

## **The earliest fossil evidence of spiny feather (pinnate-leaved) palms from the K-Pg of Gondwana**

**Sanchita Kumar, Tao Su, Robert A. Spicer, and Mahasin Ali Khan**

### **ABSTRACT**

Palms, a plant family that forms a major component of lowland tropical rainforests worldwide, are represented by a large number of fossils from Cenozoic sedimentary successions and K-Pg sediments of India, but no spiny palm has been reported from there to-date. Here, we report fossilized 'feather' (well-separated leaflets that are attached to a single leaf axis, similar to a feather) palm leaf specimens that bear spines from the latest Maastrichtian (Late Cretaceous)-earliest Danian (Early Paleocene) sediments of the Deccan Intertrappean beds of Madhya Pradesh, central India. They provide the first evidence that spiny pinnately-leaved palms were present in India during Chron 29R, which spans the K-Pg transition, and when the bulk of the subcontinent was still in the Southern Hemisphere. Other reliable records of pinnate palms are from the Northern Hemisphere (Europe) and are much younger (Eocene, Oligocene, and Miocene) than the fossils reported here. Although our data are limited, the new finds suggest that Cenozoic palm dispersal may be consistent with the "Out-of-India" hypothesis seen in several other plant groups. This report also provides new information on the distribution, diversification, and evolution of spiny palms in deep time. The evidence of fossilized spiny palms dating to the latest Cretaceous may link to a defense mechanism evolved as protection against predation from large herbivores, presumably dinosaurs.

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**Keywords:** Spiny pinnate palms; Arecaceae; K-Pg; Madhya Pradesh; new species; biodiversity

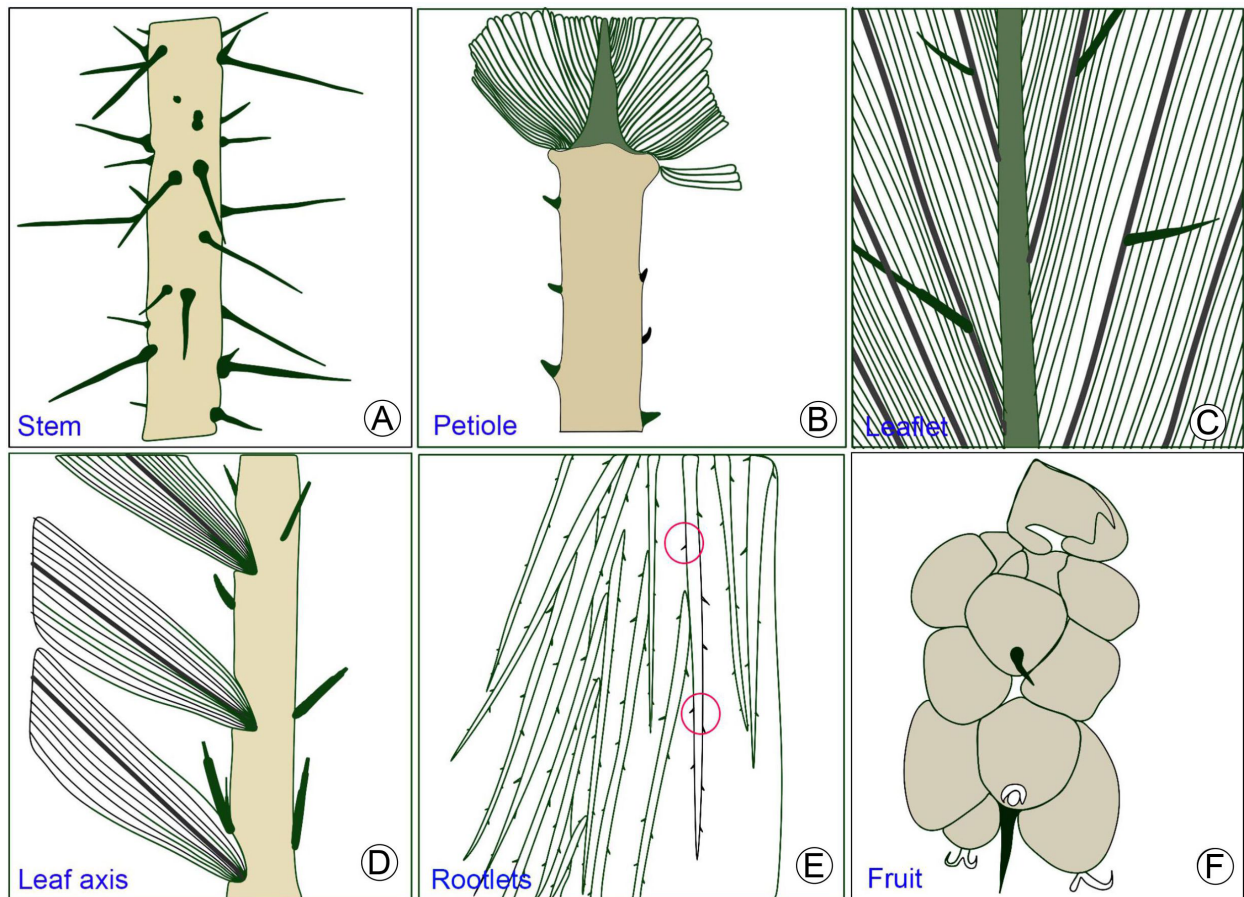
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## INTRODUCTION

Spines in palms are restricted to certain taxonomic groups and so have systematic value (Tomlinson, 1961, 1962a; Fisher, 1981). Spines may originate from superficial structures or internal vascular tissues (vascular spines) or endogenously developed organs (root- and rootlet spines). They result from a modification of an existing aerial organ, such as in leaflet spines, rachilla spines, and petiole spines, as well as emergences from superficial tissue, that is to say not a modification of an existing organ. Moreover, different spine categories are determined by their location. Spines may occur on vegetative organs (leaflet margins, leaflet midribs, petiole margins, surfaces of the leaf axis or rachis, stem surfaces) and reproductive

organs (bracts, inflorescence axes, and even fruits) (Clement and Manshardt, 2000) (Figure 1). The function of these spines does vary since in some climbing palms they serve in support, but otherwise, the function of spines in palms seems to be mainly for physical protection against large herbivores.

