Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Research Article

Turk J Bot
(2024) 48: 105-119
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doi:10.55730/1300-008X.2799

A new permineralized Corypha-type coryphoid palm stem from K-Pg of India: Anatomy, systematics, saprophytic fungi, and paleoecology

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Received: 15.08.2023 • **Accepted/Published Online:** 16.11.2023 • **Final Version:** 19.03.2024

Abstract: Palms are known to be an important and diverse angiosperm component in the Deccan Intertrappean beds of Central India. However, the report of fossilized palm stems inhibiting saprophytic fungal remains is empty in the field of paleobotany. Here, we document for the first time the occurrence of fungal remains in a petrified palm stem collected from the latest Maastrichtian (Late Cretaceous)-earliest Danian (early Paleocene) sediments of the Deccan Intertrappean beds of Madhya Pradesh, Central India. The anatomical features of the fossil stem are characterized by the presence of Corypha-type general stem pattern (progressive decrease of fibrous parts of fibrovascular bundles, fvbs from the periphery towards the center), vaginata-shaped fvbs with dorsal fibrous sclerenchymatous part (dcap) adjacent to the phloem, metaxylem vessel element varying from 1 in the outer part to 2 and more (>4) in the inner central zone, and abundant fibrous bundles in the central zone. Based on these anatomical characteristics, our Deccan specimen is confidently placed under extant Corypha-type coryphoid palm taxa belonging to the family Arecaceae and is recognized as a new species *Palmoxylon coryphaoides* Ali, Roy et Khan sp. nov. The detailed anatomical study of the fossil stem specimen also reveals that it is endogenously infected with well-preserved fungal conidia similar to the modern saprophytic fungus *Epicoccum* Link. ex Schlecht that are profusely distributed in the metaxylem vessels. The evidence of the current palm species and earlier-reported fossil palm species similar to Coryphoideae collectively indicate the existence of a tropical, warm, and humid environment in the Deccan Intertrappean Beds of Madhya Pradesh during the time of deposition.

Key words: Anatomy, Coryphoideae, Deccan Intertrappean beds, fungal remains, Madhya Pradesh, *Palmoxylon*

1. Introduction

Coryphoid palms, the second largest subfamily of Arecaceae (palms), consist of 47 genera and 518 species (Dransfield and Uhl, 1986; Dransfield et al., 2008; Baker and Dransfield, 2016) and are subdivided into eight tribes such as Borasseae, Caryoteae, Chuniophoeniceae, Corypheae, Cryosophileae, Phoeniceae, Sabaleae, and Trachycarpeae (Asmussen et al., 2006; Dransfield et al., 2008). Coryphoideae is sister to a clade comprising Arecoideae and Ceroxyloideae and is considered one of the earliest diverging members of Arecaceae (Asmussen et al., 2000). Based on molecular data, the divergence of Coryphoideae occurred at about 87 Ma (95% HPD 86–88) in Laurasia (Baker and Couvreur, 2013a, b).

Coryphoid palms show some significant anatomical characteristics in their stem pattern (Tomlinson et al., 2011). Generally, two stem patterns namely, Cocos-type (no notable change i.e. increase or decrease of fibrous part of fvbs from the periphery towards the center; so, fvbs homogeneously distributed throughout the cross-section) and Corypha-type (gradual decrease of fibrous part of fvbs from the periphery towards the centre) are common in coryphoid palm stems. Cocos-type is found in the members of tribes such as Hyphaenieae (Hyphaene), Chuniophoeniceae, Cryosophileae, and Phoeniceae, while Corypha is found in the members of other tribes such as Hyphaenieae (*Bismarckia*), Lataniieae, Corypheae, Sabaleae, and Trachycarpeae. The tribe Caryoteae exhibits a Mauritia-type stem pattern (abrupt decrease of fibrous part of fvbs from the subcortical to the central zone).

To date, very few permineralized coryphoid palm stems are reported from the Deccan Intertrappean sediments (Mahabale, 1958; Sahni, 1964; Lakhanpal et al., 1979; Prakash and Ambwani, 1980; Ambwani, 1983; Ambwani and Mehrotra, 1989; Gayakwad and Patil, 1989; Rao and Shete, 1989; Bonde et al., 2008; Roy, 2013; Khan et al., 2020). However, earlier paleobotanists did not mention the Corypha-type general stem pattern and did not find

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fungal remains in their observed fossil coryphoid palm stem. So, our discovery of palm stem-inhibiting fossil fungi is remarkable. Here, we report for the first time a Corypha-type coryphoid fossil palm stem endogenously infected with saprophytic fungi similar to the modern ascomycetous fungus *Epicoccum* from the Cretaceous-Paleogene sediments of India. The presence of the coryphoid palm stem with fungal infection indicates warm and humid conditions in the area during the deposition of Deccan Intertrappean sediments.

The present manuscript aims to (1) describe a Corypha-type coryphoid palm stem, (2) report the fungal remains associated with it, and (3) comment on its palaeoecological implications.

2. Materials and methods

2.1 Fossil locality and geological setting

The well-preserved petrified palm stem was collected from the surface exposure of Deccan Intertrappean beds of Umaria village (23°05'26.41" N, 80°37'35.25" E) in Dindori District, Madhya Pradesh, Central India (Figure 1). Based on radiometric dating ($^{40}Ar/^{39}Ar$ dating), planktonic foraminifera, and magnetostratigraphy, the age of the Deccan Intertrappean sediments is considered to be the latest Maastrichtian (Late Cretaceous)-earliest Danian (early Paleocene) (67.5–63 Ma with the bulk of the eruption at 65 ± 1 Ma) (Khosla, 1999; Hofmann et al., 2000; Chenet et al., 2009; Renne et al., 2015; Schoene et al., 2015; Srivastava et al., 2015a; Smith et al., 2015).

2.2 Sample preparation and photography

Thin anatomical sections (tangential and radial) of the present fossil stem are prepared following the standard grinding, polishing, and mounting method for permineralized material (Haas and Rowe, 1999). The thin sections were examined with a transmitted light compound microscope with a photographic attachment (Zeiss Axioskop 2) (Figures 2–4). In our study, fluorescence microscopy (Carl Zeiss with a green filter cube with a 510–530 nm excitation band) is also applied to better investigate the anatomical features of the palm stem. The fossil specimen is identified with the aid of xylotomical databases, website (http://www.infosyslab.fr/Palm-ID/ Thomas 2011), and published articles (Tomlinson, 1961; Tomlinson et al., 2011; Thomas and Franceschi, 2013).

2.3 Cladistic analysis

A cladistic parsimony analysis using PAST ver. 4.03 statistical software (Hammer et al., 2001) was undertaken to correlate the phylogenetic affinities of our fossil palm stem specimen with its NLRs (nearest living relatives) of coryphoid palms. Cladistic analyses were conducted as unordered characters for unweighted parsimony analysis and implemented using the "heuristics" menu option in the program's past. Eighteen anatomical characteristics of palm stem were scored together with those of 19 extant genera of coryphoid palm and our fossil palm stem specimen (see supplementary material). The cladogram was rooted in the result.

2.4 Repository

The holotype palm stem specimen (SKBU/PPL/U12) and prepared section slides (SKBU/PPL/U12/T1; SKBU/PPL/ U12/T2; SKBU/PPL/U12/T3; SKBU/PPL/U5/L1) are housed in the museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, West Bengal, India.

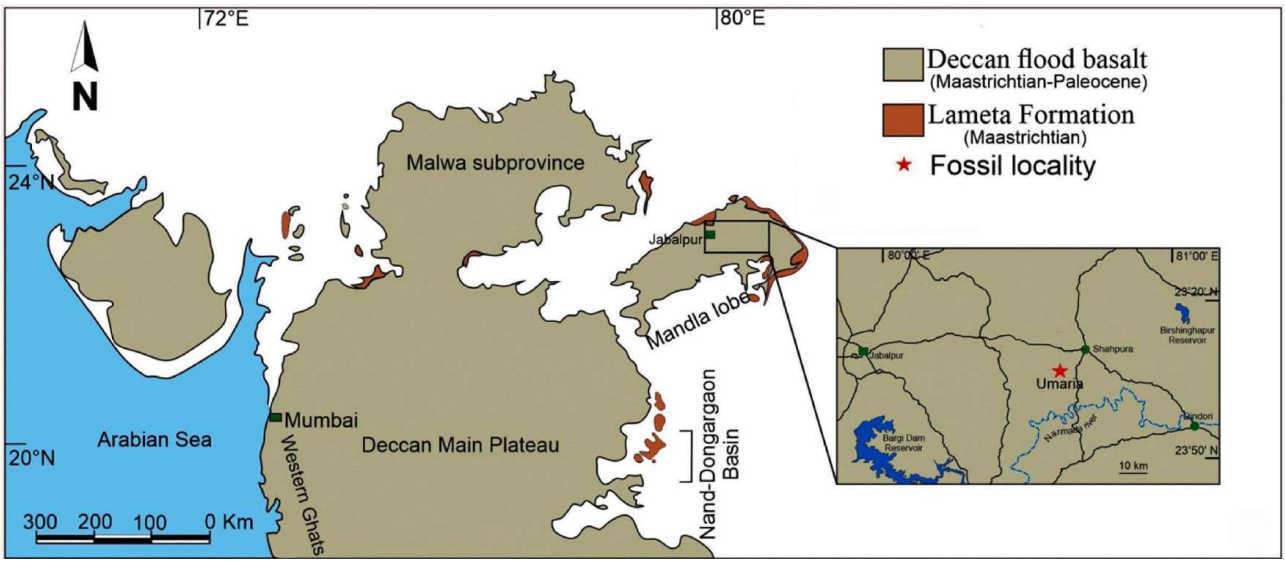

Figure 1. Map showing Deccan Volcanic Province (DVP). The fossil locality is marked by red star (modified after Smith et al., 2015).

