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A Cretaceous Gondwana origin of the wax palm subfamily (Ceroxyloideae: Arecaceae) and its paleobiogeographic context

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ABSTRACT

Here we study a well-preserved petrified palm stem from the latest Maastrichtian (Late Cretaceous) to earliest Danian (early Paleocene) sediments (*c.* 66–65 Ma old) of the Deccan Intertrappean Beds of Madhya Pradesh, Central India. We infer its systematic relationships and relevance to palm evolution. The significant anatomical attributes of the fossil include the presence of fibrovascular bundles (fvbs) with reniform dorsal fibrous sclerenchyma (dcap), 2 to >4 metaxylem vessel elements in each fvb, lacunar ground parenchyma tissue, and centrifugal differentiation of the fibrous dcap parts of the fvbs. These features reveal a close resemblance to extant taxa of the wax palm subfamily Ceroxyloideae, now with a disjunct distribution in America, Australia, Madagascar and the Comoros. The Cretaceous stem is described here as *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov. This is the oldest reliable occurrence of Ceroxyloideae in the fossil record. Present fossil evidence indicates that the sub-family was already present in India in the Late Cretaceous (Maastrichtian), about 10–15 million years before the collision of India with Eurasia. Post-collision the subfamily may have been dispersed to East Asia and then to North America via the Bering land bridge (BLB), finally reaching South America via the Isthmus of Panama link during the Miocene. However, the present-day distribution of Ceroxyloideae in Australia, Madagascar and Comoros may be explained by a historical long-distance dispersal (LDD) hypothesis.

1. Introduction

The Ceroxyloideae is a small but, in terms of morphology and biogeography, a heterogeneous sub-family of palms (Arecaceae) (Trénel et al., 2007). It is also known as the wax palm subfamily (Trénel et al., 2007, 2008), and now comprises of three tribes (Cyclospatheae Cook, Ceroxyleae Satake and Phytelepheae Horan.) with only 8 genera (*Ceroxylon*, *Juania*, *Oraniopsis*, *Ravenea*, *Pseudophoenix*, *Ammandra*, *Aphandra* and *Phytelephas*) and 42 species (Dransfield and Uhl, 1998; Dransfield et al., 2005). It is ecologically exceptional and spans a wide range of latitudes (25°N–33°S) and altitudes, including a species (*Ceroxylon parvifrons*) that can sustain natural populations 3500 m above sea level. It is placed in the family Arecaceae (Borchsenius et al., 1998). The subfamily also occupies a diverse array of habitats including seasonally dry forests (Cyclospatheae, Ceroxyleae), lowland rainforests (Phytelepheae, Ceroxyleae), and mountain forests (Ceroxyleae). It even includes the world's only aquatic palm species *Ravenea musicalis* (Dransfield and Beentje, 1995).

The Deccan Intertrappean beds, deposited in central India near the boundary of the Cretaceous and Cenozoic, contain abundant and well-preserved angiosperm plant remains that offer valuable insights into the diversity, evolution, and biogeography of the Indian flora at a time when India was an apparently geographically isolated landmass (Kapgate, 2005; Ali and Aitchison, 2008; Chatterjee et al., 2013; Smith et al., 2015). Palms have been recognized as an important component of this fossil flora, known from numerous stems (*Palmoxylon* species), leaves, roots, pollen, inflorescences and fruits. However, they are not a significant component of the present-day vegetation of central India (Matsunaga et al., 2019).

The systematic affinities of most of the palm stem fossils in the Deccan Intertrappean beds are poorly understood due to the lack of detailed anatomical knowledge of modern palm stems. The present study reports the discovery of a well-preserved petrified palm stem, containing fibro-vascular bundles with anatomical characters diagnostic of the subfamily Ceroxyloideae, from the Cretaceous–Paleogene boundary of central India. We determine its taxonomic position based on anatomical

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(stem vascular architecture) comparison with similar modern and fossil specimens. This palm stem, about 66–65 Ma old, represents the oldest known example of the wax palm subfamily. The Late Cretaceous (Maastrichtian) ceroxyloid palm stem documented here provides compelling evidence for the origin of the wax palm on insular India, when the bulk of the subcontinent was still in the Southern Hemisphere. In addition, this discovery provides evidence for a Gondwanan origin of this subfamily and represents an important source of data for understanding the evolution, diversification and paleobiogeographical history of the wax palm subfamily in deep time.

2. Materials and methods

The petrified stem described here was collected from surface exposures of the Deccan Volcanic Province (DVP) near Barga village (N23°13.574′, E080°34.903′; elevation: 564.8 m) in the Dindori District, Madhya Pradesh, Central India (Fig. 1). The fossil site is situated about 61 km east of Jabalpur and lies on a plateau in the eastern part of the Satpura Hills. We have collected a large number of permineralized angiospermous woods (both palms and eudicots) from the surface exposures of the fossil locality. The DVP of India, one of the largest continental flood basalts in Earth's history, was deposited across lacustrine and fluviatile environments that developed during quiescent periods between volcanic activities (Chatterjee et al., 2013). Based on radiometric dating (^{40}Ar/^{39}Ar dating), planktonic foraminifera and magnetostratigraphy, recent studies indicate that the age of these Intertrappean sediments is latest Maastrichtian–earliest Danian (*c.* 67–64 Ma, chrons 30 N–29 N; Hooper et al., 2010; Srivastava et al., 2014; Renne et al., 2015; Schoene et al., 2015; Smith et al., 2015). The present fossil locality occurs in the Mandla sub-province of the DVP (Smith et al., 2015) and falls within Chron 29R, which straddles Cretaceous–Paleogene (K–Pg) boundary (Pathak et al., 2017).

Anatomical sections from the periphery towards the center of the fossil stem reported here were prepared using standard thin sectioning techniques, and studied using a transmitted light compound microscope with a photographic attachment (Zeiss Axioskop 2). Thin anatomical sections (transverse and transverse longitudinal section) were prepared following the standard method of grinding, polishing and mounting for permineralized material (Hass and Rowe, 1999). The prepared slides were identified with the aid of published xylotomical databases, an online resource (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/B4) and prepared slides (SKBUH/PPL/B4/T1; SKBUH/PPL/B4/T2; SKBUH/PPL/B4/T3; SKBUH/PPL/B4/L1) are deposited at the repository of the Department of Botany, Sidho-Kanho-Birsha University, West Bengal, India.

3. Results

3.1. Systematic paleobotany

Family: Arecaceae Schultz Sch. 1832
Subfamily: Ceroxyloideae Drude 1877
Genus: **Palmoxylon** Schenk 1882
Species: *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov.

Diagnosis: Mauritia-type general stem organization; prominent reniform-shaped dorsal fibrous sclerenchyma (dcap) present; 2 to >4 metaxylem vessel elements in each fibrovascular bundles (fvb), vessel end walls oblique, leaf trace bundles (ltbs) with 2–10 small protoxylem vessels; both tabular and radiating parenchyma absent; median sinus round to slightly concave; stegmata absent; fibrous and diminutive fibrovascular bundles absent; lacunar ground tissue; centrifugal differentiation of fibrous part of fvb as well as zone of transition (TZ) between SZ (sub-cortical zone) and CZ (central zone).