In India, fossil palm leaves are mostly in the form of impressions of palmate leaves (Sahni, 1964; Achuthan, 1968; Trivedi and Chandra, 1971; Bonde, 1986; Mathur et al., 1996; Singh and Patnaik, 2012). They are described under the fossil genera *Palmacites* or *Palmites*, or more appropriately *Palmophyllum*. In addition, a few costapalmate leaves have been reported and described under the fossil genus *Sabalites* (Srivastava et al., 2014; Roy et al., 2020; Kumar et al., 2022a). Only



**FIGURE 1.** Spines on different palm organs (A) stem; (B) leaf petiole; (C) leaflet; (D) leaf axis (Rachis); (E) rootlet; (F) fruit.



three reliable fossil species of pinnately compound palm leaf remains have been reported in the Indian fossil record (Guleria and Mehrotra, 1998; Guleria et al., 2005; Singh et al., 2012), but no reliable spiny pinnate palm has been reported from there to-date. By contrast, palmate palms with spines have been reported from the Eocene of Tibet (spine-like structures mainly on the costa) (Su et al., 2019), North America (Berry, 1924), New Zealand (Hartwich et al., 2010), the Oligocene of China (Wang et al., 2015), England (Chandler, 1957), and the Miocene of France (Huard, 1967).

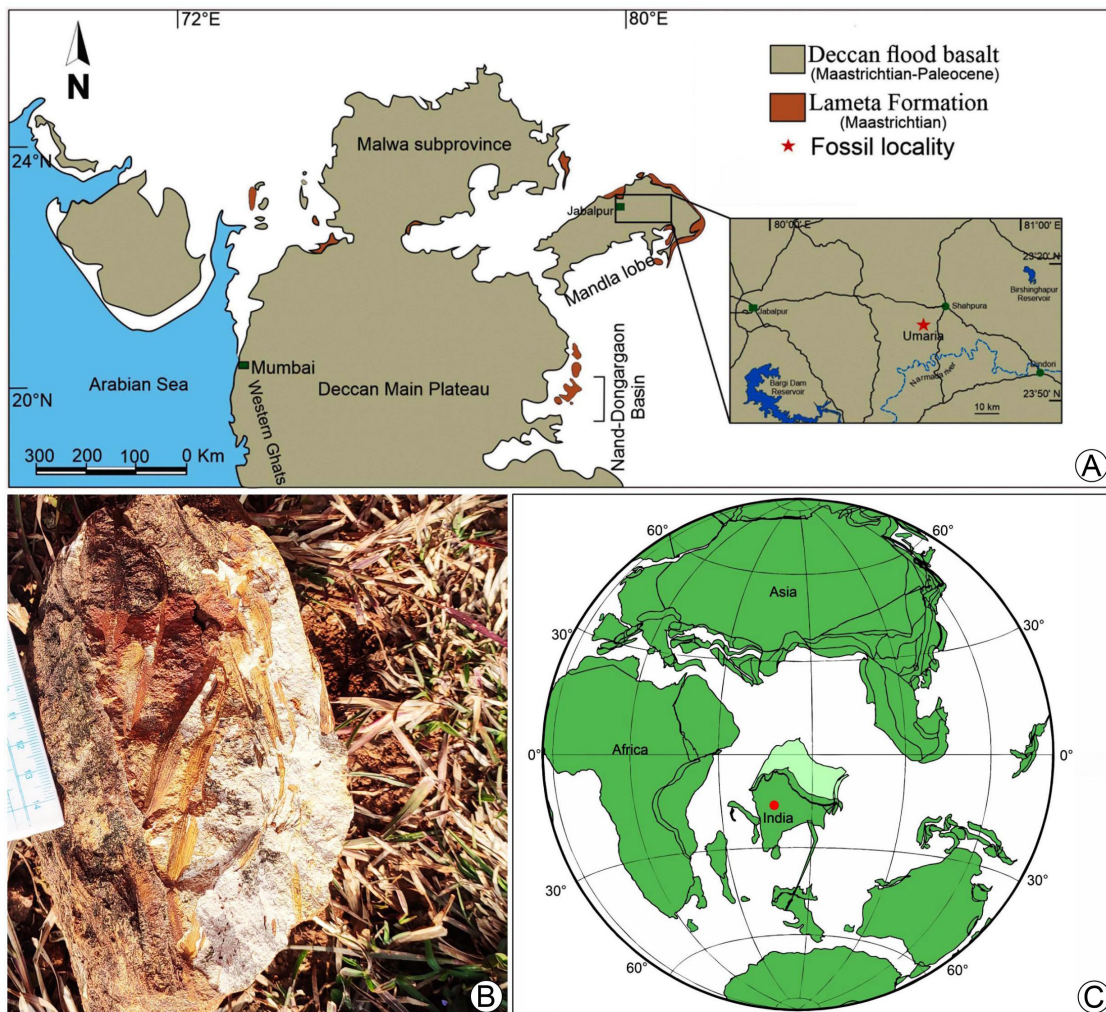
In this study, we describe under a new fossil genus two pinnately compound spiny palm leaves from the latest Maastrichtian (Late Cretaceous)-earliest Danian (Early Paleocene) sediments of the Deccan Intertrappean beds of Madhya Pradesh,

central India (Figure 2). These fossil pinnate palm leaves with well-preserved spines and spine scars represent the earliest reliable fossil record of spiny palms and also inform our understanding of their early-stage evolutionary and biogeographic histories.