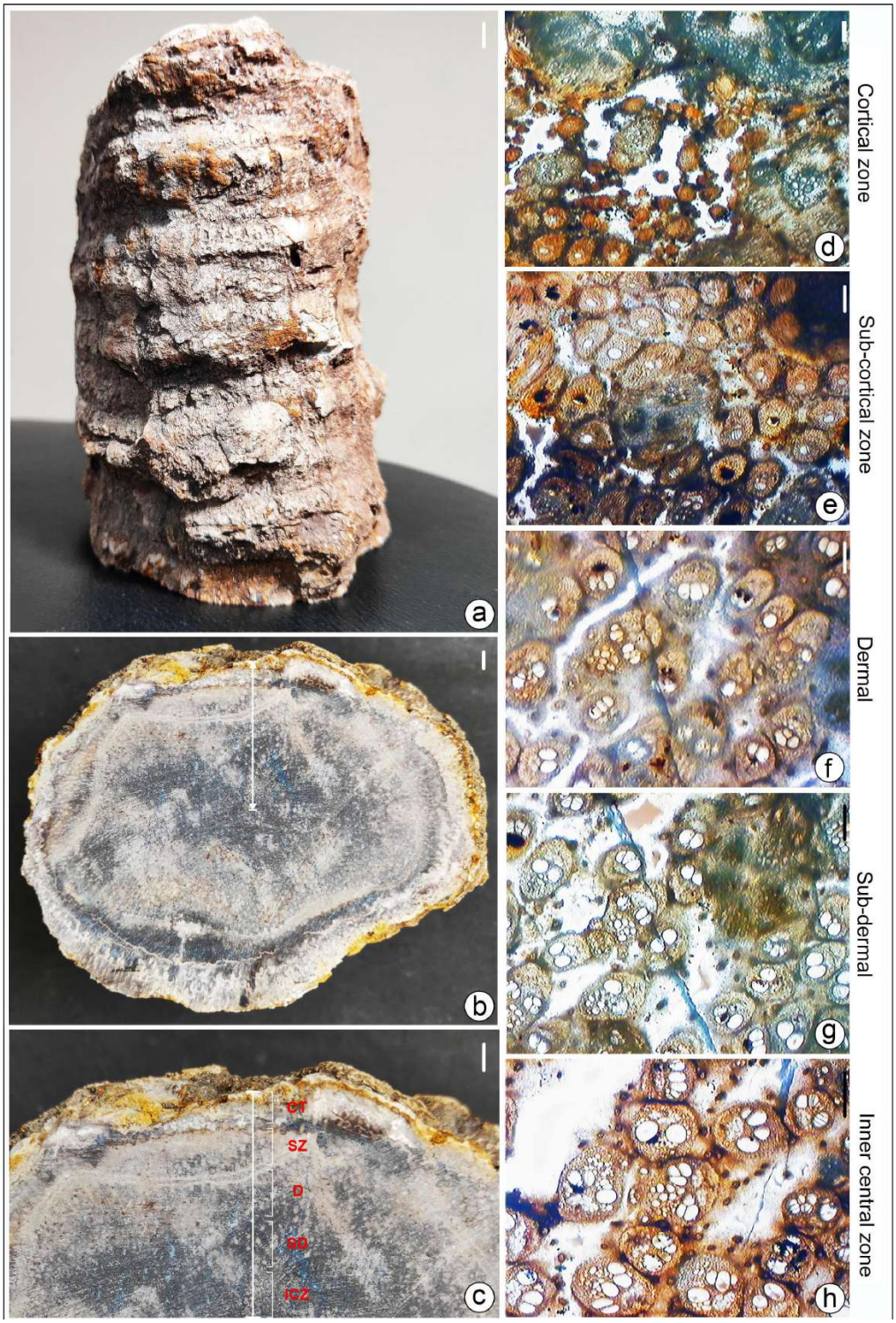

Figure 2. (a) Overview of recovered fossil stem of *Palmoxylon coryphaoides* Ali, Roy et Khan sp. nov (Holotype: SKBU/PPL/U12); (b) Top view of fossil stem showing periphery to center (marked by white arrow); (c) An enlarged view of figure b indicating cortical (CT), subcortical (SZ), dermal (D), subdermal (SD) and Inner Central zone (ICZ); (d–h) Light microscopic images of transverse sections of outermost cortex to innermost central zones of fossil palm stem *P. coryphaoides* sp. nov. Scale bars = 1 cm for a, b and c; Scale bars = 200 µm for d–h.

3. Results and discussion

3.1 Systematic description of fossil palm stem

Family: Arecaceae Schultz Sch. 1832

Genus: ***Palmoxylon*** Schenk 1882

Palmoxylon coryphaoides **Ali, Roy et Khan sp. nov.** (Figure 2)

Etymology: The specific epithet "*coryphaensis*" recognizes the Corypha type of stem organization of the fossil specimen

Holotype: SKBU/PPL/U12 (Figure 2a)

Stratigraphic horizon: Deccan Intertrappean beds; latest Maastrichtian (Late Cretaceous) - earliest Danian (early Paleocene).

Type locality: Umaria Ryt. village (location: 23°05'26.41" N, 80°37'35.25" E, , elevation 1607.61 ft a.s.l) in Dindori district, Madhya Pradesh, Central India.

Specific diagnosis

Corypha-type general stem organization; more or less irregularly oriented fvbs with one, two, and more (>4) metaxylem vessels throughout the transverse section; the size of the fvbs ranges from 100 × 250 µm and 400 × 600; the presence of 2 to >10 prominent small protoxylem vessels in both subdermal (SD) and inner central zone (ICZ); vaginata and lunaria-shaped dcap adjacent to the phloem; loosely packed ground tissue and no sustained growth in the ground parenchyma; fibrous bundles present throughout the central zone (subdermal and partly in the inner central zone); absence of centrifugal differentiation of fibrous part of fvbs or the zone of transition between subcortical zone (SZ) and central zone (CZ); tabular and radiating parenchyma absent around the fvb; strongly found gradual decrease of fibrous part of fvbs from SZ to CT.

Description

The yellowish-brown colored permineralized stem is a maximum of 20 cm in length and 9 cm in diameter (Figure 2a) and is well preserved, revealing all detailed anatomical characteristics for its identification. The cross-section shows pale grey-colored fvbs (lightly distributed) and mesh-like ground parenchyma (Figures 2b , c), typical of the palm stem.

CT (Cortical zone) (Figures 2d, 3a)

Well-developed cortex (CT); more contiguous fibrovascular bundles (fvbs), sizes vary from 80 × 100 to 130 × 250 µm, slightly smaller than the SZ; ground tissue highly compact.

SZ (Sub-cortical zone) (Figure 3b)

Distribution of fvb slightly more spaced than in the CT, sizes vary from 110 × 250 to 200 × 400 µm, mostly 1 meta xylem vessel element in all fvbs, fibrous part well developed in each fvb; higher density of the fibrous vascular bundles, d(fvb) than the CT; ratio between the d(fvb) of the sub-cortical zone (1000/cm^2) and the d(fvb) of the central zone (550/cm^2) $d(fvb)_{out}/d(fvb)_{in}$ = 1.81; absence of zone of transition (TZ) between SZ and CT and no centrifugal differentiation of the fibrous part.

DZ (Dermal zone) (Figures 2f, 3c)

Sparsely placed fvbs, sizes vary from 250 × 400 to 300 ×600 µm, shape generally round to oval, regularly oriented; frequency of fibrovascular bundles varies from 80 to 100 per cm^2; the f/v ratio ranges from 3/1 to 5/1; ground tissue not prominent; 2 to 3 metaxylem vessels connecting to the phloem; vaginata to lunaria shaped dcap present; absence of auricular sinus; presence of small fibrous bundles and absence of diminutive bundles throughout the transverse section; tabular and radiating parenchyma absent; leaf-trace bundles frequently visible.

SDZ (Subdermal zone) (Figures 2g, 3d)

Slightly bigger, more sparsely placed, and regularly oriented fvbs, sizes vary from 280 × 450 to 350 × 550 µm, shape round to slightly elongated, frequency of fibrovascular bundles varies from 70 to 80 per cm^2; f/v ratio 4/1 to 7/1; vaginata-lunaria shaped dcap present adjacent to the phloem; presence of 2–4 metaxylem vessels and 2–10 small protoxylem vessel element; leaf trace bundles present; irregularly distributed small fibrous bundles around the fvb; absence of both tabular and radiating parenchyma; ground tissue badly preserved.

ICZ (Inner central zone) (Figures 2h, 3e,f)

More sparsely placed fvbs as compared to those of D and SD zones, more or less regularly oriented, sizes vary from 300 × 500 to 400 × 600 µm, shape spheroid to elongated, vaginata to lunate shape dcap; presence of 2–4 and >4 metaxylem vessels and 5 to >10 small protoxylem vessel element (Figure 4); frequency of fibrovascular bundles varies from 60 to 70 per cm^2; f/v ratio ranges from 5/1 to 8/1; stegmata absent; presence of single-strand phloem; leaf-trace bundles present; absence of both tabular and radiating parenchyma; numerous fibrous bundles present.

