43—81.

Dransfield, J., 1981. *A synopsis of the genus Korthalsia (Palmae: Lepidocaryoideae)*. *Kew Bulletin*, pp.163—194.

Dransfield, J., Uhl, N.W., Asmussen, C.B., Baker, W.J., Harley, M.M., Lewis, C.E., 2008. *Genera Palmarum*. *The Evolution and Classification of Palms*. *Kew Publishing*, 2, 744.

Dubost, G., 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. *Journal of Mammalogy*, 65(2), 298—316.

Dutta, D., Ambwani, K., Estrada-Ruiz, E., 2011. Late Cretaceous palm stem *Palmoxylon lametaei* sp. nov. from Bhisi Village, Maharashtra, India. *Revista Mexicana de Ciencias Geológicas*, 28(1), 1—9.

Dutta, D., Ambwani, K., Prasad, M., 2007. Occurrence of Upper Cretaceous fossil palm wood, *Palmoxylon bhisiensis* sp. nov. from the Lameta Formation of Bhisi Village, Maharashtra, India. *Journal of Applied of Bioscience*, 33, 8—13.

Faurby, S., Eiserhardt, W.L., Baker, W.J., Svenning, J.C., 2016. An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution*, 100, 57—69.

Fisher, J.B., Dransfield, J., 1977. Comparative morphology and development of inflorescence adnation in rattan palms. *Botanical Journal of the Linnean Society*, 75(2), 119—140.

Fisher, J.B., 2002. Indeterminate leaves of Chisocheton (Meliaceae): Survey of structure and development. *Botanical Journal of the Linnean Society*, 139(2), 207—221.

Harley, M.M., Baker, W.J., 2001. Pollen aperture morphology in Arecaceae: Application within phylogenetic analyses, and a summary of record of palm-like pollen the fossil. *Grana*, 40, 45—77. https://doi.org/10.1080/00173130152591877.

Hartwich, S.J., Conran, J.G., Bannister, J.M., Lindqvist, J.K., Lee, D.E., 2010. Calamoid fossil palm leaves and fruits (Arecaceae: Calamoideae) from late Eocene Southland, New Zealand. *Australian Systematic Botany*, 23(2), 131—140.

Hass, H., Rowe, N.P., 1999. Thin sections and wafering. In: Jones, T.P., Rowe, T.P. (Eds.), *Fossil Plants and Spores: Modern Techniques*. *Geological Society, London*, pp. 76—81.

Hofmann, C., Feraud, G., Courtillot, V., 2000. ^{40}Ar/^{39}Ar dating of mineral separates and whole rocks from the

Western Ghats lava pile: Further constraints on duration and age of the Deccan traps. *Earth and Planetary Science Letters*, 180, 13—27.

Jablonszky, J., 1914. A Tarnoczi Mediterrankoru Flora [The Mediterranean Flora of Tarnócz]. *A Magyar Állami Földtani Intézet Évkkönyve*, 22(4), 228—273 (in Hungarian).

Kale, V.S., 2020. Cretaceous Volcanism in Peninsular India: Rajmahal—Sylhet and Deccan Traps. In: Gupta, N., Tandon, S. (Eds.), *Geodynamics of the Indian Plate*. Springer Geology. https://doi.org/10.1007/978-3-030-15989-4_8.

Kapgate, D.K., Manchester, S.R., Stuppy, W., 2017. Oldest fruit of Phyllanthaceae from the Deccan Intertrappean Beds of Singpur, Madhya Pradesh, India. *Acta Palaeobotina*, 57, 33—38.

Keller, G., Adatte, T., Bajpai, S., Mohabey, D.M., Widdowson, M., Khosla, A., Sharma, R., Khosla, S.C., Gertsch, B., Fleitmann, D., Sahni, A., 2009. K—T transition in Deccan Traps of central India marks major marine seaway across India. *Earth and Planetary Science Letters*, 282(1—4), 10—23.

Khan, M.A., Hazra, M., Mahato, S., Spicer, R.A., Roy, K., Hazra, T., Bandopadhaya, M., Spicer, T.E., Bera, S., 2020b. A Cretaceous Gondwana origin of the wax palm subfamily (Ceroxyloideae: Arecaceae) and its paleobiogeographic context. *Review of Palaeobotany and Palynology*, 283, 104318.

Khan, M.A., Mandal, K., Bera, S., 2019. A new species of permineralized palm stem from the Maastrichtian—Danian sediments of Central India and its palaeoclimatic signal. *Botany Letters*, 166, 189—206.