## MATERIAL AND METHODS

### Locality

The fossil spiny palm leaf remains described here were collected during fieldwork in 2020 and 2021. They were recovered from the latest Maastrichtian (Late Cretaceous) to earliest Danian (Early Paleocene) sediments of the Mandla Lobe, Deccan Intertrappean beds of Umariya Ryt. village (N 22°46'26", E 80°32'19", 490 m a.s.l.), Dindori



**FIGURE 2.** (A) Map showing Deccan Volcanic Province (DVP), red star showing fossil locality (modified after Smith et al., 2015); (B) Recovered spiny feather palms from surface exposures of Deccan sediments; (C) Palaeocontinental map showing the position of the surviving Indian plate and the fossil locality (red dot) at 65.5 Ma. Note that the now subducted 'Greater India' is not shown as its dimensions are poorly constrained, nor is the Tethyan Himalaya microterrene (base maps from <https://www.odsn.de/odsn/services/paleomap/paleomap.html>).

district, Madhya Pradesh, central India (Figure 2A, B). The fossil locality was situated at a low palaeo-latitude of  $\sim 18^\circ$  S (Figure 2C) (<http://www.odsn.de/odsn/index.html>; accessed November 21, 2021) at the time the leaves were deposited.

### Geological Setting and Age

The Deccan Traps of western, central, and southern parts of India, one of the largest continental flood basalts in Earth's history, were formed as a result of the outpouring of lava onto the Indian peninsula associated with the movement of the Indian Plate over the Reunion hotspot (Chatterjee et al., 2013). Geographically, the Deccan Volcanic Province is divided into three main sub-provinces, namely the Malwa lobe, the Mandla lobe, and the Central Deccan Provinces. Sediments commonly known as Deccan Intertrappean beds are composed of shales, porcellanitic shales, cherts, limestone, and clays.

The Mandla Lobe of the Deccan Volcanic Province (DVP), comprises a 900 m thick package of 29 flows dated as primarily belonging to Chron 29R (Pathak et al., 2017), with deposition lasting  $<1$  Ma and spanning the Cretaceous–Paleogene (K–Pg) transition. In the Mandla Lobe, sediments represent lacustrine and fluvial environments deposited during quiescent periods between episodes of volcanic activity, often lasting thousands of years. The age of these Deccan Intertrappean sediments is generally assigned to the latest Maastrichtian–earliest Danian based on radiometric ( $^{40}\text{Ar}/^{39}\text{Ar}$ ) dating, planktonic foraminifera, and magnetostratigraphy (Venkatesan et al., 1997; Khosla, 1999; Hofmann et al., 2000; Chenet et al., 2009; Keller et al., 2009; Renne et al., 2015; Schoene et al., 2015; Shrivastava et al., 2015; Smith et al., 2015).

### Deccan Floristic Composition

The Deccan Intertrappean Beds are highly fossiliferous and contain a rich biota (Prasad et al., 1995; Bajpai, 2009; Khosla and Verma, 2015; Kapur et al., 2019). The Deccan Intertrappean (Maastrichtian–Danian) flora hosts one of the richest fossil plant assemblages in India and offers valuable insights for understanding the diversity, evolution, and palaeobiogeography of the Indian flora during the K–Pg transition when India was still a relatively isolated landmass (Kapgate, 2005; Chatterjee et al., 2013; Smith et al., 2015). It is interesting to note that palms have been recognized as an important component of this flora, represented by numerous permineralized stems of

*Palmoxyton* (Prakash and Ambwani, 1980; Ambwani, 1984a, b; Manchester et al., 2016; Khan et al., 2019, 2020a, b), fruits (Prakash, 1960; Bande et al., 1982; Mehrotra, 1987; Bonde, 1990; Srivastava and Srivastava, 2014; Manchester et al., 2016; Matsunaga et al., 2019) as well as several species of leaf remains (Sahni 1964; Bonde, 1986; Srivastava et al., 2014; Roy et al., 2021; Kumar et al., 2022a). In addition to palm woods, other abundant plant megafossils reported from the Deccan Traps are silicified dicot woods (Lakhanpal et al., 1979; Bande and Khatri, 1980; Bande and Prakash, 1980, 1983; Bande et al., 1986; Mehrotra, 1989; Srivastava, 2010; Baas et al., 2017), and a few dicot leaf fossils (Prasad et al., 2013; Khan et al., 2020c).

### Observation

The two studied fossil spiny palm leaf impressions (Figures 3, 4) were first cleaned with a chisel and hammer and then photographed in natural low-angled light using a digital camera (NIKON D3300). Line drawings of fossil specimens (Figure 5) were made using CorelDraw ver. 20 software. To determine the reliable taxonomic affinity of recovered Deccan palm leaf fossil specimens, we compare them with vouchers of modern taxa of pinnately compound spiny palm leaf species featured in digital herbarium catalogues, specifically the Kew Herbarium catalogue (<https://apps.kew.org/herbcat/gotoCiteUs.do>), and the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)). In addition, we also compare our specimens with previously reported fossil pinnate palm leaf species from India and elsewhere. Terms used to describe the K–Pg palm leaves conform to the standard terminologies used for architectural description of fossil palm leaves (Read and Hickey, 1972).