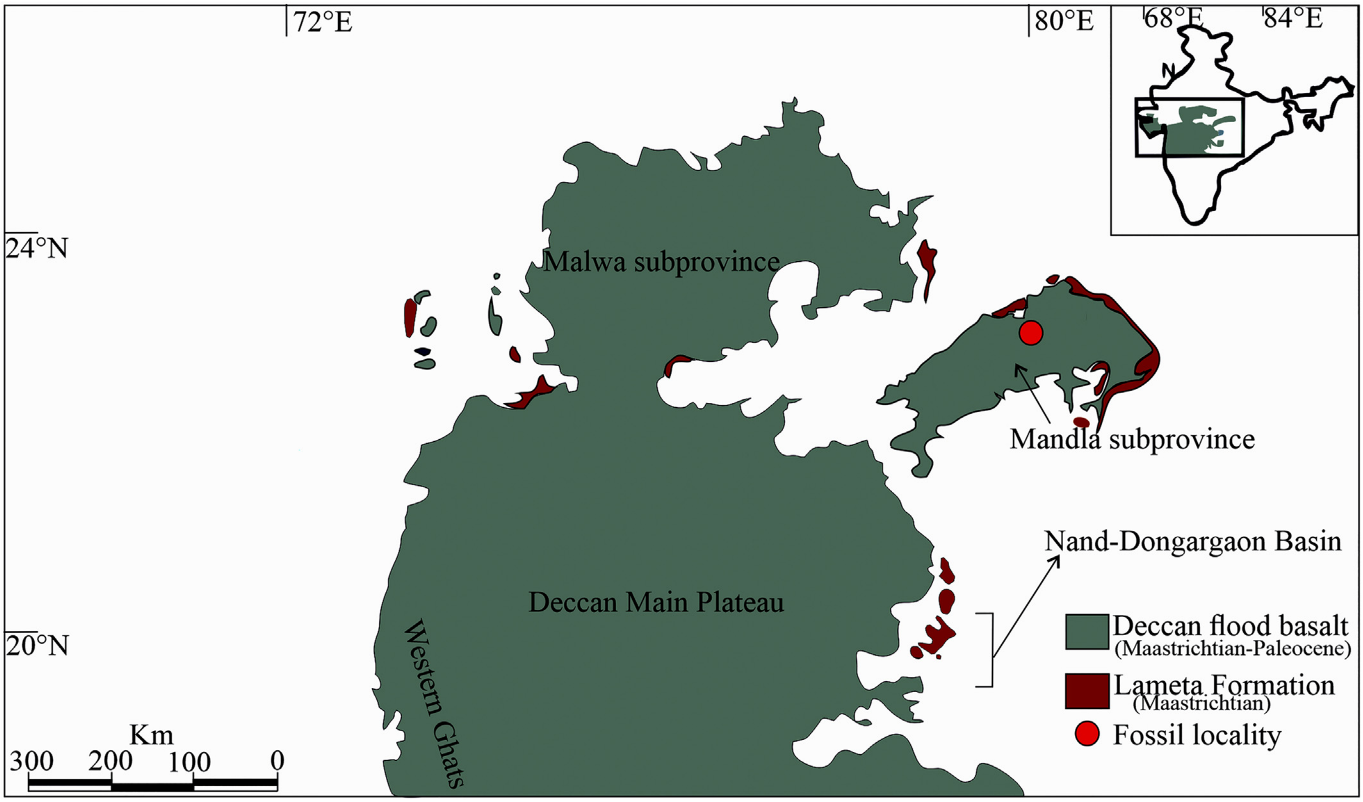

Fig. 1. Map showing Deccan Volcanic Province (DVP), red star showing fossil locality (modified after Smith et al., 2015).

Description: Petrified stem well-preserved, yellowish brown, maximum 12 cm in length and 17 cm in diameter; anatomically divisible into SZ and CZ; cortex not clearly developed; CZ with fvbs slightly more widely spaced than in the SZ where the density of the fibrous vascular bundles, d(fvb), is more or less constant; a zone of transition (TZ) present between the SZ and the CZ; characteristic centrifugal differentiation of the fibrous part of the fvb is present (Fig. 2C) and results in a change in cell differentiation around the cells adjacent to the fibrous part above the phloem, in transverse section the area of the fibrous part strongly decreases from the subcortical to the central zone of the central cylinder (i.e. the inner fvbs have a poorly developed fibrous part, whereas the outer fvbs have a well-developed fibrous part) (Fig. 2C; Plates I, 1–6; II, 1–6); based on the orientation, the distribution of fvbs, and nature of ground tissue in the CZ, is also divided into three zones termed dermal (D), sub-dermal (SD) and innermost central zones CZ(in); in the vascular part (v) of each fvb there are 2 to >4 metaxylem vessel elements (Plates I, 2, 5; II, 4, 6), 2 to 10 narrow and small protoxylem vessels, which become well-developed in the fvb connecting a leaf (the leaf trace) and phloem; ltbs easily distinguished by their protruded tongue-like vascular part (Plate I, 1, 4), with a number of small protoxylem vessels slightly larger in size than the normal fvbs (Plate I, 1, 4); vessel end walls are very oblique to oblique; small fibrous bundles and diminutive fvbs totally absent; the fvbs have the following mean dimension: H_{max} (maximal height of the fvb) = 1200 μm, L_{max} (maximal width of the fvb) = 650 μm, H_{vasc} (height of the vascular part) = 950 μm, L_{vasc} (width of the vascular part at the auricular sinus level) = 370 μm; vessel mean diameter = 150 μm; reniform shaped dcap present in SZ and D adjacent to the phloem, fibrous sheath with thick-walled, polygonal sclerenchymatous cells; the median sinus round to slightly concave and the auricular sinus angular; stegmata completely absent; tabular parenchyma around the dcap of the fvb, and radiating parenchyma around vascular part of the fvb absent; ground parenchyma undergoes a sustained growth, ground tissue well preserved and composed of thick-walled, oval to elongated parenchyma cells (100–160 μm in length and 70–80 μm in breadth) with large intercellular air spaces (Plates I, 1–6; II, 1–6).

Holotype: Specimen number: SKBU/PPL/D4; Type locality: Barga village (location: N23°13.574′, E080°34.903′; elevation: 564.8 m) in Dindori District, Madhya Pradesh, Central India; Type horizon: Deccan Intertrappean Beds; latest Maastrichtian (Late Cretaceous)-earliest Danian (early Paleocene); Collecting date: December 28, 2018; Collectors: Mahasin Ali Khan and Kaustav Roy; Repository: Specimen is kept at the Museum of the Department of Botany, Sidho-Kanho-Birsha University (SKBUH).

Etymology: The specific epithet "*ceroxyloides*" recognizes subfamily Ceroxiloideae, the modern comparable form of the present fossil stem.