Khan, M.A., Roy, K., Hazra, T., Mahato, S., Bera, S., 2020a. A new coryphoid palm from the Maastrichtian—Danian sediments of Madhya Pradesh and its palaeoenvironmental implications. *Journal of the Geological Society of India*, 95(1), 75—83.

Khosla, S.C., 1999. Costabuntonia, a new genus of Ostracoda from the intertrappean beds (Paleocene) of east coast of India. *Micropaleontology*, 45, 319—324.

Khosla, A., Verma, O., 2015. Paleobiota from the Deccan volcano-sedimentary sequences of India: Paleoenvironments, age and paleobiogeographic implications. *Historical Biology*, 27, 898—914.

Kissling, W.D., Balslev, H., Baker, W.J., Dransfield, J., Göldel, B., Lim, J.Y., Onstein, R.E., Svenning, J.C., 2019. PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data*, 6(178). https://doi.org/10.1038/s41597-019-0189-0.

Kumar, S., Hazra, T., Spicer, R.A., Hazra, M., Spicer, T.E., Bera, S., Khan, M.A., 2023. Coryphoid palms from the K—Pg boundary of central India and their biogeographical implications: Evidence from megafossil remains. *Plant Diversity*, 45(1), 80—97.

Lahm, S.A., 1986. Diet and habitat preference of Mandrillus sphinx in Gabon: Implications of foraging strategy. *American Journal of Primatology*, 11(1), 9—26.

Lakhanpal, R.N., Prakash, U., Ambwani, K., 1979. Two petrified palm woods from the Deccan Intertrappean Beds of Mandla District, Madhya Pradesh. *Paleobotanist*, 26, 119—129.

Mahabale, T.S., 1958. Resolution of the artificial palm genus, Palmoxylon: A new approach. *Palaeobotanist*, 7, 76—84.

Manchester, S.R., Bonde, S.D., Nipunage, D.S., Srivatava, R., Mehrotra, R.C., Smith, S.Y., 2016. Trilocular palm fruits from the Deccan Intertrappean Beds of India. *International Journal of Plant Sciences*, 177(7), 633—641.

Mathew, A., Bhat, K.M., 1997. Anatomical diversity of Indian rattan palms (Calamoideae) in relation to biogeography and systematic. *Botanical Journal of the Linnean Society*, 125, 71—86.

Matsunaga, K.K., Manchester, S.R., Srivastava, R., Kapgate, D.K., Smith, S.Y., 2019. Fossil palm fruits from India indicate a Cretaceous origin of Arecaceae tribe Borasseae. *Botanical Journal of the Linnean Society*, 190(3), 260—280.

McClatchey, W., Manner, H.I., Elevitch, C.R., 2006. Metroxylon amicarum, M. paulcoxii, M. sagu, M. salomonense, M. vitiense, and M. warburgii (sago palm), Traditional Trees of Pacific Islands: Their Culture, Environment, and Use. Species Profiles for Pacific Island Agroforestry: Ecological, Economic, and Cultural Renewal. *Permanent Agriculture Resources*. ISBN: 970254458. http://www.traditionaltree.org/.

Molnar, P., Stock, J.M., 2009. Slowing of India's convergence with Eurasia since 20 Ma and its implications for Tibetan mantle dynamics. *Tectonics*, 28(3). https://doi.org/10.1029/2008TC002271. TC3001.

Morley, R.J., 1998. Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. *Biogeography and Geological Evolution of SE Asia*, 1998, 211—234.

Morley, R.J., 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1—2), 5—20.

Nair, K.K.K., Bhusari, B., 2001. Stratigraphy of Deccan Traps: A Review. *Geological Survey of India Special Publication*, 64, 477—492.

Pan, A.D., Jacobs, B.F., Dransfield, J., Baker, W.J., 2006. The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28—27 Mya) of north-western Ethiopia. *Botanical Journal of the Linnean Society*, 151, 69—81.

Pathak, V.S., Patil, K., Shrivastava, J.P., 2017. Tectonomagmatic setting of lava packages in the Mandla Lobe of the eastern Deccan Volcanic Province, India: Palaeomagnetism and magnetostratigraphic evidence. *Journal of the Geological Society of India*, 445, 69—94.

Prakash, U., Ambwani, K., 1980. A petrified Livistona-like palm stem, *Palmoxylon livistonoides* sp. nov. from the Deccan Intertrappean Beds of India. *Palaeobotanist*, 26(3), 297—306.