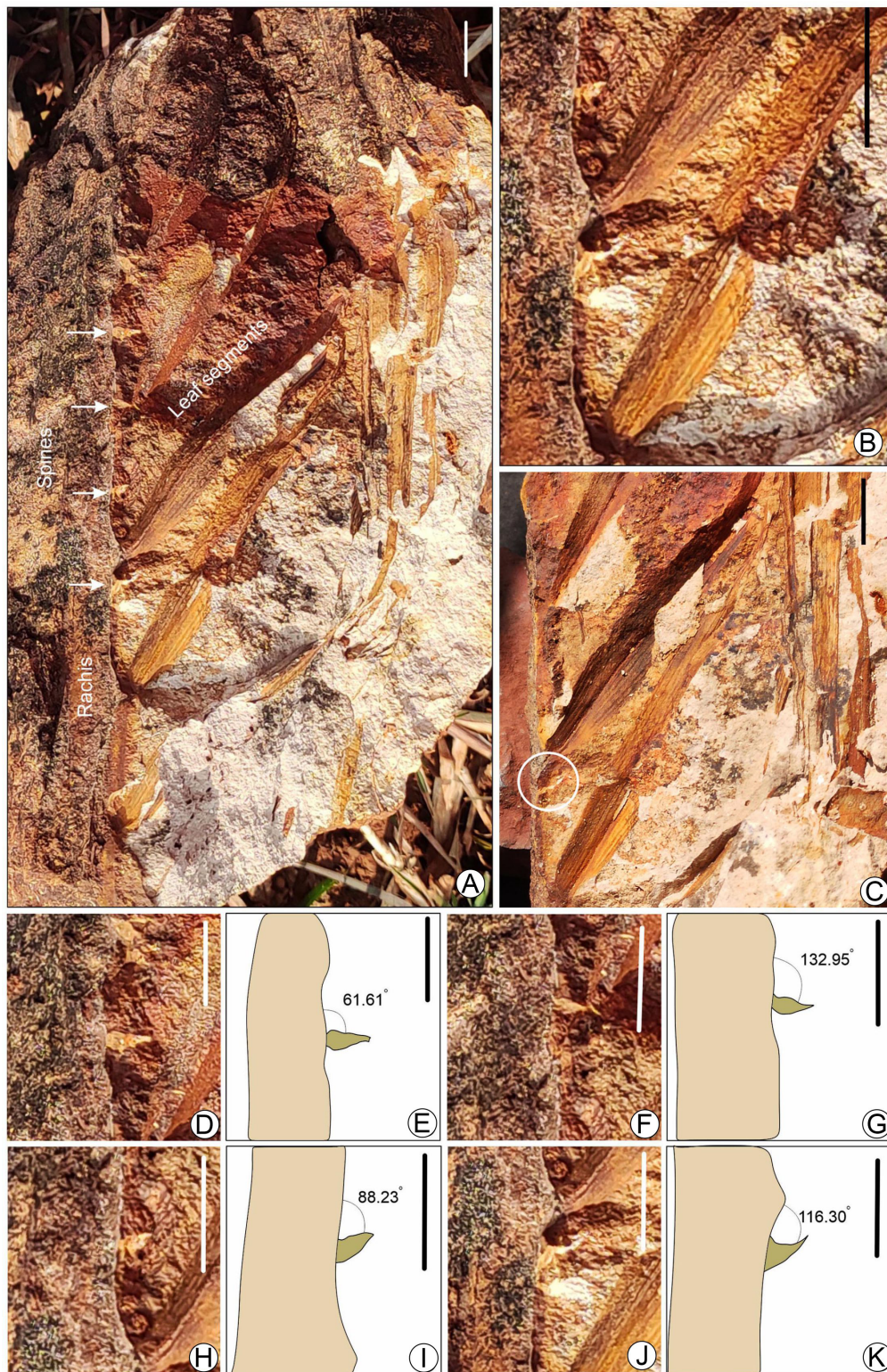
### Repository

The recovered specimens (SKBUH/PPL/Um/L/48, Figure 3A, B (part), Figure 3C (counterpart); SKBUH/PPL/UL28, Figure 4A) are deposited in the Museum of the Department of Botany, Sidho-Kanho-Birsha University (SKBUH), Purulia, India. The new names are registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany,

## SYSTEMATIC PALAEONTOLOGY

**Family.** Arecaceae Schultz Sch.





**FIGURE 3.** Fossil species *Spinopinnophyllum acanthorachis* S. Kumar, T. Su and M. A. Khan sp. nov. (SKBUH/PPL/Um/L/48). (A) A palm leaf specimen showing a stout rachis with well-preserved spines (marked by white arrows) and well-separated plicate leaf segments; (scale bar = 1 cm); (B) A part of the fossil leaf specimen showing two prominent spines on the rachis (scale bar = 1 cm); (C) Counterpart of SKBUH/PPL/Um/L/48 (scale bar = 1 cm); (D, F, H, J) Enlarged views of *S. acanthorachis* leaf showing the different orientation of spines on the rachis; (E, G, I, K). Line drawing of (D, F, H, J) (scale bars = 1 cm).





**FIGURE 4.** Fossil species *Spinopinnophyllum acanthorachis* S. Kumar, T. Su and M. A. Khan sp. nov. (SKBUH/PPL/UL28). (A) Fossil palm leaf specimen showing a distinct rachis with well-separated leaf segments and scars of spine bases (marked by 1, 2, 3, and 4) (scale bar = 1 cm); (B) A modern palm leaf of *Calamus* L. (Arecaceae) showing a robust rachis with spines and leaf segments (scale bar = 1 cm); (C) An enlarged view of fig. A showing a robust rachis with scars of spine bases and leaf segments (scale bar = 1 cm); (D) A large view of scar of the base of the spine (scale bar = 0.3 cm).