3.2. Taxonomic considerations of fossil palm stem

3.2.1. Why Corypha-type palm?

Palms (Arecaceae) show significant anatomical characteristics in their stem pattern (von Mohl's classification 1823–1850). These are Cocos-type (uniform distribution of fibrous part of fvbs throughout the cross-section, fvbs are similar in their size and structure); Corypha-type (progressive decrease of fibrous part of fvbs from the outer cortex towards the centre); Mauritia-type (abrupt decrease of the fibrous part from the outer cortex towards the centre); Calamus-type (relatively uniform density of fvbs and have among the widest vessels in palms); Geonoma-type (absence of fibrous part centrifugal differentiation and have compact ground parenchyma but without lacunae). So, the present fossil specimen shows

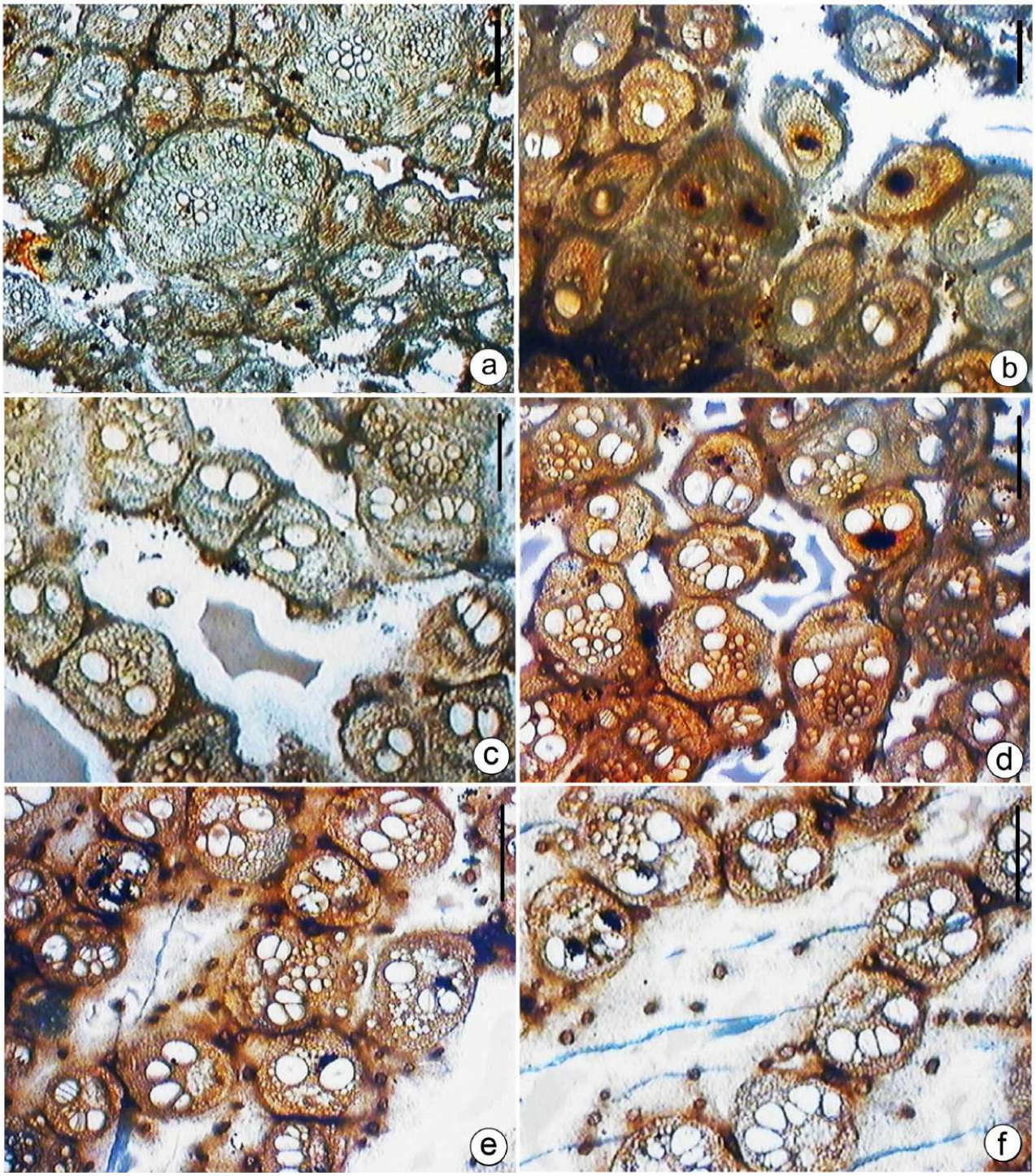

Figure 3. Light microscopic images of the transverse section of outer cortical to inner central zones of fossil palm stem *P. coryphaoides* sp. nov. (a) A well-developed cortical zone of the fossil stem; (b) Size, shape, orientation, and distribution of the fibrovascular bundles with mostly one metaxylem vessel element in the sub-cortical zone; (c) Size, shape, orientation, and distribution of the fibrovascular bundles with mostly two metaxylem vessels in the dermal zone; (d) Size, shape, orientation, distribution of fibrovascular bundles with xylem vessels in the subdermal zone; (e–f) Size, shape, orientation, distribution of fibrovascular bundles with xylem vessels and small fibrous bundles in the innermost central zone Scale bars = 200 µm.

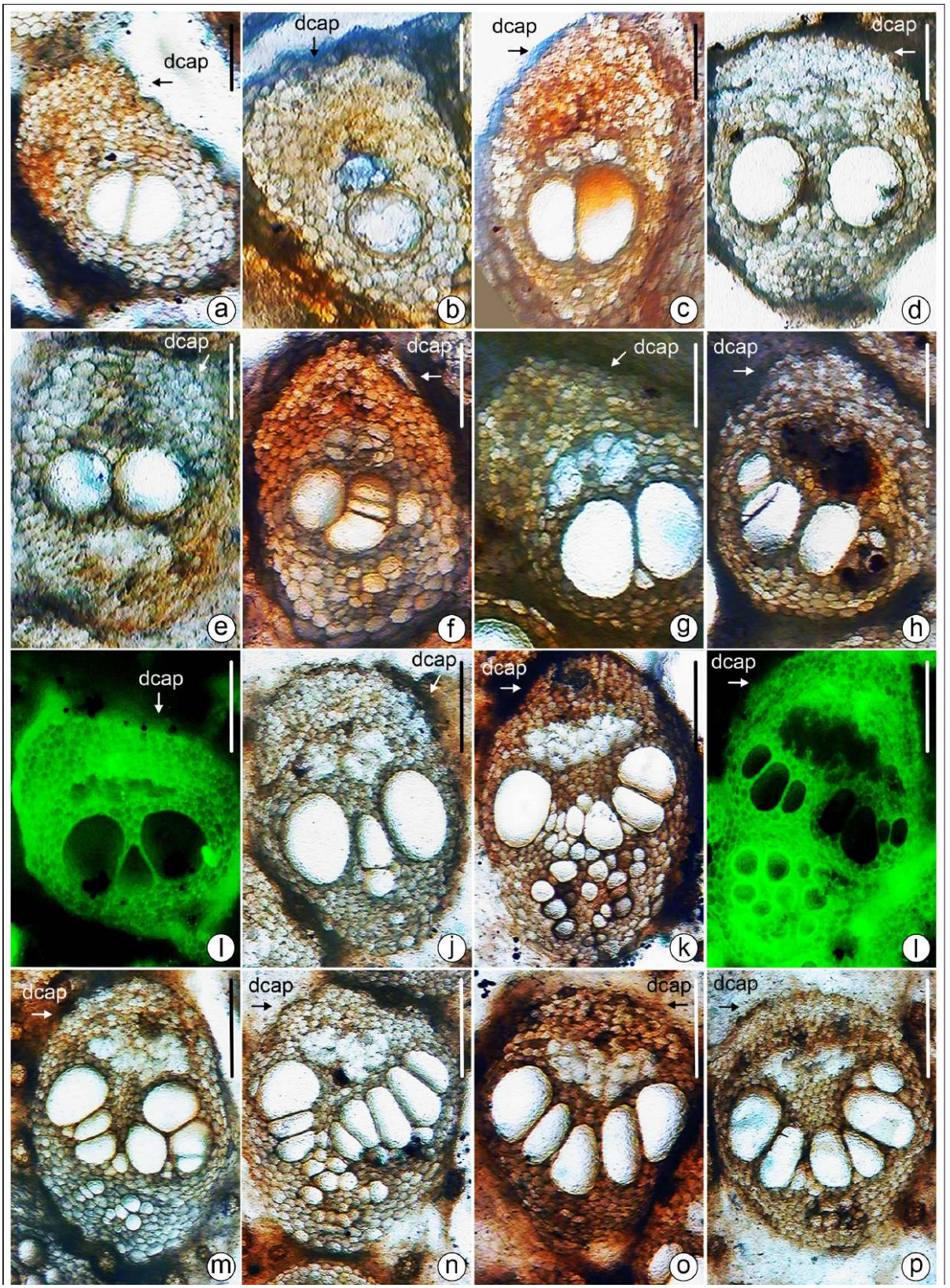

Figure 4. Light microscopic image of single fibrovascular bundles from the outer cortex to the inner central zone showing a gradual decrease of the fibrous part (dcap) of the fossil palm stem *P. coryphaoides* sp. nov. Scale bars = 100 µm.

the closest similarity with Corypha-type general stem organization, as the proportion of fibrous part of fvbs is less developed in the inner central zone, gradual decrease of fibrous part towards the centre and no sudden transition of the fibrous part between the outer and inner part of the stem is observed (Figure 5).