Prasad, M., Khare, E.G., Singh, S.K., 2013. Plant fossils from the Deccan intertrappean sediments of Chhindwara District, Madhya Pradesh, India: Their palaeoclimatic significance. *Journal of the Palaeontological Society of India*, 58(2), 229—240.

Rage, J.C., 2003. Relationships of the Malagasy fauna during the Late Cretaceous: Northern or southern routes? *Acta Palaeontologica Polonica*, 48, 661—662.

Renne, P.R., Sprain, C.J., Richards, M.A., Self, S., Vanderkluysen, L., Pande, K., 2015. State shift in Deccan volcanism at the Cretaceous—Paleogene boundary, possibly induced by impact. *Science*, 350, 76—78.

Roy, K., Hazra, T., Hazra, M., Mahato, S., Bera, S., Khan, M.A., 2021. A new coryphoid costapalmate palm leaf from the Maastrichtian—Danian of India. *Botany Letters*, 168(2), 155—166.

Salard-Cheboldaeff, M., 1981. Palynologie Maestrichtienne et Tertiaire du Cameroun. Résultats botaniques. *Review of Palaeobotany and Palynology*, 32, 401—439. https://doi.org/10.1016/0034-6667(81)90021-X.

Schenk, A., 1882. Die von den Gebrüdern Schlagenwelt in Indien gesammelten fossilen Hölzer. Botanischer Jahrbücher fur Systematik. *Pflanzengeschichte und Pflanzengeographie*, 3, 353—358.

Schoene, B., Samperton, K.M., Eddy, M.P., Keller, G., Adatte, T., Bowring, S.A., Khadri, S.F., Gertsch, B., 2015. U—Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. *Science*, 347(6218), 182—184.

Schrank, E., 1994. Palynology of the Yesomma Formation in Northern Somalia: A study of pollen, spores and associated phytoplankton from the Late Cretaceous Palmae Province. *Palaeontographica Beitrage Zur Naturgeschichte Der VorZeit Abteilung B: Palaeophytologie*, 231, 63—112.

Schultz, C.H., 1832. *Natürliches System des Pflanzenreichs: Nach Seiner Inneren Organisation, Nebst Einer Vergleichenden Darstellung der Wichtigsten Aller Früheren Künstlichen und Natürlichen Pflanzensysteme*. A. Hirschwald, Berlin, Germany, p. 317 (in German).

Sheth, H.C., Pande, K., Bhutani, R., 2001. ^{40}Ar—^{39}Ar ages of Bombay trachytes: Evidence for a Palaeocene phase of Deccan volcanism. *Geophysical Research Letters*, 28(18), 3513—3516.

Smith, S.Y., Manchester, S.R., Samant, B., Mohabey, D.M., Wheeler, E., Baas, P., Kapgate, D., Srivastava, R., Sheldon, N.D., 2015. Integrating paleobotanical, paleosol, and stratigraphic data to study critical transitions: A case study from the Late Cretaceous—Paleocene of India. *Paleontological Society Papers*, 21, 137—166.

Smith, S.Y., Kapgate, D.K., Robinson, S., Srivastava, R., Benedict, J.C., Manchester, S.R., 2021. Fossil fruits and seeds of Zingiberales from the Late Cretaceous—Early Cenozoic Deccan Intertrappean Beds of India. *International Journal of Plant Sciences*, 182(2), 91—108.

Srivastava, R., Srivastava, G., Dilcher, D.L., 2014. Coryphoid palm leaf fossils from the Maastrichtian—Danian of Central India with remarks on phytogeography of the Coryphoideae (Arecaceae). *PLoS One*, 9, e111738.

Shrivastava, J.P., Duncan, R.A., Kashyap, M., 2015. Post-K/PB younger ^{40}Ar—^{39}Ar ages of the Mandla lavas: Implications for the duration of the Deccan volcanism. *Lithos*, 224, 214—224.

Stocker, G.C., Irvine, A.K., 1983. Seed dispersal by cassowaries (Casuarius casuarius) in North Queensland's rainforests. *Biotropica*, 15(3), 170—176.

Stur, D., 1873. Vorkommen einer Palmenfrücht-Hülle Lepidocaryopsis Westphaleni, n. g. et sp. im Kreide-Sandstein der Peruzer Schichten bei Kaunitz in Böhmen. *Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 1—4, 1—2.

Teodoridis, V., Kvaček, Z., Agostini, S., Martinetto, E., Rossi, M.A., Cavallo, O., 2015. Feather palm foliage from the Messinian of Italy (Capo di Fiume, Palena and Pollenzo near Alba) within the framework of northern Mediterranean late Miocene flora. *Historia Naturalis*, 72(3—4), 301—314.