**FIGURE 5.** (A, B) Line drawing of the fossil species *Spinopinnophyllum acanthorachis* S. Kumar, T. Su and M. A. Khan sp. nov. (Scale bars = 1 cm).

**Genus.** *Spinopinnophyllum* S. Kumar, T. Su and M.A. Khan gen. nov.

**PFN003225**

**Type species.** *Spinopinnophyllum acanthorachis* S. Kumar, T. Su, and M. A. Khan sp. nov.

**PFN003226**

**Etymology.** “*spino*” is used to symbolize the presence of the spine and “*pinnophyllum*” refers to the pinnately compound leaves.

**Species.** *Spinopinnophyllum acanthorachis* S. Kumar, T. Su, and M.A. Khan sp. nov.

**Diagnosis.** Leaf pinnately compound, leaflets attached to stout rachis; prominent pointed spines (Figure 3) or scars of the base of spines (Figure 4A) present on the rachis; preserved leaflets narrow emerging straight from one side of the rachis at an acute angle (Figures 3, 4); thick and prominent midvein in each leaflet; mid-vein paralleled by prominent secondary lateral veins, oblique and transverse cross veins also present on both sides of the secondary lateral vein.

**Holotype.** SKBUH/PPL/Um/L/48 (Figure 3A)

**Paratype.** SKBUH/PPL/UL28 (Figure 4A)

**Etymology.** The specific epithet “*acanthorachis*” is used to symbolize the presence of spines on the rachis of palm leaves.

**Type locality.** Umariya Ryt. village (N 22°46'26”, E 80°32'19”, 490 m a.s.l.) in Dindori district, Madhya Pradesh, central India.

**Description.** The fossil specimens preserve the middle portion of the pinnate leaves, both the petiole and apical portion are not observed; length is 9.2–14.4 cm and width is 1.3–6.9 cm; leaflets are observed on one side of the prominent rachis (Figures 3A; 4A); rachis is stout, 14.2 cm in length and 0.8–1.1 cm in breadth, some faint longitudinal fiber-like structures are also seen on the surface of rachis; 6–7 leaflets are preserved one side of the rachis (Figures 3A; 4A), and the leaflets are attached to the rachis by the entire base, leaflets are narrower at the point of attachment, the terminal portion of the leaflets is not preserved; leaflets are 1.1–6.5 cm long, 0.4–1 cm wide, unarmed, plicate, plication induplicate, emerging at a narrow acute angle from the rachis, thick, coriaceous, and the angle of divergence of leaf segments is 30°–35°; venation is pinnate, decurrent, and each leaflet has a characteristic thick, distinct, midvein, or primary vein (0.4 mm thick) that is strong and uniform (Figures 3B, C; 4C); about 4–7 distinct lateral veins run parallel on each side of the midvein (Figures 3B; 4C) equidistant from each other, 2° veins are 0.1–0.2 mm apart, some lateral veins lack

oblique cross-veins; four spines are clearly observed on the rachis, distinct and well-preserved on a stout rachis; spines are 0.2–0.6 mm long and pointed (Figures 3A–C; 4D), and present along the margin of the rachis at an angle of ~61–116° (Figure 3D–K); In one specimen, four scars of the base of spines are observed on the rachis (Figure 4A, C), distinct spines are also well-preserved within some spine bases (Figure 4C, D).

**Horizon and age.** Deccan Intertrappean beds; latest Maastrichtian (Late Cretaceous)-earliest Danian (Early Paleocene), Chron 29R.

### Taxonomic Determination of the New Palm

#### Genus

The above-mentioned diagnostic features, such as a thick coriaceous pinnate leaf, entirely separated pinnae joined to the strong spiny rachis by their entire narrow bases, pinnate venation, a strong prominent primary vein, and numerous parallel secondaries on either side of the primary vein indicate that our Deccan fossil specimens belong to parts of pinnately leaved palms, especially spiny pinnate palms (family Arecaceae). Given their fragmentary nature and lack of cuticular information, it is not possible to assign them to a particular modern tribe or genus in Arecaceae. This is because such induplicate types of pinnate leaves are found in a large number of palms, e.g., *Areca* L., *Bentinckia* Berry ex Roxb., *Cocos* L. (Arecoideae), *Calamus* L., *Plectocomia* Martius and Blume (Calamoideae), and *Phoenix* L. (Coryphoideae) (Tomlinson, 1990). In addition, Read and Hickey (1972) have pointed out that numerous similarities in the form and external macromorphological features of palm leaves make it difficult to assign fossil palm leaves to modern palm genera based only on external gross morphology. They also have suggested that no attempt should be made to place fossil palm fragments in modern palm genera unless unquestionably identifiable to them. They provided a key for assigning fragmentary true palm leaves to six fossil genera. They described unarmed palm leaf segments under the fossil genus *Amesoneuron*, with armed leaf segments on one side under *Bactrites*, a costapalmate palm leaf with a prominent costa under *Sabalites*, a palmate leaf segment without any costa under *Palmacites*, a pinnately compound leaf with pinnae reduplicate on the adaxial surface and without any spines under *Phoenicites* and a pinnately compound leaf with induplicate pinnae on the adaxial surface, but with lowermost pinnae on the rachis spine-like (like modern genus *Phoenix*), under the fossil genus

*Phoenix*. Thus, in being different from Read and Hickey's fossil genera, especially the pinnately compound fossil leaf genera *Phoenicites* and *Phoenix*, we propose a new fossil genus, *Spinopinophyllum* S. Kumar, T. Su, and M. A. Khan gen. nov. for the fossil spiny pinnate palm leaf specimens described here.