3.2.2. Why Corypha-type coryphoid palm?

Among the modern palm subfamilies, the Nypoideae,

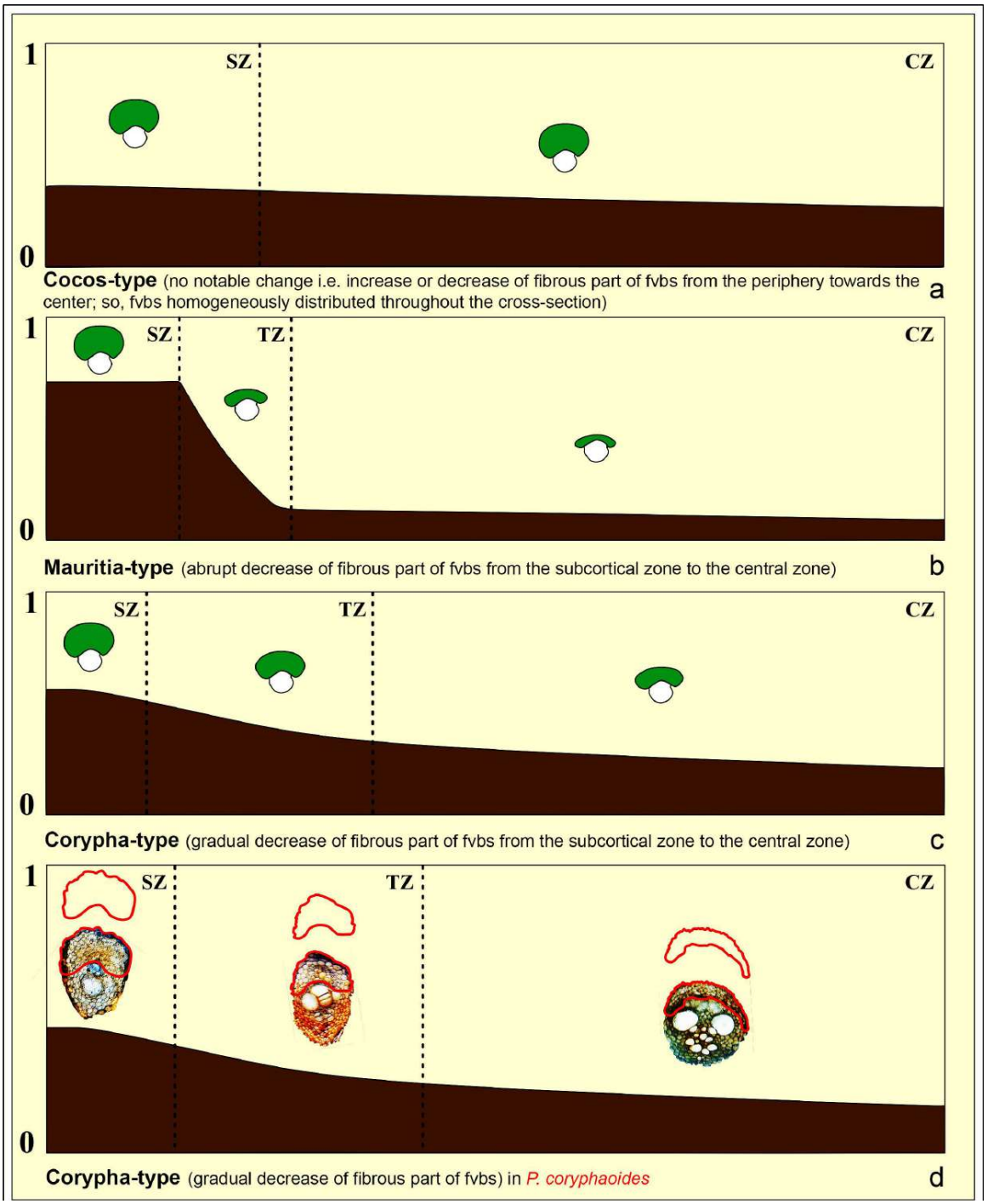

Figure 5. The graphical representation of different general stem patterns of palm shows the proportion of the fibrous part (dcap) of fvbs in different zones (a–c) modern palm; (d) present fossil palm stem namely *P. coryphaoides* sp. nov. (SZ: subcortical zone; TZ: zone of transition; and CZ: central zone).

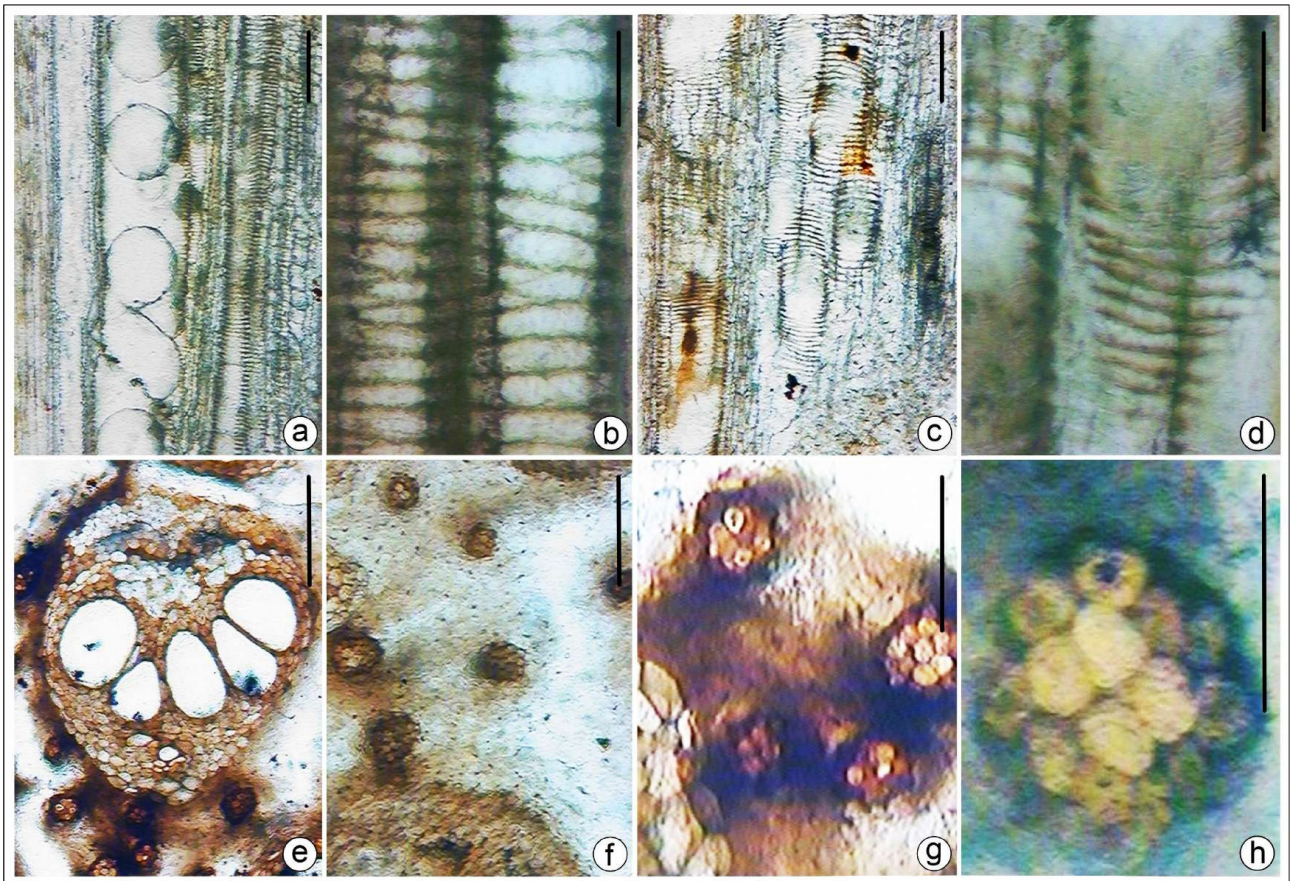

Figure 6. (a–d) Light microscopic images of the longitudinal section of a part of the fossil palm stem *P. coryphaoides* sp. nov. showing fibers and metaxylem vessels with scalariform pitting of a metaxylem vessel; (e) Light microscopic image of a single fibrovascular bundle with numerous small fibrous bundles; (f) Distribution of six fibrous bundles in the ICZ of the present fossil palm stem; (g) Enlarged view of fibrous bundles shown in e; (h) Enlarged view of a single fibrous bundle of the present fossil palm stem *P. coryphaoides* sp. nov. Scale bar = 100 µm for a–f; Scale bar = 50 µm for g; and Scale bars =25 µm for h.

and Ceroxyloideae are distinguishable from the present specimen as they show Cocos, and Mauritia type general stem organization respectively. Calamoideae exhibits Mauritia or Calamus type of stem organization. Corypha-type is mostly found in Coryphoideae and a few members of Arecoideae. However, Arecoideae differs in several lines of anatomical characteristics, such as the presence of sagittate and reniforma-shaped fibrous parts in fvbs, the absence of fibrous bundles in the central cylinder, and the presence of only 1 or 2 metaxylem elements. In our specimen, metaxylem vessel elements vary from 1 in the outer part to 2 and more (>4) in the inner central zone, and abundant fibrous bundles are present in the central zone (Figure 6). Of the known anatomy of different genera of modern palm subfamilies, our new palm species shows more anatomical similarities with members of Corypha-type coryphoid palm than other palm subfamilies.