Remarks: The precise affinities of fossil palm stems have always been difficult to determine due to the lack of thorough anatomical knowledge of all modern palm stems. However, Thomas and Franceschi (2013) showed that the five palm subfamilies, Ceroxyloideae, Nypoideae, Coryphoideae, Calamoideae, Arecoideae and their tribes, have useful distinguishing characters. This provides important perspectives for identifying fossil palm stems, and shows that their identification using standardized anatomical descriptors is potentially possible at the genus, tribe and/or subfamily levels (Thomas and Franceschi, 2012, 2013). The most useful anatomical characters of modern palm stems for systematic purposes are: general stem pattern (von Mohl's classification 1823–1850), shape of fibrous part or dcap in transverse section, number of metaxylem element per fvb, presence or absence of the centrifugal differentiation of fibrous part, and the nature of the ground parenchyma (Thomas and Franceschi, 2013). The other anatomical characters such as the presence or absence of radiating parenchyma, tabular parenchyma, diminutive fvbs, fibrous bundles, auricular sinuses etc. also have taxonomic value, but depend on stem development or the position of the stem section.

Significant anatomical features of the fossil stem described here, such as the presence of lacunose ground parenchyma, the zone of transition between SZ and CZ, the sustained growth of the central cylinder of ground parenchyma, and the centrifugal differentiation of the fibrous part of the fvb suggest that our Deccan specimen belongs to the Mauritia-type general stem organization of modern erect palms (Fig. 2A, B, C). Another principal organization type of modern erect palm stems in transverse section (TS) is the Cocos-type, which differs from the Mauritia-type in having a compact ground parenchyma and an absence of centrifugal differentiation of the fibrous part (Thomas and Franceschi, 2013).

For the taxonomic determination of the fossil specimen reported here we followed the scheme of stem anatomical descriptors for modern palms compiled by Thomas and Franceschi (2013). Based on the Mauritia-type general stem organization with centrifugal differentiation of fibrous parts, the structure of the fvbs (reniform type dcap, 2 to >4 metaxylem vessel elements in each fvb), as well as the nature of ground parenchyma tissue (highly lacunose), our fossil specimen shows closest similarity with modern genera of the sub-family Ceroxyloideae, and is distinct from other sub-families of the Arecaceae such as the Nypoideae, Coryphoideae, Calamoideae and Arecoideae. The number of metaxylem vessel elements per fvb is an important anatomical character at the subfamily level (Thomas and Boura, 2015). The subfamily Arecoideae is the only subfamily that never presents fvbs with 2 or more vessels. Generally, members of the sub-family Coryphoideae have 1, 2, or more metaxylem elements per fvb (Couvreur et al., 2011), whereas the other subfamilies (Calamoideae and Nypoideae) systematically present only 1 or 1 and 2 metaxylem elements in each fvb (Thomas and Franceschi, 2013). However, the subfamily Ceroxyloideae presents two specific patterns: members of Cyclospatheae (*Pseudophoenix*) have two vessels per fvb, whereas the other two tribes (Ceroxyleae and Phytelepheae) have several (3 or 4 or >4) vessels per fvb. Centrifugal differentiation of the sheath of fibers is present in other subfamilies including Ceroxyloideae, but is not found in the Coryphoideae (except in the tribe Caryoteae having 1 and 2 metaxylem vessel elements in each fvb). However, Cocos-type organization is absent in Ceroxyloideae (except in the genus *Phytelephas* of tribe Phytelepheae having >4 metaxylem vessel elements in each fvb).

Of the known anatomy of different tribes of modern Ceroxyloideae palms (Thomas and Franceschi, 2013), our fossil specimen shows anatomical similarities to South American representatives of tribe Ceroxyleae in the size, shape, structure of fvbs and the nature of ground tissue (Table 1). The tribe Cyclospatheae differs in having 2(3–4) metaxylem vessel elements per fvb. However, the current specimen has 2 to >4 metaxylem vessel elements in each fvb. Phytelepheae differs in having Cocos-type general stem organization compared with the Mauritia type stem organization seen in our fossil specimen. In addition, it differs in having >4 metaxylem vessel elements in each fvb and fibrous bundles in the central cylinder of the stem. Our specimen lacks tabular parenchyma around the dcap of fvb, which also differentiates it from the aforesaid tribe.

One fossilized stem, *Phytelephas sewardii* Kaul (1943), having affinity with the modern stem of *Phytelephas* (Phytelepheae) of the Ceroxyloideae, has been reported from the Miocene sediments of Antigua, West Indies (Table 2). Our Deccan fossil stem differs in having well-preserved vessels in the fvbs, as compared with the lack of vessels in the stem of Kaul's specimen. Recently, Chate et al. (2019) reported a petrified phytelephantoid palm stem with roots (*Palmoxylon phytelephantoides*) from the late Cretaceous-early Paleocene sediments of the Deccan Intertrappean Beds of Central India. Our specimen differs in having centrifugal differentiation of the fibrous part of the fvb and lacunar ground parenchyma tissue, while *P. phytelephantoides* has compact ground tissue. It also differs from our specimen in having tabular parenchyma around the dcap of the fvb. As our fossil stem is anatomically different from *Phytelephas sewardii* and *P. phytelephantoides*, it is regarded as a new species, namely *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov.