## DISCUSSION

### Spines as a Valuable Taxonomic Character in Palms

Spiny palms are unevenly distributed throughout the major tribes (Tomlinson et al., 2011). The Bactridinae and lepidocaryoid palms are highly spinous (Tomlinson, 1961; Dransfield et al., 2008). In the climbing palms of the lepidocaryoid group, spines are developed for physical support as well as defense, whilst other genera (*Metroxylon*, *Pigatetta*, *Raphia*, and *Salacca*) in this group have protective spines (Bailey, 1941; Tomlinson, 1962a).

The subfamily Calamoideae is predominantly spiny; the spines are present generally either on the leaves, leaf sheaths, inflorescences, and leaf rachis (abaxially), or on the extended terminal cirrus and may be modified into hooks in the climbing species. Structures that are associated with climbing are facilitated by the elongation of stems, the presence of spines or reflexed leaflets, or a combination of all of these features. They are most frequent among the four subtribes of Calamoideae (Korthalsiinae, Plectocomiinae, Ancistrophyllinae, and Calaminae), and three unrelated tribes of Arecoideae (Chamaedoreae, Cocoseae, and Areceae) (Dransfield et al., 2008). The Calamoideae exhibit a wide diversity of emergent spines on leaves, leaf sheaths, and inflorescences (Figure 6).

In some species of *Calamus* and *Daemonorops*, the interweaving adjacent whorls of spines form galleries in which ants live. The rachis of climbing palms (*Desmoncus*, *Chamaedorea*, and *Ancistrophyllum*) is extended into a long cirrus along which the pairs of leaflets are widely spaced. Each leaflet develops as a rigid, backwardly directed grapnel spine or hook. Grapnel spines occur on the back of the leaf axis and are usually restricted to the long terminal cirrus of certain scandent palms. Grapnel leaflets of *Desmoncus* are almost offensive weapons compared with the passive nature of more orthodox spines (Tomlinson, 1962a). A second climbing organ, i.e., the flagellum identified as a sterile inflorescence, which may bear grapnel spines is found in the genus *Calamus*. In *Salacca* spines are aggregated on the peti-

ole in a transverse arrangement to form a linear series (Tomlinson et al., 2011).

Many coryphoid groups such as Borasseae, Phoeniceae, and Rhipidinae also produce significant spines. Spines are mostly present on the petiole margin, but basal leaflets reduced to a stiff, pointed spine-like structure are usually referred to as an acanthophyll, and are diagnostic in Phoeniceae. In Rhipidinae, leaf sheath vascular spines are present in *Guihaia*, *Maxburretia*, *Trachycarpus*, and *Rhipidophyllum*. Most members of Trachycarpeae have marginal petiolar spines, and occasionally only the juvenile leaves have spines (*Saribus*, *Washingtonia*). Some members (Cocoseae, Areceae, and Iriarteeae) of the large palm group Arecoideae are spiny, and within Cocoseae members of the Bactridinae, Attaleinae, and Elaeidinae bear spines. Bactridinae are usually heavily spiny with spines on the leaf rachis and leaf blade. Leaf-sheath vascular spines are found in some genera (*Butia*, *Syagrus*) of Attaleinae. Spines are also present on the leaf sheath of genera of the Onco-spermatinae within the Areceae (Tomlinson, 1962a, b; Tomlinson et al., 2011).

We compare our Deccan spiny palm leaf specimens with modern pinnate palm leaves having spines on the rachis. Spines on rachises exist in many extant palm species. This character is not taxonomically restricted and commonly occurs in a range of different genera (*Astrocaryum*, *Bactris*, *Acrocomia*, and *Aiphanes*) of Bactridinae palms. Some members of the subfamily Calamoideae (climbing lepidocaryoid palms) are also predominantly spiny and spines are present on the leaf rachis such as in *Calamus acamptostachys* (Becc.) Baker, 2015; *Desmoncus chinantlensis* Liebm. ex Martius, 1853; and *Plectocomia dransfieldiana* Madulid, 1981 (Tomlinson, 1962a, b; Tomlinson et al., 2011). The spines are variable in morphology being long and needle-like, or short and broad. The bactroid (Tribe Cocoseae; Subtribe Bactridinae) group of palms is exclusively American and is particularly heavily spiny (Bailey, 1941; Tomlinson et al., 2011). Spines on the rachis of different extant palm species such as *Acrocomia aculeata* (Jacq.) Lodd. ex Martius, 1834; *A. totai* Martius, 1844; *Aiphanes horrida* (Jacq.) Burret, 1932; *Astrocaryum sciophilum* (Miq.) Pulle, 1906; *A. murumuru* Martius, 1824; *Bactris gasipaes* Kunth, 1816; and *B. setiflora* Burret, 1939 of the subtribe Bactridinae (Bailey, 1941; de Lima et al., 2018; Table 1; Figure 6) are more or less morphologically equivalent to those of our fossil spiny palm leaves where spines are located on the rachises of the pinnate





**FIGURE 6.** Spines on the rachises of different species of modern pinnate palms. (A) *Astrocarium sciophilum* (Miq.) Pulle, 1916; (B) *Plectocomia dransfieldiana* Madulid, 1981; (C) *Aiphanes horrida* (Jacq.) Burret, 1932; (D) *Acrocomia totai* Martius, 1944; (E) *Astrocarium murumuru* Martius, 1824; (F) *Bactris gasipaes* Kunth, 1816; (G) *Desmoncus chinantlensis* Liebm. ex Martius, 1853; (H) *Aiphanes verrucosa* Borchsenius and Balslev, 1990; (I) *Astrocarium mexicanum* Liebm. ex Martius, 1853 (scale bars = 1 cm, source: The Herbarium Catalogue, Royal Botanic Garden, Kew, published on the internet <http://www.kew.org/herbcat>).