3.2.3. Comparisons with modern genera of coryphoid palms

To identify our specimen up to the generic level, we compare it with the stem anatomy of different modern genera of coryphoid palms such as *Bismarckia* Hildebr. and H.Wendl., *Brahea* Mart. ex Endl., *Borassus* L., *Chamaerops* L., *Chuniophoenix* Burret, *Coccothrinax* Sarg., *Copernicia* Mart., *Corypha* L., *Lodoicea* Comm. ex DC., *Livistona* R.Br., *Licuala* Wurmb, *Nannorrhops* (Griff.) Aitch., *Pritchardia* Seem. and H. Wendl., *Rhapis* L.f. ex Aiton., *Sabal* Adans., *Serenoa* Hook.f., *Trachycarpus* H.Wendl., *Washingtonia* H. Wendl. and *Wallichia* Roxb. Some coryphoid palm taxa such as *Wallichia*, *Chuniophoenix*, *Rhapis*, *Coccothrinax*, *Nannorrhops*, *Chamaerops*, and *Trachycarpus* can be easily distinguished by their general stem pattern. *Wallichia* exhibits mauritia-type, both *Chuniophoenix* and *Rhapis* show geonoma-type, *Coccothrinax*, *Nannorrhops*,

Chamaerops, and *Trachycarpus* possess cocos-type of general stem pattern in comparison to corypha type stem pattern in the present fossil specimen. *Bismarckia* stem is characterized by the presence of reniform-shaped fvbs with 2 (3–4) metaxylem vessels and the absence of fibrous bundles in the central cylinder whereas our specimen is characterized by vaginata to lunate-shaped fvbs with mostly 1, 2, and >4 number of metaxylem vessels and the presence of distinct fibrous bundles in the central cylinder. *Borassus* is distinguished by only 1 metaxylem vessel element. In *Serenoa* and *Pritchardia*, fvbs are reniform and fibrous bundles are absent in the central cylinder. *Brahea*, *Copernicia*, *Sabal,* and *Washingtonia* differ by having reniform fvbs with 2 (3–4) metaxylem vessels. However, some palm genera namely, *Corypha*, *Lodoicea*, *Livistona*, and *Licuala* exhibit corypha type of general stem pattern. They are also characterized by the presence of fibrous bundles in the central cylinder, and the absence of tabular parenchyma as found in our specimen. But *Corypha* and *Licuala* differ in their shape of fvbs. So, based on the suite of the above-mentioned anatomical characteristics, it is likely that our Deccan specimen is more similar to *Lodoicea* and *Livistona*. This conclusion is also supported by cluster analysis (Figure 7).

3.2.4. Comparison with earlier reported fossil stem species of coryphoid palms

As the present fossil palm stem possesses a corypha-type general stem pattern and exhibits a close resemblance with coryphoid palms, we compare the current specimen with those of extinct coryphoid palms. To date, only five reliable fossil species similar to coryphoid palms are reported from the Late Cretaceous to early Paleocene of Deccan Intertrappean beds of Central India (see supplementary material; Mahabale, 1958; Lakhanpal et al., 1979; Prakash and Ambwani, 1980; Ambwani, 1983; Khan et al., 2020). The fossil species are *Palmoxylon* sp. (Mahabale, 1958), *P. parapaniensis* and *P. mandlaensis* (Lakhanpal et al., 1979), *P. livistonoides* (Prakash and Ambwani, 1980), *P. shahpuraensis* (Ambwani, 1983), and *P. dindoriensis* (Khan et al., 2020). *Palmoxylon* sp. differs from our fossil specimen in the shape of fvbs and the number of metaxylem vessel elements. The Mahabale's species has cordate, sagittate, and reniform-shaped fvbs with mostly two metaxylem vessel elements in the transverse section in comparison to vaginata to lunate-shaped fvbs and mostly one, two, and more (>4) metaxylem vessels in our specimen. *P. parapaniensis* differs from the present specimen in having a cocos-type of general stem pattern. *P. mandlaensis* has reniform to cordate-shaped fvbs with 1–2 layers of tabular parenchyma. *P. livistonoides* is easily distinguished from our specimen by the reniform-shaped fvbs with only 1–2 metaxylem vessels. *P. shahpuraensis* differs in the absence of fibrous bundles in the central cylinder and reniform to cordate-shaped fvbs. *P. dindoriensis* has a cocos-type general stem pattern, reniform fvbs with two-layered tabular parenchyma, and a smaller number of metaxylem vessels than that of our specimen. Undoubtedly, the present fossil palm stem is different from the previously described coryphoid palm stem fossil species. These differences support the recognition of a new taxon. As our fossil stem specimen possesses all internal anatomical characteristics of the genus *Palmoxylon* Schenk and mainly corypha-type general stem pattern, it is designated here as a new species, *Palmoxylon coryphaoides* Ali, Roy et Khan sp. nov.

3.3 Systematic description of palm stem-inhibiting fungus

Family: Didymellaceae

Class: Ascomycetes

Genus: *Epicoccum* Link 1816 (Figure 8)

cf. *Epicoccum* sp.

Description

Fungal conidia endogenously well-preserved in both the transverse (Figure 8a) and longitudinal sections (Figure 8b) of the fossil palm stem, conidia warted and spherical, dark brown, mostly 10–28 µm in diameter, formed singly or mostly densely compacted in colonies, nonspecialized, determinant, conidiophores not seen, presence of young conidia with funnel-shaped base and attachment scar, mature conidia multicellular with an irregular or verrucose external surface, mycelium not preserved, however very few hyphal branches present in longitudinal section of the fossil stem (Figure 8c).

Remarks

The morphological features (darkly pigmented, spherical-shaped multicellular conidia with a verrucose cell wall the funnel-shaped base, and fungal hyphae) (Figures 8d–f) of fungal remains indicate their affinity with those of the modern genus *Epicoccum* Link. of Ascomycetes (Figures 8g, h). This monotypic genus *E. nigrum* Link (synonym *E. purpurascens* Ehrenb.) is a saprophytic endophyte mostly found in dissolving and recycling senescent plant tissues and forms pustules (composed of sporodochia and conidia) on it (Schol-Schwarz, 1959).

3.4 Palaeoecological implications

In Deccan Intertrappean sediments of India, most of the reports focus on the systematics of angiosperm flora, while the fungal remains that often cooccur with them have not received much attention. Some lines of reliable evidence of plant-fungus interactions are previously documented from the Deccan Intertrappean sediments of Central India (Srivastava et al., 2009). Fungal parasitism and saprophytism in fossil fruits, seeds, and wood, as well as dispersed fungal spores, are known from Deccan Intertrappean beds (Lakhanpal et al., 1967; Chitaley and Patil, 1970, 1972; Trivedi and Verma, 1971; Singhai, 1972,