Thomas, R., Boura, A., 2015. Palm stem anatomy: Phylogenetic or climatic signal? *Botanical Journal of the Linnean Society*, 178(3), 467—488.

Thomas, R., Franceschi, D., 2013. Palm stem anatomy and computer-aided identification: The Coryphoideae (Arecaceae). *American Journal of Botany*, 100(2), 289—313.

Tomlinson, P.B., Fisher, J.B., Spangler, R.E., Richer, R.A., 2001. Stem vascular architecture in the rattan palm Calamus (Arecaceae—Calamoideae—Calaminae). *American Journal of Botany*, 88(5), 797—809.

Tomlinson, P.B., Spangler, R., 2002. Developmental features of the discontinuous stem vascular system in the rattan palm Calamus (Arecaceae—Calamoideae—Calamineae). *American Journal of Botany*, 89(7), 1128—1141.

Tomlinson, P.B., Zimmermann, M.H., 2003. Vascular architecture of the American climbing palm Desmoncus (Bactridinae-Arecoideae-Arecaceae). *Botanical Journal of the Linnean Society*, 142, 243—254.

Tomlinson, P.B., Fisher, J.B., 2000. Stem vasculature in climbing monocotyledons: A comparative approach. In: Wilson, K.L., Morrison, D.A. (Eds.), *Monocotyledons: Systematics and Evolution*. CSIRO Publishing, Melbourne, Australia, pp. 89—97.

Tomlinson, P.B., 1961. Palmae. In: Metcalfe, C. (Ed.), *Anatomy of the Monocotyledons*, vol. 2. Oxford University Press, Oxford, UK, p. 306.

Tomlinson, P.B., Horn, J.W., Fisher, J.B., 2011. *The Anatomy of Palms*. Oxford University Press, Oxford, UK.

Trivedi, B.S., Surange, K.R., 1970. *Palmoxylon mohgaonensis*, a new species of petrified palm stem from the Deccan Intertrappean Series of India. *Palaeobotanist*, 18(1), 1—7.

Trivedi, B.S., Verma, C.L., 1972. Petrified palm *Palmoxylon penchense* sp. nov. from the Deccan Intertrappean Beds of Madhya Pradesh, India. *Palaeobotanist*, 21(3), 352—358.

Uhl, N.W., Dransfield, J., 1987. *Genera Palmarum. A classification of palms based on the work of Harold E. Moore, Jr (No. Le0216)*. Allen Press.

Uhl, N.W., Dransfield, J., Davis, J.I., Luckow, M.A., Hansen, K., Doyle, J.J., 1995. Phylogenetic relationships among palms: Cladistic analyses of morphological and chloroplast DNA restriction site variation. *Monocotyledons: Systematics and Evolution*, 2, 623—661.

Van Hoeken-Klinkenberg, P.M.J., 1964. A palynological investigation of some Upper Cretaceous sediments in Nigeria. *Pollen et Spores*, 6, 209—231.

Velitzelos, D., Iamandei, S., Iamandei, E., Velitzelos, E., 2019. Palaeoxylotomical studies in the Cenozoic petrified forests of Greece. Part one — Palms. *Acta Palaeobotanica*, 59(2), 289—350.

Venkatesan, T.R., Kumar, A., Gopalan, K., Al'Mukhamedov, A.I., 1997. ^{40}Ar—^{39}Ar age of Siberian basaltic volcanism. *Chemical Geology*, 138(3—4), 303—310.

Verma, O., Khosla, A., 2019. Developments in the stratigraphy of the Deccan Volcanic Province, peninsular India. *Comptes Rendus Geoscience*, 351, 461—476.

Winkworth, R.C., Wagstaff, S.J., Glenny, D., Lockhart, P.J., 2002. Plant dispersal news from New Zealand. *Trends in Ecology and Evolution*, 17(11), 514—520.

Xu, H.C., Rao, A.N., Zeng, B.S., Yin, G.T., 2000. Research on rattans in China, conservation, cultivation, distribution, ecology, growth, phenology, silviculture, systematic anatomy and tissue culture. International Plant Genetic Resources Institution, Selangor, Malaysia. http://www2.bioversityinternational.org/publications/Web_version/576/.

Zona, S., Henderson, A., 1989. A review of animal-mediated seed dispersal of palms. *Selbyana*, 11, 6—21.