**TABLE 1.** Selected extant pinnate palm species having spines on their rachis.

| Palm Subfamilies                                       | Species  |
|--|--|
| Coryphoideae   | <i>Phoenix</i> spp.  |
| Calamoideae  | <i>Plectocomia dransfieldiana</i> Madulid, 1981                  |
| Arecoideae   | <i>Astrocaryum murumuru</i> Martius, 1824                        |
|  | <i>Astrocaryum sciophilum</i> (Miq.) Pulle, 1906                 |
|  | <i>Acrocomia aculeata</i> (Jacq.) Lodd. ex R.Keith, 1834         |
|  | <i>Acrocomia totai</i> Martius, 1844                             |
|  | <i>Astrocaryum mexicanum</i> Liebm. ex Martius, 1853             |
|  | <i>Aiphanes tricuspidata</i> Borchsenius, Bernal, and Ruíz, 1989 |
|  | <i>Aiphanes horrida</i> (Jacq.) Burret, 1932                     |
|  | <i>Aiphanes verrucosa</i> Borchsenius and Balslev, 1989          |
|  | <i>Bactris gasipaes</i> Kunth, 1816                              |
|  | <i>Bactris setiflora</i> Burret, 1939                            |
|  | <i>Bactris guineensis</i> (L.) H.E. Moore, 1963                  |
| <i>Desmoncus chinantlensis</i> Liebm. ex Martius, 1853 |  |

leaves. Most of the Bactridinae grow today in the tropical forests of Central and South America (Dransfield et al., 2008).

### Comparison with Previously Reported Fossil Pinnate Palms from India and Elsewhere

Here, we also compare the recovered fossil palm leaf specimens with earlier reported fossil pinnate leaf taxa not only from India but also more widely. Mahabale (1966) reported a fossil specimen showing a resemblance to the pinnate leaf of *Phoenix* as *Palmophyllum mohgaonense* based on the basal part of the leaf exhibiting spines on the axis or rachis. However, the fragmentary nature of Mahabale's specimen does not permit a detailed comparison with the present fossil specimens. As far as we are aware, there are only some limited records of fossilized pinnately compound palm leaf remains from India (Guleria and Mehrotra, 1998; Singh et al., 2012; Guleria et al., 2005). Our fossil leaf specimens are different from them in the arrangement of pinnae on the rachis and the length and thickness of the rachis. In addition, incomplete pinnate leaves are also reported from the Rajahmundry Sandstones (Cretaceous) of Bommuru, Andhra Pradesh (Mahabale and Rao, 1973), and the Eocene sediments of the Garo Hills, Assam (Lakhanpal, 1964).

Pinnate palm leaves (*Phoenicites jungii*; *P. spectabilis*; *P. angustifolius*; *P. borealis*; *P. pumila*; *P. pallavicinii*; *P. italica*; *P. danteana*; *P. densifolia*, etc.) are also reported from the Cenozoic (Eocene, Oligocene, and Miocene) sediments of Europe (Brongniart, 1828; Arenes and Depape, 1956; Massalongo, 1858; Visiani, 1864; Friedrich, 1883; Spitzberger, 1989; Teodoridis et al., 2015). We compared our fossil leaf specimens with them and found that the Deccan specimens differ in their arrangement of pinnae on the rachis, and the length and thickness of the rachis. Our specimens also differ in having spines on their rachises.

The Calamoideae (rattan palm) leaf species *Calamoides pikopiko* reported by Hartwich et al. (2010) from the Late Eocene (Beaumont Formation) sediments of Pikopiko, Southland, New Zealand, has prominent punctate prickles (?) scars along the leaf veins. Huard (1967) reported fossil species *Spinophyllum* from the Neogene (Miocene) Arjuzanx leaf assemblage of France, where lignite adjacent to leaf-bearing sands yielded spiny sheaths belonging to palm stems. Berry (1924) reported the fossil leaf palm species *Bactrites pandanifoliolus* from the Eocene sediments (Lisbon Formation) of Georgia, USA. The North American species possess spiny leaf fragments with small teeth on one margin. In a few leaves, the primary veins bore spines on one or both surfaces as shown by two specimens in which the spines are preserved. The fossil species *Calamus daemonorops* reported by Chandler (1957) from the Oligocene sediments of South Devon, England, exhibits spines and spine bases. The above-mentioned four non-Asian fossil spiny palm species can also be distinguished from the Deccan material described here based on spine position. They have spines on the leaflets, whereas our Deccan specimens possess spines on the rachis. Therefore, we assign these newly discovered pinnate spiny palm leaves as *Spinopinnophyllum* S. Kumar, T. Su, and M.A. Khan gen. nov.

### Palaeobiogeographic Significance

Palms are represented by a large number of fossils from India and elsewhere (Rao and Achuthan, 1973; Harley, 2006; Dransfield et al. 2008; Kumar et al., 2022b). However, the spiny palms have a poor fossil record in deep time, making hypotheses concerning their origin and dispersal difficult to evaluate. From this point of view, our finding of well-preserved spiny pinnate palms from the latest Maastrichtian (Late Cretaceous) to early Danian (earliest Paleocene) sediments (Chron

29R, c. 66–65 Ma) of the Mandla Lobe of the Deccan Intertrappean Beds of Madhya Pradesh, Central India, before good evidence of direct India-Eurasia land contact, is important because it represents the oldest reliable fossil record of spiny pinnate palms, and supports their Gondwanan origin.