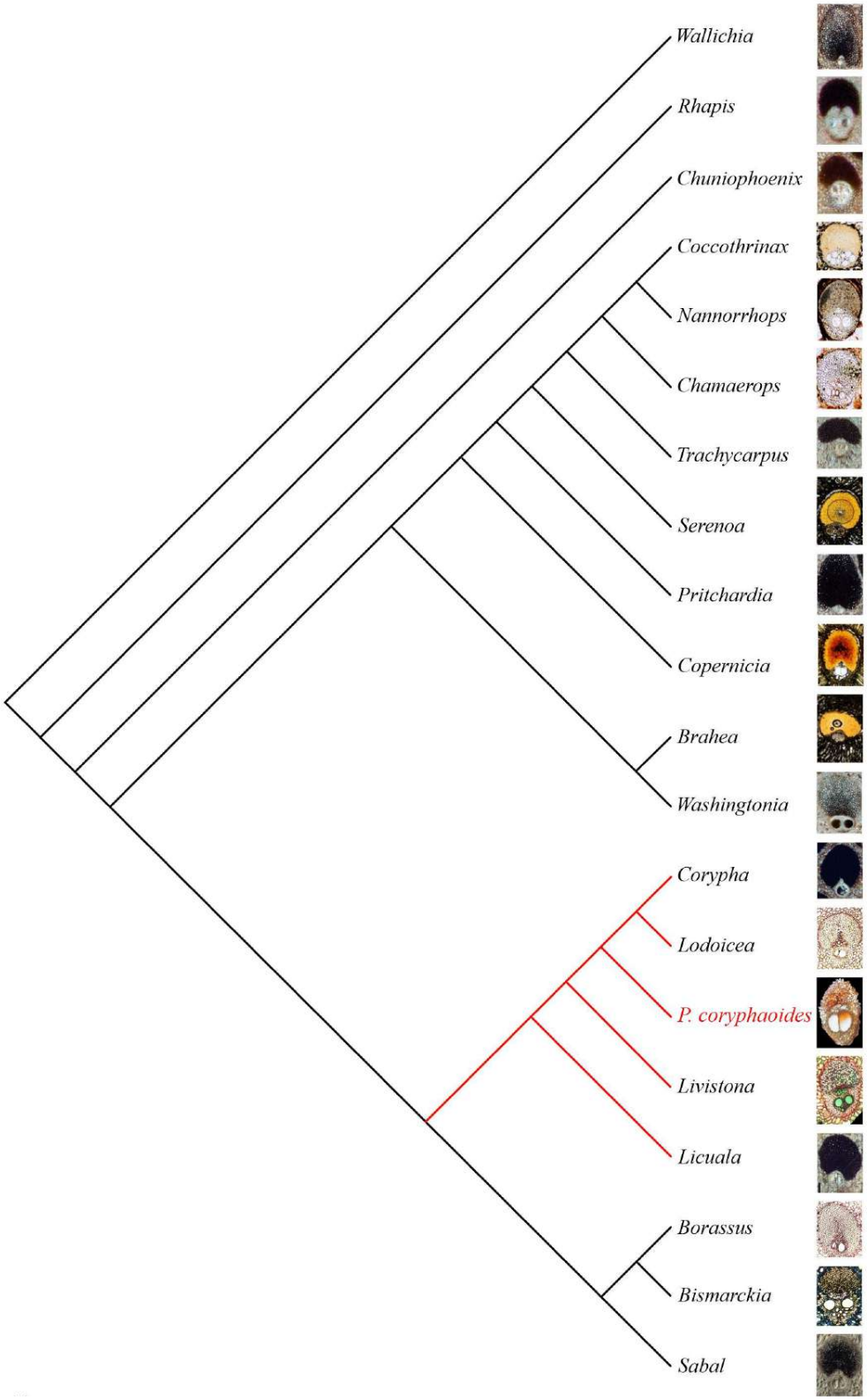

Figure 7. Cluster analysis dendrogram using PAST software showing the characteristic relationship of the fibrovascular bundle between the present fossil species and the other modern species of coryphoid palms.

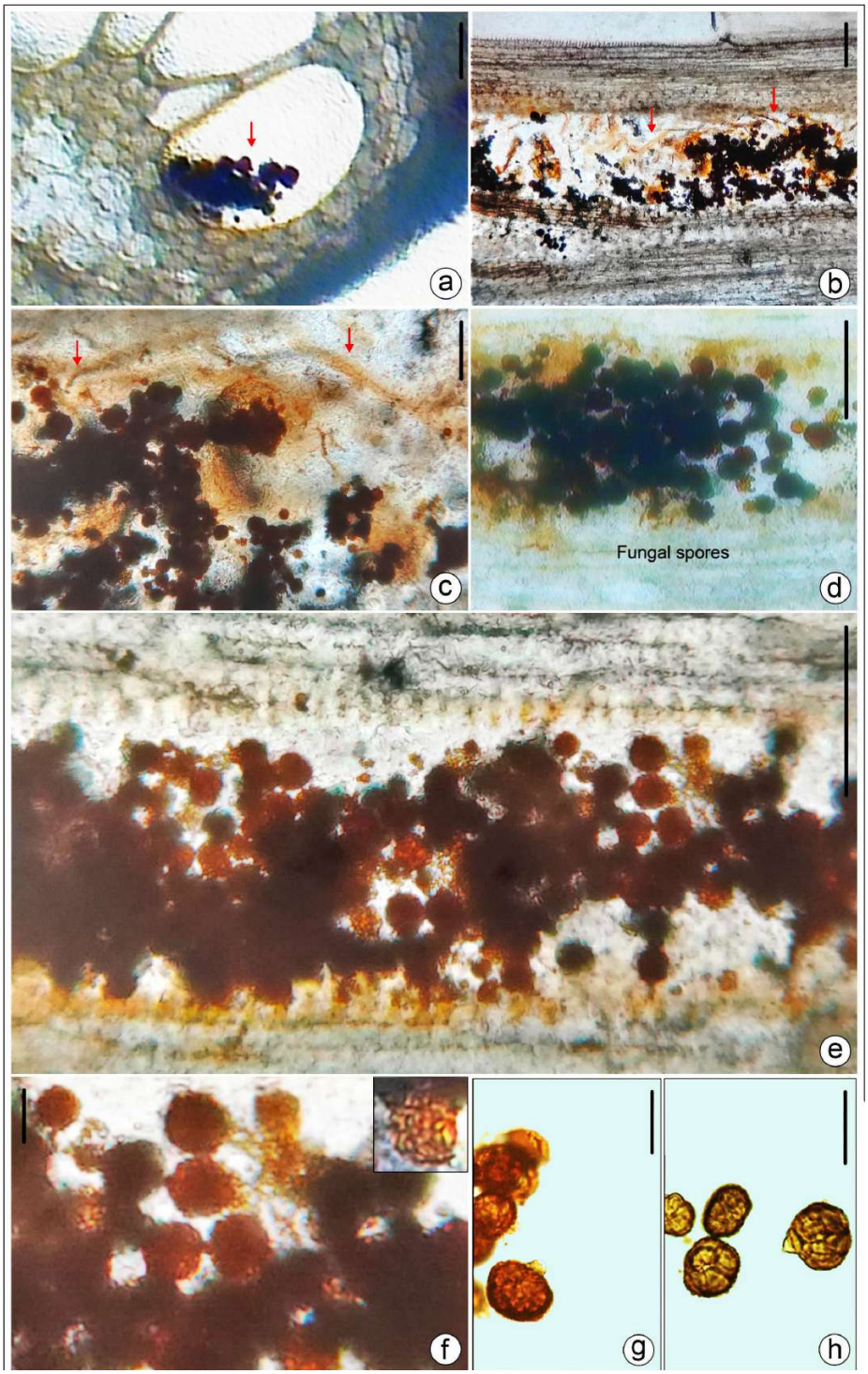

Figure 8. (a) Light microscopic image of the cluster of fungal spores (red arrow) found in the metaxylem vessel in transverse view; (b) Light microscopic image of fungal spores and hyphal branch (marked by red arrow) in longitudinal section of the fossil palm stem *P. coryphaoides* sp. nov.; (c) Enlarged the view of Figure b; (d) Colony of dark brown coloured fungal spores; (e) Warted and spherical dark brown coloured numerous mature and immature conidia; (f) Mature conidia showing multicellular structure with the external verrucose surface; (g, h) Conidia of modern *Epicoccum* (source link doi:10.1371/journal.pone.0014828.g002) Scale bars = 100 µm for a, c–e; Scale bar = 200 µm for b; and Scale bars = 20 µm for f–h.

1974; Chitaley and Yawale, 1978; Barlinge and Paradkar, 1982; Kalgutkar et al., 1993; Patil and Datar, 2002; Srivastava, 2004, 2008; Srivastava et al., 2009; Lanjewar et al., 2015; Kapgate, 2016; Sonkusare et al., 2017). It is interesting to note that, despite palm fossil plants being abundant (Kumar et al., 2022) in Deccan Intertrappean beds, no fossil fungi have been documented in palm fossils to date. Here, we report for the first time the occurrence of fungal remains (conidia and hyphae) similar to *Epicoccum* in a petrified palm stem from the latest Maastrichtian-earliest Danian sediments of Madhya Pradesh, Central India. This record expands our current knowledge of fungi-plant interaction in the ancient forests of Madhya Pradesh. In addition, the fossil evidence of coryphoid palm (host) with saprophytic fungus *Epicoccum* collectively provides significant information about their palaeoecology and past habitat.

Epicoccum nigrum is a widespread, highly robust, ubiquitous mitosporic ascomycete (Dothideomycetes) that colonizes different types of substrates of dissolving and recycling senescent plant tissues as secondary invader and associates with plant primary decomposition (Andrews and Harris 2000; Ahumada-Rudolph et al., 2014). This cosmopolitan endophytic fungal species is common in many water-damaged materials, such as gypsum boards, floors, wood, paper, textiles, seeds, insects, human skin, and sputum (parasitic). It inhabits the interior of the host plant without inducing disease symptoms or producing external structures (Azevedo and Araujo, 2007). It can grow between –3 ˚C and 45 ˚C (26–113 ˚F), with ideal growth at 23–28 °C (73–82 °F), and 5.0–6.0 pH (Anderson et al., 1981). It has been found to grow colonies on leaves submersed in water as cold as 0 °C (32 °F), and isolated from sediment, sponges, algae, and other sea plants (Ahumada-Rudolph et al., 2018). Moreover, *Epicoccum* is also considered a facultative marine fungus (Cole, 2012). The conidia of *Epicoccum* are actively released depending on temperature, light, and relative humidity conditions (Meredith, 1966). It is interesting to note that, *Epicoccum* is greatly diversified in the host plants of tropical regions (Blackwell, 2011; Suryanarayanan, 2011).