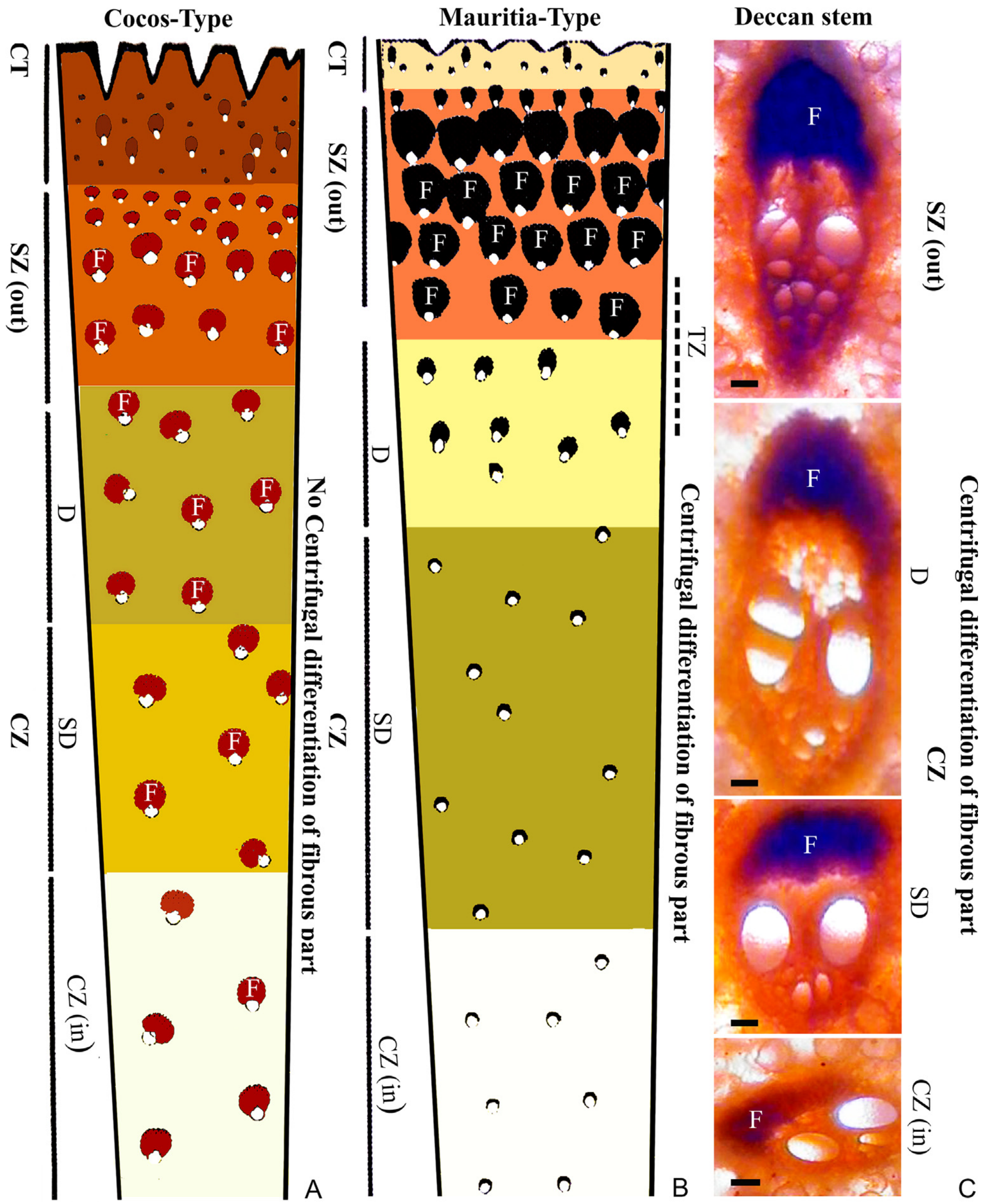

Fig. 2. Comparisons of Deccan palm stem *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov. with Cocos and Mauritia-type general stem organization of the modern erect palm in transverse section (TS). (A) Cocos-type organization of the modern erect palm stems in transverse section (Thomas, 2011); (B) Mauritia-type organization of the modern erect palm stems in transverse section (Thomas, 2011); (C) Light microscopic images of transverse section of sub-cortical and central zones of fossil palm stem (scale bar = 100 μm), Abbreviations: CT, cortex; SZ (out), outer sub-cortical zone; CZ, central zone; D, dermal; SD, sub-dermal; CZ (in), innermost central zone; TZ, zone of transition.

4. Discussion

4.1. Origin of Ceroxyloideae

Fossilized plant remains inform us of the past distribution of a taxon's ancestors, (Tiffney and Manchester, 2001). So, the fossil evidence of Ceroxyloideae is essential for understanding its deep evolutionary and biogeographical history. The fossil record for the wax palm subfamily is mainly limited to microfossils (Harley, 2006). Biswas (1962) reported a simple-tectate fossil pollen, *Palmaepites eocenica* resembling *Juania* (tribe Ceroxyleae), from Eocene sediments within India. In addition, Saxena et al. (1990) described a monoporate, spinose pollen fossil, *Echimonoporopollis grandiporus*, similar to pollen of extant *Ravenea* (tribe Ceroxyleae) from the lower to middle Eocene sediments (Neyveli Formation) of Tiruchirapalli District, Tamil Nadu, India, but its identification is questionable (Harley, 2006). Other microfossils of Ceroxyloideae include the semitectate, monosulcate fossil pollen *Liliaciditus tritus* resembling modern *Pseudophoenix* (tribe Cyclospatheae) from Paleocene to lower Oligocene strata of south-eastern North America (Frederiksen, 1980; Melchior, 1998); the monoporate fossil pollen, *Jacobipollis,* resembling *Ammandra* (tribe Phytelepheae), from the Miocene sediments of India (Harley, 2006); coarsely reticulate fossil pollen, *Luminidites,* resembling modern *Ceroxylon* (tribe Ceroxyleae) from the late Oligocene–early Miocene of New Zealand (Pocknall and Mildenhall, 1984), and the coarsely reticulate fossil pollen, *Longapertitis,* resembling modern *Ceroxylon*, from the Paleocene of northern Pakistan (Frederiksen, 1994), the Late Cretaceous to late Eocene of Africa (Pan et al., 2006), and late Eocene strata of Colombia (Jaramillo and Dilcher, 2000). However, the specimens of *Longapertitis* are of uncertain affinity and are a questionable pollen genus. Until they can be re-examined, they do not represent a reliable record for this tribe. The pollen genus *Longapertites*, present in Africa