There are only a few unarmed pinnate palms in the fossil record, and these are reported from the Cenozoic (Eocene, Oligocene, and Miocene) sediments of Europe (Italy, France, and Germany) and Africa (Brongniart, 1828; Arenes and Depape, 1956; Massalongo, 1858; Visiani, 1864; Friedrich, 1883; Spitzlberger, 1989; Pan et al., 2006; Teodoridis et al., 2015). The material described here allows us to propose probable migration pathways of pinnate palms from India to Europe after the docking of the Indian subcontinent with Eurasia during the early Paleogene. The exact time at which this occurred is still debated but the earliest evidence for very close proximity between India and Eurasia is at ~ 61 Ma (An et al., 2021). However, this may represent the docking of a breakaway Indian plate fragment that now makes up the Tibetan Himalaya, with the main part of India making contact at ~ 53 Ma (Yuan et al., 2022). Our finding of spiny pinnate palm leaves at the K/Pg therefore, although preliminarily, supports an “Out-of-India” dispersal hypothesis. Such a proposal runs counter to a prevailing hypothesis that suggests a Laurasian palm origin (Baker et al., 2013a, b), but this dated molecular phylogenetic analysis lacked the benefit of our new well-dated fossils, and a re-analysis is now called for.

Some researchers have suggested that biotic exchange between India and Eurasia may not have required direct contact between the two landmasses (Chatterjee and Scotese, 2010). As an alternative, the biotic exchange may have occurred via African-Arabian connections between India and Eurasia (Greater Somalia or Oman- Kohistan-Dras Island Arc) towards the end of the Cretaceous. This hypothesis depends on the presence of pinnate palm megafossils in Africa (Pan et al., 2006). As both pinnate and palmate palm leaf fossils are reported from Africa, our data support the “Out-of-India” hypothesis and that pinnate palms entered Europe either directly from the Indian subcontinent or on the breakaway Indian plate fragment that became the Tibetan Himalaya.

Our pinnate spiny palm materials, together with the previously reported spineless palms from the same locality, indicate that palms were one of the major angiosperm components of the Madhya Pradesh Deccan flora. It is worth noting that pin-

nate spiny palms are absent in the fossil locality at the present day. Climate variability over evolutionary time and monsoon intensification might be key reasons for the loss of spiny palms from the present-day vegetation there.

### **The Relevance of Spiny Palm Fossils to the History of Palm Physiology and Palaeoecology**

The role of spines on palm leaves is not completely understood and is likely multifunctional, but the main function of the spines is as a defense mechanism against larger herbivores (Tomlinson, 1962a; Zhang et al., 2022). The large animals against which the spiny defensive mechanisms of palms evolved are now extinct (Tomlinson, 1962a). Apart from signifying an age for spiny palms that goes back at least to a period when the forests were inhabited by much larger herbivores than occur today, these fossils also suggest that spines are a primitive feature in palms. More recently-evolved palms have no defensive mechanisms because the need has reduced and there are many small spineless delicate palms (Tomlinson, 1962a). Also, it may be that ancient spineless palms originated in areas free from herbivorous predators, and the existence of so many genera of spineless arecoid palms on isolated islands in the Pacific area might support this view (Tomlinson, 1962a). So, the evidence of fossil spiny palms from the latest Maastrichtian-earliest Danian sediments of the Deccan Intertrappean beds of Madhya Pradesh may be a rough measure of the former distribution and predation intensity of large herbivores that are now extinct. We assume these large herbivores might have been dinosaurs and not mammals because Late Cretaceous mammals tend to be much smaller than those that exist today, or in the early Cenozoic (Grossnickle et al., 2019). Based on evidence from the western USA, it seems that it was only after the K-Pg that mammal body mass began to exceed 50 kg (Lyson et al., 2019).

The function of spines in several climbing palms is not for protection, but as grapnels that serve to attach the leaves of the palm to the surrounding foliage and branches of taller trees, so that the palm grows into the forest canopy with the support of adjacent vegetation, rather than by investing in its mechanical tissues. These spines are architecturally and functionally different from the ones appearing in our fossil material.

Spines on other angiosperms are most pronounced today in low productivity semi-arid open environments, where there is heavy grazing pressure from herbivores and competition for plant food

is intense (Charles-Dominique et al., 2016; Ratnam et al., 2016). However, modern heavily spined palm genera (such as *Bactris* and *Astrocaryum*) generally grow in moist and shady environments (Tomlinson, 1962a).

## CONCLUSIONS

Pinnately-leaved spiny palm fossils collected from the K-Pg sediments of the Deccan Intertrappean beds of Madhya Pradesh, central India, are assigned to the new fossil genus *Spinopinnophyllum*. Our finding indicates that such pinnate spiny palms lived in what is now Madhya Pradesh during the Late Cretaceous-early Paleocene, and suggests that palms had already diversified there at that time. As fossil pinnate spiny palms are little known, the present report provides important evidence for exploring the evolutionary history of these palms. The present fossil evidence of pinnate spiny palms supports the “Out-of-India” hypothesis, i.e., pinnate palms originated in Gondwana and were subsequently “ferried” to Europe on the “raft” of India, spreading within Eurasia fol-

lowing the establishment of the India-Eurasia land contact early in the Cenozoic. The presence of spiny pinnately-leaved palms at the K-Pg suggests defense mechanisms offering protection from large herbivores developed during the late Cretaceous when the only common large herbivores were dinosaurs. Further studies on fossil records of spiny palms are necessary to properly demonstrate the significance of our current hypotheses.

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