The core distribution of the modern coryphoid palms is in tropical climates with MAT (mean annual temperature) of 8.9–30 °C, MART (mean annual range of temperature) of 0.4–22.3 °C, CMMT (cold month mean temperature) of 0–8 °C and CQtrMT (lowest coldest quarter mean temperature) of 3.3–28.3 °C (Reichgelt et al., 2018). Early palm lineage fossils from the Cretaceous were most likely growing in tropical conditions (Manchester et al., 2010) and have diversified from tropical environments during the late Paleogene and Neogene (Svenning et al., 2008; Couvreur et al., 2011). So, the recovery of our new permineralized corypha-type coryphoid palm and other reported palm fossils from the Deccan Intertrappean beds of Madhya Pradesh (Rode, 1933b; Sahni and Rode, 1937; Mahabale, 1950; Prakash, 1954, 1960c; Chitaley, 1960; Mahabale and Udwadia, 1960; Sahni, 1964; Trivedi and Chandra, 1971, 1973; Chitaley and Kate, 1974; Bande et al., 1982; Lakhanpal et al., 1982; Ambwani, 1984c; Bonde, 1987; Mehrotra, 1987; Bonde, 1990a, b, 1995; Chitaley and Nambudiri, 1995; Bonde et al., 2000; Prasad et al., 2013; Srivastava and Srivastava, 2014; Srivastava et al., 2014; Manchester et al., 2016) states that the palms were diverse, as well as abundant, in a tropical warm, humid environment favored by the high rate of precipitation during the K-Pg time in Madhya Pradesh. The occurrence of the petrified palm stem, along with the saprophytic fungus *Epicoccum* indicates that warm and moist conditions prevailed in the area during the time of deposition.

Acknowledgments

AL., M. A. K., and K. R. gratefully acknowledge the Department of Botany, Sidho-Kanho-Birsha University for providing infrastructural facilities to accomplish this work.

References

Ahumada-Rudolph R, Cajas-Madriaga D, Rudolph A, Reinoso R, Torres C et al. (2014). Variation of sterols and fatty acids as an adaptive response to changes in temperature, salinity, and pH of a marine fungus *Epicoccum nigrum* isolated from the Patagonian Fjords. Revista de Biología Marina y Oceanografía. 49 (2): 293-305. doi:10.4067/S0718-19572014000200009.

Ahumada-Rudolph R, Novoa V, Becerra J (2018). Morphological response to salinity, temperature, and pH changes by marine fungus *Epicoccum nigrum*. Environ Monit Assess. 191 (1): 35.

Ambwani K (1983). *Palmoxylon shahpuraensis* sp. nov., a fossil palm resembling *Licuala* from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh. Palaeobotanist 31: 52-59.

Ambwani K (1984c). *Palmostroboxylon arengoidum* sp. nov., a fossil palm peduncle resembling *Arenga* from the Deccan Intertrappean beds of Shahapura, Madhya Pradesh. Palaeobotanist 32: 134-139.

Ambwani K, Mehrotra RC (1989). A new fossil palm wood from the Deccan Intertrappean bed of Shahpura, Mandla District, Madhya Pradesh. Geophytology 19: 70-75.

Anderson KH, Domsch W, Gams Traute-Heidi (1981). Compendium of soil fungi. London: Academic Press. ISBN 978-0-12-220401-2.

Andrews JH, Harris RF (2000). The ecology and biogeography of microorganisms on plant surfaces. Annual Review of Phytopathology 38: 145-180.

Asmussen CB, Baker WJ, Dransfield J (2000). Phylogeny of the palm family (Arecaceae) based on rps16 intron and trnL-trnF plastid DNA sequences. In: Wilson, K., Morrison, D., (Eds), Proceedings of II International Conference on Comparative Biology of Monocotyledons. Australia, Sydney: CSIRO. pp. 525-535.

Asmussen CB, Dransfield J, Deickmann V, Barfod AS, Pintaud JC et al. (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.

Azevedo JL, Arau´jo WL (2007) Diversity and applications of endophytic fungi isolated from tropical plants. In: Ganguli BN, Deshmukh SK, eds. Fungi: multifaceted microbes. Boca Raton: CRC Press. pp 189-207.

Baker WJ, Couvreur TLP (2013a). Global biogeography and the diversification of palms shed light on the evolution of tropical lineages. I. Historical biogeography. Journal of Biogeography 40: 274-285.

Baker WJ, Couvreur TLP (2013b). Global biogeography and the diversification of palms shed light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. Journal of Biogeography 40: 286-298.

Baker WJ, Dransfield J (2016). Beyond Genera Palmarum: progress and prospects in palm systematics. Botanical Journal of the Linnean Society 182 (2): 207-233.

Bande MB, Prakash U, Ambwani K (1982). A fossil palm fruit *Hyphaeneocarpon indicum* gen. et sp. nov. from the Deccan Intertrappean Series, India. Palaeobotanist 30: 303-309.

Barlinge SG, Paradkar SA (1982). Records of new fossil algal and fungal forms from the Deccan Intertrappean of Mohgaon-Kalan, M.P., India. Botanique 10: 163-174.

Blackwell M (2011) The Fungi: 1, 2, 3 … 5.1 million species? American Journal of Botany 98: 426-438.

Bonde SD (1987). *Parapalmocaulon surangei* gen. et sp. nov. from the Deccan Intertrappean beds of Umaria, District Mandla, Madhya Pradesh. Biovigyanam 13: 78-80.

Bonde SD (1990a). A new palm peduncle *Palmostroboxylon umariensis* (Aracaceae) and a fruit *Pandanusocarpon umaraiense* (Pandanaceae) from the Deccan Intertrappean beds of India. In, Dougles, J.G., Christophel, D.C., Proc. 3rd International Organisation of Palaeobotany Conference 59-65. Melbourne.

Bonde SD (1990b). *Arecoidocarpon kulkarnii* gen. et sp. nov, an arecoid palm fruit from Mohgaon Kalan, Madhya Pradesh. Palaeobotanist 38: 212-216.

Bonde SD (1995). A palm peduncle and fruit from the Deccan Intertrappean beds of India; In, Pant, D. D., Proceedings of the Birbal Sahni Birth Centenary International Conference: Symposium on Global Environment and Diversification of Plants through Geological Time 63-69. Birbal Sahni Centenary Volume. Allahabad, India.

Bonde SD, Kumbhojkar MS, Aher RT (2000). *Phoenicicaulon mahabalaei* gen. et sp. nov. a sheathing leaf base of *Phoenix* from the Deccan Intertrappean beds of India. Geophytology 29: 11-16.

Bonde SD, Chate SV, Gamre PG, Nipunage, DS (2008). A dichotomously branched fossil palm stem from the Deccan Intertrappean beds of India. Current Science 94 (2): 182-183.

Chenet AL, Courtillot V, Fluteau F, Ge´rard M, Quidelleur X et al. (2009). Determination of rapid Deccan eruptions across the Cretaceous-Tertiary boundary using paleomagnetic secular variation: 2. Constraints from analysis of eight new sections and synthesis for a 3500-m-thick composite section. Journal of Geophysical Research: Solid Earth 114, B06103.

Chitaley SD (1960). A new specimen of *Nypa* fruit from Mohgaon cherts. Nature 186, 495.

Chitaley SD, Kate UR (l974). *Deccananthus savitrii,* a new petrified flower from the Deccan Intertrappean beds of India. Palaeobotanist 21 (3): 317-320.

Chitaley SD, Nambudiri EMV (1995). Anatomy of *Nypa* fruits reviewed from new specimens from the Deccan Intertrappean flora of India; In Pant D D, Proceedings of the Birbal Sahni Birth Centenary International Conference: Symposium on Global Environment and Diversification of Plants through Geological Time, Birbal Sahni Centenary 83-94. Allahabad, India.

Chitaley SD, Patil GV (1970). An acanthaceous fossil wood with deuteromyceteous fungus from the Deccan Intertrappean beds of Mohgaonkalan, India. Proc. 57th Indian Science Congress Kharagpur 3 (Abst): 337-338.

Chitaley SD, Patil GV (1972). Ebenaceous fossil wood infected with deuteromyceteous fungus from the Deccan Intertrappean beds of India. Botanique 3 (2): 99-106.

Chitaley SD, Yawale NR (1978). Fungal remains from the Deccan lntertrappean beds of Mohgankalan, India. Botanique 7 (4): 189-194.

Cole GT ed. (2012). Biology of conidial fungi. Elsevier.

Couvreur TL, Forest F, Baker WJ (2011). Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. BMC Biology 9, 44. doi:10.1186/ 1741-7007-9-44

Dransfield J, Uhl NW (1986). An outline of a new classification of palms. Principes 30: 3-11.

Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM et al. (2008). Genera Palmarum: The evolution and classification of palms. Kew, UK, Royal Botanic Gardens.

Gayakwad BB, Patil G (1989). On two palm woods from the Deccan Inter-trappean beds of Betul District, Madhya Pradesh. In: Biradar, N.V. (Ed.), Proceedings of the Special Indian Geophytological Conference, Pune 1986. University of Poona, Pune, pp. 31-38.

Haas H, Rowe NP (1999). Thin sections and wafering. In Jones T P and Rowe T P Fossil Plants and spores: modern techniques 76-81. The Geological Society, London.

Hammer O, Harper DAT, Ryan PD (2001). PAST: Paleontological statistics software package for education and data analysis. Palaeontologia electronica 4: 1-9.

Hofmann C, Feraund G, Courtillot V (2000). 40Ar/Ar40 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 (1-2): 13-27.

Kalgutkar RM, Nambudiri EMV, Tidwell WD (1993). *Diplodites sweetii* sp. nov. from the late Cretaceous (Maastrichtian) Deccan Intertrappean beds of India. Review of Palaeobotany and Palynology 77 (1-2): 107-118.

Kapgate VD (2016). Fossil Fungi from Deccan Intertrappean Cherts of Madhya Pradesh, India International Journal of Life Sciences A6: 117-120.