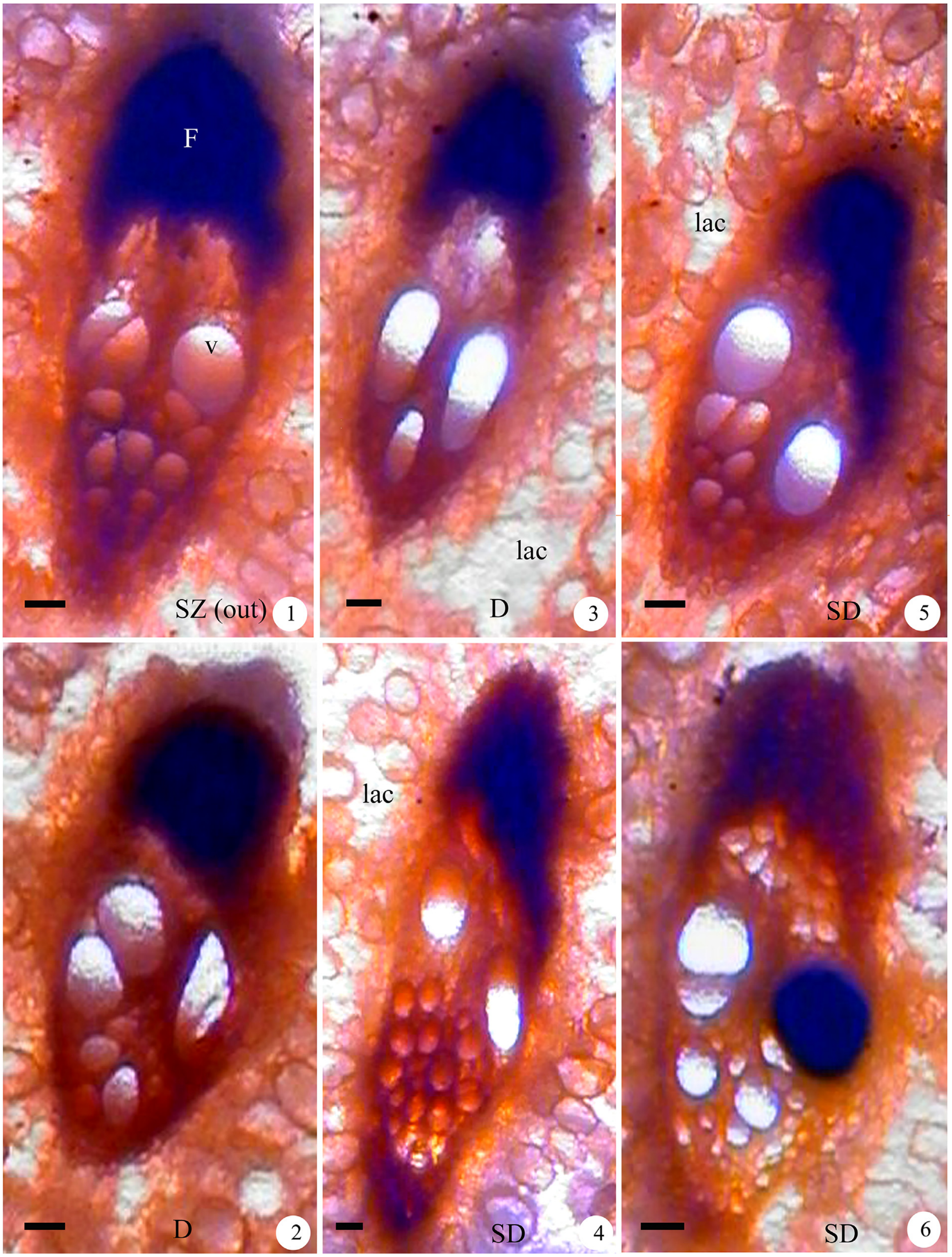

Plate I. Light microscopic images of transverse section of outer sub-cortical, dermal and sub-dermal zones of fossil palm stem *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov. A. (1) fibrovascular bundle and lacunar nature of ground tissue in outer sub-cortical zone, SZ (out); (2, 3) Fibrovascular bundles in dermal zone (D); (4, 5, 6) Fibrovascular bundles in sub-dermal zone (SD) (scale bar = 100 μm), Abbreviations: F, Fibrous part of fibrovascular bundle; V, metaxylem vessel part of fibrovascular bundle; lac, lacunar.

in the Late Cretaceous, is thought by Morley (2000) to be ancestral to the calamoid *Eugeissona* (subtribe Eugeissoneae, tribe Calamoideae) (Dransfield et al., 2005).

Because pollen can be transported over long distances (e.g. Rousseau et al., 2008), and reworked from older to younger sediments prior to final deposition without showing clear signs of abrasion or damage,

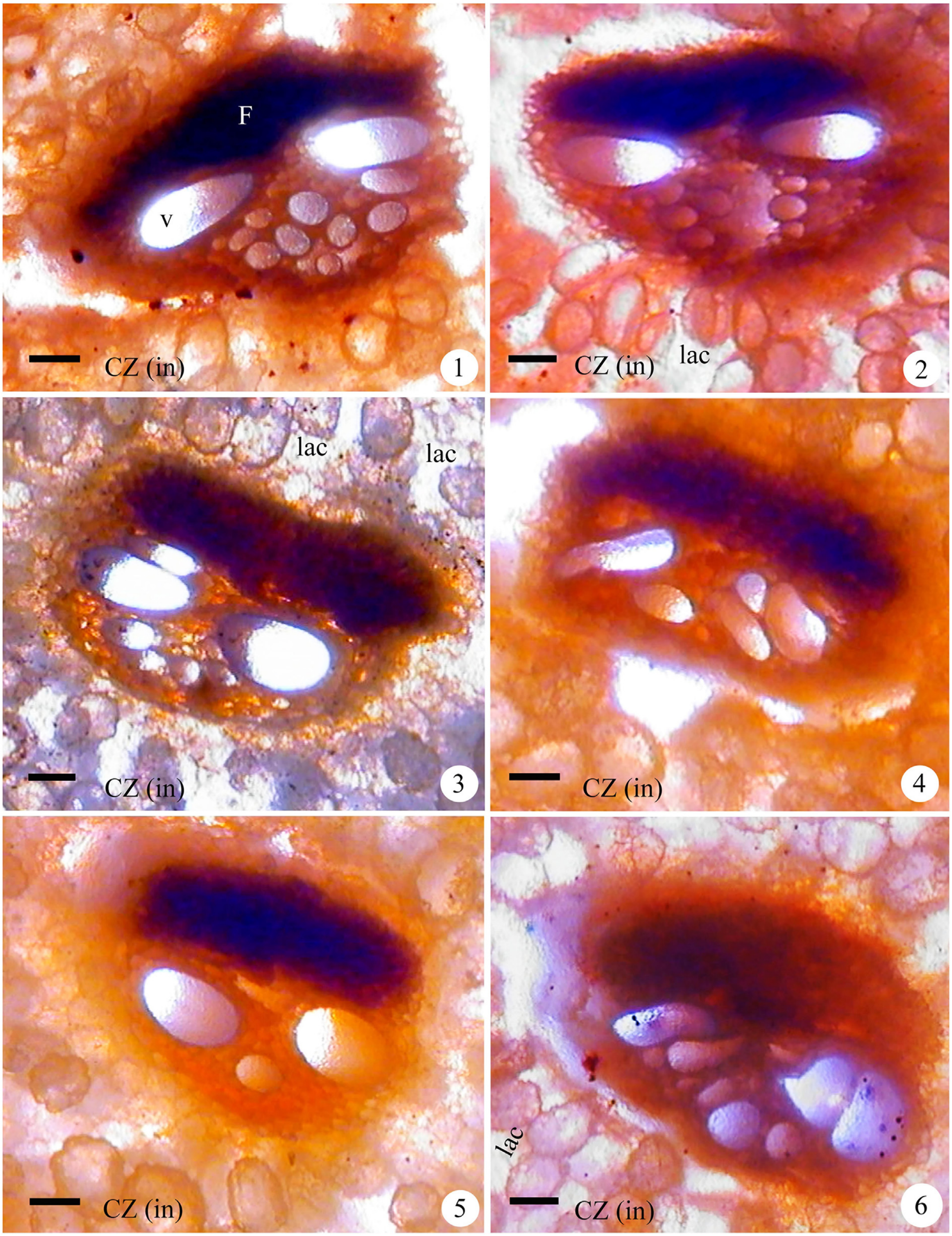

Plate II. Light microscopic images of transverse section of inner central zone of fossil palm stem *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov. (1–6) Fibrovascular bundles and lacunar nature of ground tissue in inner central zone, CZ (in) (scale bar = 100 μm), Abbreviations: F, Fibrous part of fibrovascular bundle; V, metaxylem vessel part of fibrovascular bundle; lac, lacunar.

preservation of more definitive megafossil evidence of the Ceroxyloideae is required to demonstrate an origin of this group of palms. Moreover, megaremains are generally believed to offer much more reliable identification than pollen (Mander and Punyasena, 2014) and are far less durable (they do not get reworked as easily and transport is betrayed by abrasion artifacts). This means identifiable megaremains are usually preserved proximal to their growth site (Ferguson, 1985).

Table 1
Comparative anatomical details of the palm fossil *Palmoxylon ceroxyloides* Khan, Hazra et Bera, sp. nov. with tribes of subfamily Ceroxyloideae.

Anatomical attributes	Modern members of subfamily Ceroxyloideae			Fossil taxon
	Tribe Cyclospatheae	Tribe Ceroxyleae	Tribe Phytelepheae	*Palmoxylon ceroxyloides* sp. nov.
Organization type (Von Mohl-type Classification)	Mauritia	Mauritia	Cocos	Mauritia
Shape of fibrous part in TS (Stenzel's classification)	Reniforma	Reniforma	Reniforma	Reniforma
Number of metaxylem vessel element/ fvb	2 (3–4)	2 (3–4) & 3–4 & >4	>4	
Fibrous part centrifugal differentiation	Present	Present	Absent	Present
Developed cortex	Absent	Present & Absent	Present	Absent
Fibrous bundles in central cylinder	Absent	Present & Absent	Present	Absent
Auricular sinus	Angular & Absent in central zone of the central cylinder	Angular & Absent in central zone of the central cylinder	Absent	Angular & Absent in central zone of the central cylinder
Radiating parenchyma	Absent	Present & Absent	Absent	Absent
Tabular parenchyma	Present & Absent	Present & Absent	Present	Absent
Nature of ground parenchyma of the central cylinder	Lacunar	Lacunar	Compact	Lacunar

To provide a clear picture for both the origin and dispersal history of the Ceroxyloideae requires reliable megafossil evidence from Paleogene or older Gondwanan sediments. As far as megafossil records are concerned, this wax palm sub-family is only reported from the late Neogene sediments of the West Indies and South America (Kaul, 1943; Brown, 1956). Brown (1956) reported a sandstone cast fossil of tagua, the Ivory-nut palm *Phytelephas olsonii* (tribe Phytelepheae), from the Punta Gorda Formation (late Miocene or early Pliocene) sediments of Ecuador in South America. In addition, Kaul (1943) described a fossilized vessel-less stem of *Phytelephas sewardii* from Miocene sediments on Antigua, West Indies. However, we do not have an extensive megafossil record of Ceroxyloideae in deep time. To-date the oldest megafossil assigned to Ceroxiloideae, *Phytelephas sewardii* (Kaul, 1943), is Miocene (23–5.3 Ma old), significantly younger than our present fossil *Palmoxylon ceroxyloides*, which is late Maastrichtian–early Danian (66–65 Ma).

From this standpoint, the occurrence of our well-preserved petrified ceroxyloid palm stem from the latest Maastrichtian (Late Cretaceous)–earliest Danian (early Paleocene) sediments of Central India is highly significant, and implies strongly that the wax palm sub-family originated in Gondwana in the Cretaceous, and only later dispersed from India into other continents (Figs. 3, 4). The alternative interpretation is that the characters observed in our fossil represent an extinct type of plant that had the characteristics of the wax palms, but which died out leaving no descendants. If this was the case it becomes a complex philosophical issue as to what any fossil represents, so the most parsimonious explanation is that these remains are indeed indicative of primitive wax palms. However, members of the wax palm Ceroxyloideae are most diverse today in South America. They are also disjunctly distributed in North and Central America, Australia, Madagascar and Comoros, but they are not found today in India or other parts of Asia. Eight genera of Ceroxyloideae are geographically restricted. Four genera such as *Ceroxylon*, *Juania*, *Oraniopsis*, *Ravenea* of the tribe Ceroxyleae occur in South America, Australia and Madagascar. A monotypic tribe Cyclospatheae (genus *Pseudophoenix*) is found only in North and Central America. The remaining three genera, namely *Ammandra*, *Aphandra* and *Phytelephas* of the tribe Phytelepheae, are endemic to South America. So, today this subfamily displays a disjunct distribution pattern in eastern and western Gondwanan continents.

4.2. Possible dispersal routes of Ceroxyloideae

In order to explain the intercontinental disjunct distribution, as well as dispersal routes of flora and fauna, four hypotheses have been proposed (Couvreur et al., 2011). These hypotheses are: migrations via different land bridges under favorable climates (geodispersal) (Nie et al., 2005); vicariance resulting from the break-up of the Gondwanan supercontinent (Raven and Axelrod, 1974); continental rafting (Conti et al., 2002); and long-distance dispersal (Wen, 1999; Givnish et al., 2016) mediated by animals, ocean currents and winds (Renner, 2004; Nie et al., 2005). Here we invoke two hypotheses, namely land bridges and long-distance dispersal, to account for the biogeography of the palm subfamily Ceroxyloideae. While we can never be certain which hypothesis is correct in any given instance, it is useful to consider what was possible, and then which was the most likely dispersal mechanism.

Major land bridges came into play after the breakup of Pangea to form Laurasia and Gondwana from the Jurassic onwards (Cox, 1974; Raven and Axelrod, 1974). These land bridges play an important role in the dispersal of many biotic elements (Brikiatis, 2014). The latest Cretaceous to early Paleocene age of our find (no older than ~66 Ma) precludes dispersal westwards to South America at low and middle latitudes because the Atlantic had opened in the mid Cretaceous (Scotese, 2014). Moreover, there is no fossil evidence of the Ceroxyloideae in Africa, which was well separated from India in the Late Cretaceous (Chatterjee et al., 2013). This means that, with currently available evidence, higher latitude routes seem most likely, which may have been possible in the hyperthermal Paleogene world (Zachos et al., 2008; Anagnostou et al., 2016).

The two important intercontinental connections of Laurasia were the trans-Atlantic connection and the trans-Beringian connection. The trans-Atlantic land bridges include various North Atlantic Land Bridges (NALBs) from the Paleocene to early Eocene connecting Europe and North America (Tiffney, 1985a, 1985b; Wen, 1999; Tiffney and Manchester, 2001; Marincovich Jr. and Gladenkov, 2001; Milne and Abbott, 2002; Ickert-Bond et al., 2009), and include transfer via Greenland. Furthermore, the connection between Europe and Greenland includes a northern “DeGeer” route and a southern “Thulean” route (McKenna, 1983). The marsupial *Maastrichtidelphys* occurring in the Maastrichtian of the Netherlands (Martin et al., 2005) provides evidence for the existence of the “DeGeer” route. On the other hand, the southern “Thulean” route was climatically more favorable for dispersal of the ancestral magnolias to Europe during the Eocene (Irving and Hebda, 2003). Vertebrate paleontological evidence also suggests that both terrestrial and freshwater vertebrates used these routes for migration. They migrated across NALBs along with the boreotropical flora. The majority of these fauna were herbivorous or omnivorous and they played an important role in the dispersal of the aforesaid flora (McKenna, 1975).

Table 2
Micro and megafossil (marked by green shading) record of Ceroxyloideae palm.