Khan MA, Roy K, Hazra T, Mahato S, Bera S (2020). A new coryphoid palm from the Maastrichtian-Danian Sediments of Madhya Pradesh and its Palaeoenvironmental Implications. Journal of Geological Society of India 95: 75-83.

Khosla SC (1999). *Costabuntonia*, a new genus of Ostracoda from the Intertrappean beds (Paleocene) of the east coast of India. Micropaleontology 45: 319-323.

Kumar S, Manchester SR, Hazra T, Khan MA (2022). A review of palm macrofossils from India and perspectives. Arabian Journal of Geosciences 15 (23): 1720.

Lakhanpal RN, Dayal R, Jain RK (1967). A fossil lagenidialean fungus from the Deccan Intertrappean beds of Mohgaon Kalan, Madhya Pradesh. Current Science 36 (8): 210-211.

Lakhanpal RN, Prakash U, Ambwani K (1979). Two petrified palm woods from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh. Paleobotanist 26: 119-129.

Lakhanpal RN, Prakash U, Bande MB (1982). A monocotyledonous inflorescence from the Deccan Intertrappean beds of India. Palaeobotanist 30 (3): 316-324.

Lanjewar SG, Puranik SD, Sakundarwar RS (2015). Fossil Fungal Spores *Dicellaeosporitesdeccani* sp. nov. of Fungi Imperfecti from Mohangaonkalan M.P. India. International Journal of Research in Biosciences, Agriculture & Technology 2347-517X.

Mahabale TS (1950). Some new fossil plants from the Deccan Intertrappeans. Palaeobotany in India, VII. Journal of the Indian Botanical Society 29 (1): 1-46.

Mahabale TS (1958). Resolution of the artificial palm genus, *Palmoxylon*: A new approach. Palaeobotanist 7: 76-84.

Mahabale TS, Udwadia NN (1960). Studies on Palms: Part IV - Anatomy of Palm Roots. Proceedings of the National Institute of Sciences, India 26 (1): 73-104.

Manchester SR, Bonde SD, Nipunage DS, Srivatava R, Mehrotra RC et al. (2016). Trilocular palm fruits from the Deccan Intertrappean beds of India. International Journal of Plant Science 177 (7): 633-641.

Manchester SR, Lehman TM, Wheeler EA (2010). Fossil palms (Arecaceae, Coryphoideae) associated with juvenile herbivorous dinosaurs in the upper Cretaceous Aguja Formation, Big Bend National Park. Texas. International Journal of Plant Science 171: 679-689.

Mehrotra RC (1987). Some new palm fruits from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh. Geophytology 17: 204-208.

Meredith DS (1966). Diurnal periodicity and violent liberation of conidia in *Epicoccum*. Phytopathology 56: 988.

Patil KS, Datar K (2002). A new Hyphomycetes fungus from the Deccan Intertrappean Beds of Wardha District, Maharashtra. Geoplhytology 30 (1&2): 3l-35.

Prakash U (1954). *Palmocarpon mohgaoense* sp. nov., a palm fruit from the Deccan Intertrappean Series, India. Palaeobotanist 3: 91-96.

Prakash U (1960c). On two palm fruits from the Deccan Intertrappean beds of Mohgaonkalan. Current Science 29: 20-21.

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

Prasad M, Singh H, Singh SK, Mukherjee D, Estrada-Ruiz E (2013). Early Eocene arecoid palm wood, *Palmoxylon vastanensis* n. sp. from vastan lignite, Gujarat, India: its palaeoenvironmental implications. Journal of the Palaeontological Society of India 58 (1): 115-123.

Rao GV, Shete RR (1989). *Palmoxylon hyphaeneoides* sp. nov. from the Deccan Intertrappean beds of Wardha District, Maharashtra. In: N V. Biradar, Proceedings of Special Indian Geophytological Conference Poona. pp. 123-128.

Reichgelt T, West CK, Greenwood DR (2018). The relation between global palm distribution and climate. Sci Rep., doi: 10.1038/s41598-018-23147-2.

Renne PR, Sprain CJ, Richards MA, Self S, Vanderkluysen L et al. (2015). State shift in Deccan volcanism at the K-Pg boundary, possibly induced by impact. Science 3: 76-78.

Rode KP (1933b). A note on fossil angiospermous fruits from the Deccan Intertrappean beds of the Central Provinces. Current Science 2 (5): 171-172.

Roy S (2013). On the occurrence of *Palmoxylon coronatum* Sahni resembling *Borassus* Linn. from the Tertiary of West Bengal, India. Ameghiniana 17: 130-134.

Sahni B (1964). Revision of Indian Fossil Plants III, Monocotyledons. Monograph No. I. Birbal Sahni Institute of Palaeobotany, Lucknow 1-89.

Sahni B, Rode KP (1937). Fossil plants from the Intertrappean beds of Mohgaon Kalan, in the Deccan, with a sketch of the geology of the Chhindwara district. Proceedings of the National Academy of Sciences, India 7 (3): 165-174.

Schoene B, Samperton KM, Eddy MP, Keller G, Adatte T et al.(2015). U-Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. Science 347: 183-184.

Schol-Schwarz M (1959). The genus *Epicoccum* Link. Transactions of the British Mycological Society 42 (2): 149-IN3. doi:10.1016/S0007-1536(59)80024-3.

Singhai LC (1972). *Deccanosporium eocenum* gen. et sp. nov. a petrified fungus from the Deccan Intertrappean Series. Journal of Ravishankar University, Raipur 1 (1): 24-28.

Singhai LC (1974). Fossil fungi from the Deccan Intertrappean beds of Madhya Pradesh, India. Journal of Biological Sciences 17: 92-102.

Smith SY, Manchester SR, Samant B, Mohabey DM, Wheeler E et al. (2015). Integrating paleobotanical, paleosol, and stratigraphic data to study critical transitions: a case study from the Late Cretaceous- Paleocene of India. *In* Polly, P.D., Head, J.J., Fox, D.L., Earth-Life Transitions: Paleobiology in the context of earth system evolution, 137-166. The Paleontological Society Papers 21, Yale Press, New Haven, CT.

Sonkusare H, Samant B, Mohabey DM (2017). Microflora from sauropod coprolites and associated sediments of Late Cretaceous (Maastrichtian) Lameta Formation of Nand-Dongargaon basin, Maharashtra. Journal of the Geological Society of India 89: 391-397.

Srivastava JP, Duncan RA, Kashyap M (2015). Post-K/PB younger 40Ar-39Ar ages of the Mandla lavas: implications for the sahniduration of the Deccan volcanism. Lithos 224-225: 214-224.

Srivastava R (2008). Fossil woods resembling *Sonneratia* with fungal infection from Deccan Intertrappean sediments of Seoni District, Madhya Pradesh. Geophytology 37: 87-92.

Srivastava R, Kar RK (2004). Record of new petrified epiphyllous fungi (*Polyhyphaethyrites*) from the Deccan Intertrappean beds of Mohgaon Kalan, Madhya Pradesh, India. Current Science 87 (7): 866-867.

Srivastava R, Srivastava G (2014). Fossil fruit of *Cocos* L. (Arecaceae) from Maastrichtian-Danian sediments of central India and its phytogeographical significance. Acta Palaeobotanica 54: 67-75.

Srivastava R, Srivastava G, Dilcher DL (2014). Coryphoid Palm leaf fossils from the Maastrichtian-Danian of Central India with remarks on phytogeography of the Coryphoideae (Arecaceae). Plos One 9 (11): 1-10.

Srivastava R, Kapgate DK, Chatterjee S (2009). Permineralized fungal remains in the fossil wood of *Barringtonia* from the Deccan Intertrappean sediments of Yavatmal District, Maharashtra, India. Journal of Palaeosciences 58 (1-3): 11-19.

Suryanarayanan TS (2011) Diversity of fungal endophytes in tropical trees. In: Pirttila¨ AM, Frank AC, editors. Endophytes of Forest Trees: Biology and Applications, Forestry Sciences. Springer Netherlands 80: 67-80.

Svenning JC, Borchsenius F, Bjorholm S, Balslev H (2008). High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. Journal of Biogeography 35: 394-406.

Thomas R (2011). Comparative anatomy of palm trees-Computer-assisted identification, applications in paleobotany and archaeobotany (Doctoral dissertation, National Museum of Natural History-MNHN PARIS).

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

Tomlinson PB (1961). Palmae In Metcalfe, C., Anatomy of the monocotyledons 2 Oxford University Press, Oxford, UK.

Tomlinson PB, Horn JW, Fisher JB (2011). The anatomy of palms Oxford University Press, Oxford, UK.

Trivedi BS, Chandra R (1971). A palm leaf from the Deccan Intertrappean Series, Mohgaonkalan, Madhya Pradesh, India. Current Science 40: 528-527.

Trivedi BS, Chandra R (1973). *Palmocarpon splendidum* sp. nov. from the Deccan Intertrappean beds of Mohgaon Kalan, Chhindwara District, M.P, India. Palaeobotanist 20 (3): 339-343.

Trivedi BS, Verma CL (1971). New fossil fungus from the Deccan intertrappean beds of Madhya Pradesh, India. The Paleobotanist Vol 2.

Von Mohl H (1823-1850). "De palmarum Structura." In Historia Naturalis Palmarum, Opus Tripartitum, eds von Martius, K.F., 1-92. Vol. 1. Leipzig, Germany: Monachii- impensis auctoris. F. Fleischer.