Fossil species	**Modern comparable forms**	**Organ**	**Fossil localities**	**Age**	**References**
Palmaepites eocenica	*Juania* (Ceroxyleae)	Pollen	India	Eocene	Biswas,1962
Echimonoporopollis grandiporus	*Ravenea* (Ceroxyleae) (?)	Pollen	India	Eocene	Saxena et al. 1992
Jacobipollis	*Ammandra* (Phytelepheae)	Pollen	India	Miocene	Harley, 2006
Liliaciditus tritus	*Pseudophoenix* (Cyclospatheae)	Pollen	North America	Paleocene - Oligocene	Frederiksen, 1980; Melchior, 1998
Luminidites	*Ceroxylon* (Ceroxyleae)	Pollen	New Zealand	Oligocene–Miocene	Pocknall and Mildenhall, 1984
Longapertitis	*Ceroxylon* (Ceroxyleae)	Pollen	Pakistan	Paleocene	Frederiksen, 1994
			Africa (?)	Cretaceous to Eocene	Pan et al., 2006
			Colombia	Eocene	Jaramillo and Dilcher, 2000
Phytelephas sewardii	*Phytelephas* (Phytelepheae)	Stem	West Indies	Miocene	Kaul, 1943
Phytelephas olsonii	*Phytelephas* (Phytelepheae)	Nut	Ecuador, South America	Miocene/ Pliocene	Brown, 1956
Palmoxylon phytelephantoides	*Phytelephas* (Phytelepheae)	Stem with root	India	Late Cretaceous- early Paleocene	Chate et al., 2019
Palmoxylon ceroxyloides Khan, Hazra et Bera, sp. nov	Ceroxyleae (Ceroxyloideae)	Stem	India	Late Cretaceous- early Paleocene	Present study

The Trans-Beringian route includes the Beringian Land Bridge (BLB) across what is now the Bering Sea, which has intermittently connected North America and Asia since the mid Cretaceous (~100 Ma). The BLB operated until the Pliocene after which the Beringian transgression led to the opening of the Bering Strait in the late Pliocene (3.5 Ma), (McKenna, 1983; Lafontaine and Wood, 1988; Tangelder, 1988).

Evidence for the importance of the BLB includes the existence of boreotropical forests, which stretched from Asia to North America through Beringia during the Paleocene (Wolfe, 1978), the dispersal of the plant *Paliurus* (Rhamnaceae) to North America from India during the Eocene, and by the middle-late Miocene (14–10 Ma) to late Pliocene (3.5 Ma) a belt of coniferous forests connected northern Asia with northern North America. The BLB appears to have acted as a major migration corridor for many plant taxa such as *Acer* L., *Amersinia* Manchester, Crane & Golovnev, *Davidia* Baill., *Dipteronia* Oliv., *Eucommia* Oliv., *Limnobiophyllum*, *Macginitiea* Manchester, *Quereuxia* Kryshtofovich ex Nevolina, and *Trochodendron* Siebold & Zucc between North America and East Asia (Manchester, 1999; Grímsson et al., 2014), as well as faunal elements such as *Viverravus* (McKenna, 1975).

The paucity of fossil evidence means that routes and directions of dispersal of Ceroxyloideae between South America and India remain uncertain. The geological history of India, including its split from other parts of Gondwana, its northward journey, and eventual collision with Eurasia, has been well documented (Ali and Aitchison, 2005; Bouilhol et al., 2013). The present fossil evidence of a ceroxyloid palm from the latest Maastrichtian sediments of India implies that the wax palm subfamily must have been present in India by latest Cretaceous time (*c.* 66–65 Ma), and this early occurrence suggests an Indian origin. Thereafter it may have dispersed to East Asia following the collision of the Indian subcontinent with Eurasia, and reached North America via the

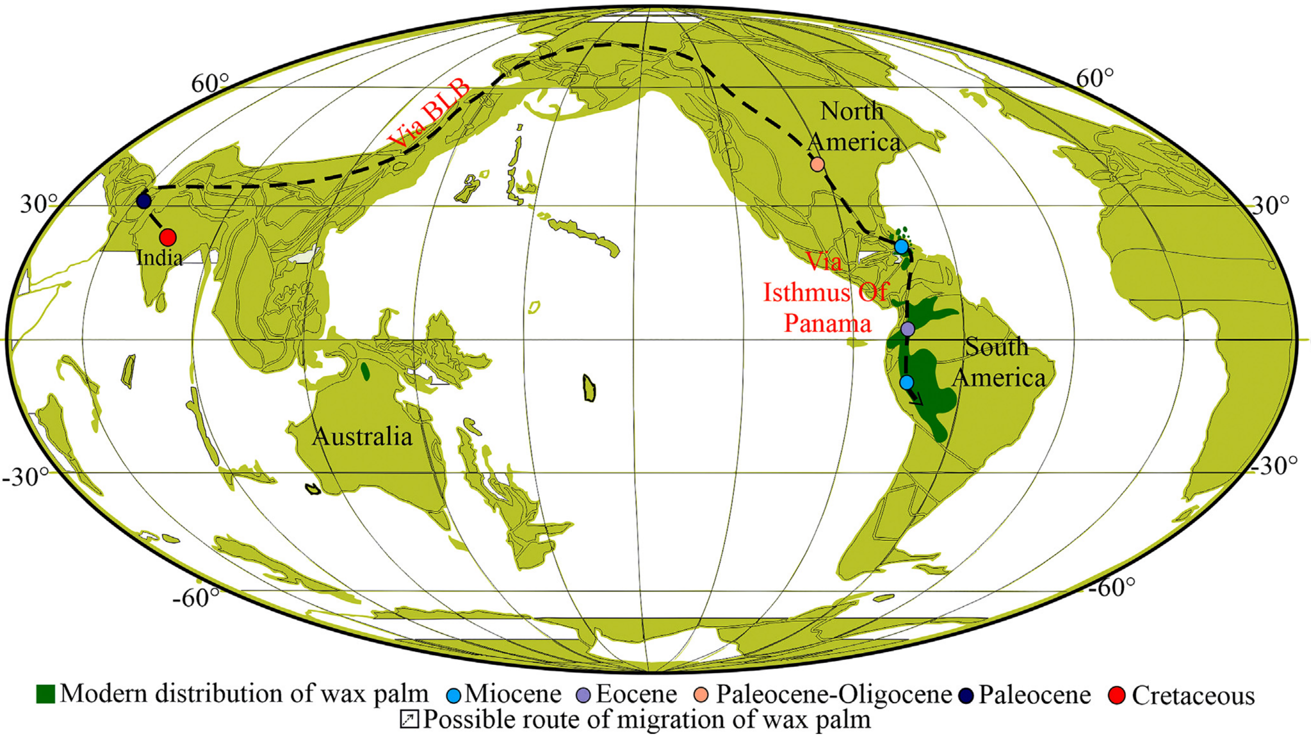

Fig. 3. Map showing the distribution of extant and extinct Ceroxyloideae and possible migratory routes to North America via Beringian Land Bridge (BLB) and to South America via the Isthmus of Panama.

BLB, which existed until sometime between 4.8 and 5.5 Ma. The occurrence of Paleocene-Oligocene microfossils of the Ceroxyloideae in North America (Frederiksen, 1980; Melchior, 1998) hints at the wax palm reaching there from India through the BLB (Fig. 3), so we suggest that the BLB (during the Eocene) is the most likely route.

During the Miocene, the Isthmus of Panama formed a land link between North America and South America (Cody et al., 2010; Bacon et al., 2015). So, after colonizing North America, the wax palm subfamily probably reached South America in the Miocene via the Isthmus of Panama link (Fig. 3). This hypothesis conforms with reliable megafossil

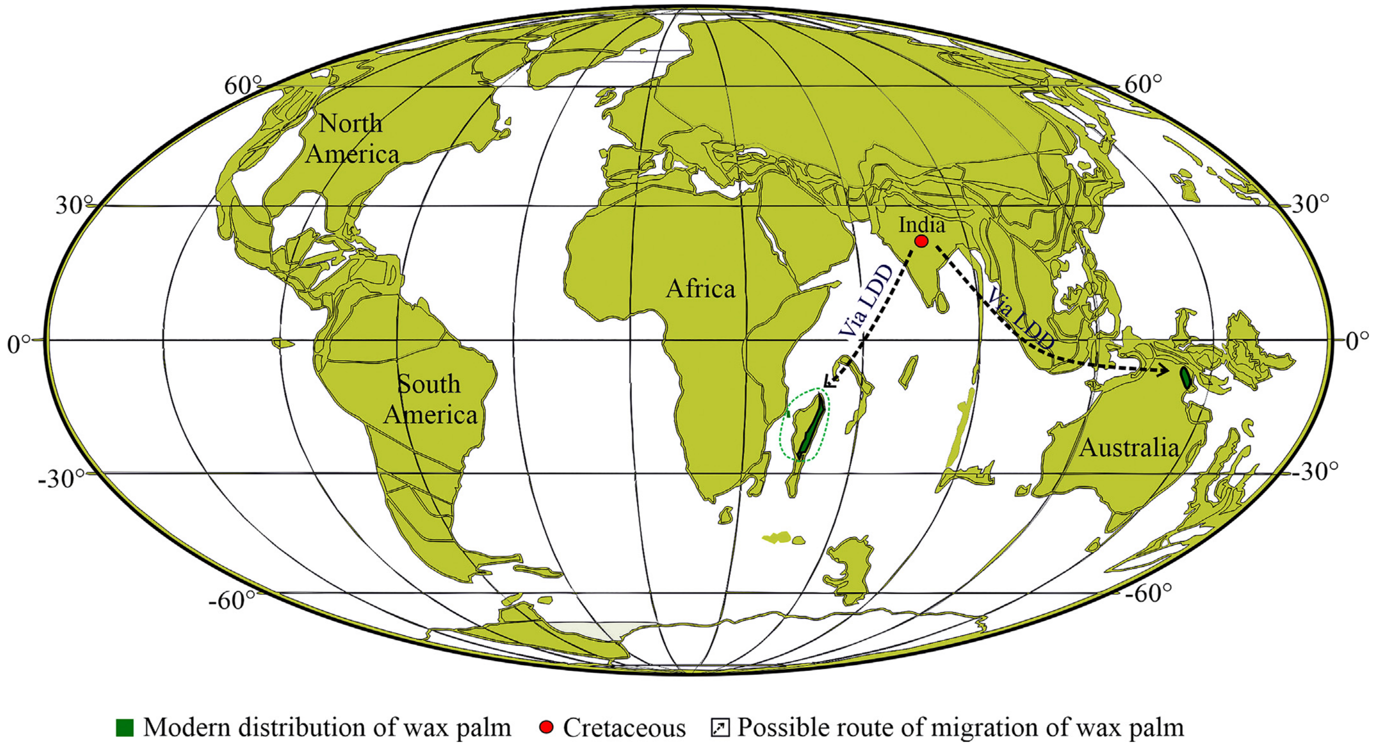

Fig. 4. Map showing the distribution of extant and extinct Ceroxyloideae and the possible migratory route from India to eastern Gondwana continents via long-distance dispersal (LDD).

evidence of the Ceroxyloideae in South America during the Miocene (Kaul, 1943; Brown, 1956). It is also supported by the "Great American Interchange" hypothesis that holds exchange of both flora and fauna took place between the North and South America (Webb, 1985).

From the Oligocene onwards Islands of southeastern Asia also formed a land link between the Asian continent and Australia (Morley, 2003), so, we suggest that Ceroxyloideae probably reached Australia via that island route.

On a more local level the Kohistan-Dras volcanic arc likely acted as a land connection between India and Pakistan from ~61 Ma (Sahni, 1988; Khan et al., 2009; Chatterjee et al., 2013). The Paleocene pollen evidence of *Ceroxylon* (tribe Ceroxyleae) from Pakistan (Frederiksen, 1994) can be thought of as the result of migration from India via the Kohistan-Dras volcanic arc.

In addition to migrations across different land bridges, several recent studies have suggested that long-distance dispersal (LDD) may have played important roles in certain intercontinental disjunctions (Nie et al., 2005; Popp et al., 2011). Intercontinental plant dispersals can be explained by abiotic transfer by water or wind (Carlquist, 1967, 1983), and biotically by birds (Winkworth et al., 2002). These two dispersal systems are not entirely independent of course in that wind patterns influence ocean currents and may facilitate bird migrations. LDD is a very common dispersal route for plant taxa between Southern Hemisphere continents such as South Africa, South America, Australia and New Zealand (Winkworth et al., 2002). Several biogeographical patterns indicate that LDD can be directional (Wardle, 1978; Les et al., 2003; Sanmartin and Ronquist, 2004), and so the Antarctic Circumpolar Current and the West-wind Drift (Colls and Whitaker, 2001), which originated after the rifting of South America and Australia from Antarctica at 38 Ma, may have given rise to the close taxonomic affinities between Australia, New Zealand, Madagascar, South Africa and South America.

That birds may act as important LDD agents was first proposed by Darwin (1859) and this has been supported by various other workers (Willis, 1970). The spread of *Lepidium* and *Microseris* between coastal California and Australia/New Zealand was likely facilitated by birds (Lincoln et al., 1998). Madagascar's geographic isolation from the other southern continents also supports biotic exchange (Schatz, 1996). Schatz considered that the Madagascar flora in the early Cenozoic migrated from Australia, India, and Southeast Asia, and the prevailing easterly wind blowing across the Indian Ocean accelerated the process of LDD.

Given these examples we suggest that the present-day distribution of Ceroxyloideae in the eastern Gondwanan continents of Australia, Madagascar and the Comoros, where obvious land bridge routes appear lacking, may be explained by long distance dispersal from India (Fig. 4). Furthermore, small, nutrition-rich seeds of some members of Ceroxyloideae palm (*Ravenea* and *Pseudophoenix*) likely attracted animal dispersants that included birds (*Saltator albicollis*, *Loxigilla noctis* and *Alectronenas madagascariensis*) (Zona and Henderson, 1989; Adany et al., 1994). So, we suggest that migrating birds may also have played a key role in long-distance seed dispersal of some members of the Ceroxyloideae.

Fossil evidence, along with molecular phylogenetic data, is important in studying the evolution and speciation of an organism. Our fossil evidence, along with the known fossil records of Ceroxyloideae, suggests that the wax palm subfamily evolved in India during the late Cretaceous and migration occurred from India to other continents. The present study also suggests that Gondwanan vicariance is unlikely as an explanation for disjunctions in Ceroxyloideae. We suggest alternative explanations for disjunctions in this palm subfamily that include a mid-Cenozoic trans-Beringian dispersal track and historical long-distance dispersal. The present finding fits well with the previous molecular phylogenetic analysis by Trénel et al., 2007 and plate tectonic models. Trénel et al. (2007) studied the biogeography of the Ceroxyloideae using nuclear and plastid DNA sequence data and considered mid-Cenozoic dispersal (not Gondwanan vicariance) as the predominant mechanism for the distribution of this palm subfamily.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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