Rhizopalamoxylon nypoides – a new palm root from the Deccan Intertrappean beds of Sagar, Madhya Pradesh, India

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A new species of fossil palm rhizome having root-mat under the organ genus *Rhizopalamoxylon* (*Rhizopalamoxylon nypoides* sp. nov.) is reported. The specimen shows the closest resemblance with the modern monotypic genus *Nypa* Wurm of the Arcaceae. The specimen was collected from the late Maastrichtian–early Danian sediments of Deccan Intertrappean beds, Mothi, Sagar district, Madhya Pradesh, India. *Nypa* is a mangrove palm naturally found in estuaries and swamps of the tropical region and represents one of the oldest records of the genus from the Deccan Intertrappean beds of central India. The abundance of palms, including *Nypa* and previously recorded coastal and mangrove elements such as *Acrostichum*, *Barringtonia*, *Cocos*, *Sonneratia* and marine algae (*Distichoplax* and *Peyssonellia*) from the Deccan Intertrappean beds indicate marine influence and existence of tropical rainforest ecosystem in the vicinity of fossil locality in contrast to the deciduous forests occurring there at present.

1. Introduction

The Deccan Volcanic Province (DVP) of India is one of the largest continental flood basalts in the earth history. The Deccan traps were formed as a result of volcanic eruption and outpouring of lava in peninsular India; this was associated with the movement of Indian Plate over the hotspot located in the Reunion Island (Chatterjee *et al.* 2013). Recent studies based on ⁴⁰Ar/³⁹Ar dating and magnetostratigraphy indicate that volcanism had extended duration of 67.5 ± 1 to 63 Ma having a bulk eruption at 65 ± 1 Ma (Chenet *et al.* 2009; Renne *et al.* 2015; Schoene *et al.* 2015; Shrivastava *et al.* 2015). Deccan Intertrappean sediments were deposited during pauses or quiescent period of the volcanic activity in lacustrine and fluvial

environments. These sedimentary beds that occur sandwiched between successive lava flows are highly fossiliferous and contain diverse biota (both flora and fauna) of late Maastrichtian–early Danian age.

It has been observed that Deccan volcanism along with meteorite impact at Chicxulub, Mexico played a significant role in global climate change at the K–Pg boundary and severely affected the existence of dinosaurs and planktic foraminifera (Khosla and Sahni 2003; Keller *et al.* 2009a, b). However, Couvreur *et al.* (2011) suggested a constant diversification of palms (Yule Process) in the tropical rain forest ecosystem until the Neogene. Our observations also suggest that palms along with other terrestrial angiosperms continued and diversified throughout K–Pg boundary mass extinction event.

Keywords. *Rhizopalamoxylon*; *Nypa*; Deccan Intertrappean beds; late Maastrichtian–early Danian; Sagar; Madhya Pradesh.

2. Material and method

The general stratigraphic sequence of rocks of the Sagar district has been given by Rajarajan (1978). The oldest rock exposed in the area is sandstone-quartzite of Rewa Group (Vindhyan Supergroup) of Neoproterozoic age, overlain by the flows of Deccan basalts (with Intertrappean beds) of late Maastrichtian–early Danian age.

The specimen of palm rhizome fossil, described here was collected from thin calcareous sandstone bed (late Maastrichtian–early Danian) of the Deccan Intertrappean (GPS coordinates of fossil recovery 23°57'35"N; 78°41'18"E), exposed between two basaltic flows (marked as Lower Flow and Upper Flow, Map 1), western slope of a Deccan Trap hill,

at 582 m elevation, near Mothi, Sagar district, Madhya Pradesh, India (figure 1).

The cross sections of the fossil rhizome were prepared following the standard method of grinding, polishing and mounting in Canada balsam for permineralized material (Lacey 1963). The thin sections were examined and photographed under the high power light microscope (Leica DFC290). Thin sections of a number of modern genera of palm roots for comparison were examined at the Birbal Sahni Institute of Palaeobotany, Lucknow (BSIP). The type slides are deposited in the museum of the institute (BSIP). The anatomical terms used in describing the rhizome are those adopted by Tomlinson (1990) and Seubert (1996a, b).

Figure 1. Geological map showing the fossil locality (marked by a star) near Mothi Village, Sagar district, Madhya Pradesh.

3. Systematic description

Order: Arecales

Family: Arecaceae

Sufamily: Nypoideae

Genus: *Rhizopalamoxylon* Gothan (1942)

Rhizopalamoxylon nypoides Kathal *et al.*, sp. nov.
(figures 2, 3)

Specific diagnosis: Roots more than 15, about 2–3.5 mm in thickness, each divisible mainly into extrastelar and stelar regions. Extrastelar region made up of rhizodermis, exodermis, cortex and endodermis; stelar region comprising vascular bundles and pith. Rhizodermis single layered. Exodermis made up of 2–3 layers of horizontally elongated thick walled cells. Outer cortex about 350–450 μm thick,

homogeneous. Inner cortex about 2 mm in thickness, aerenchymatous with well developed radially elongated air chambers or cavities in 1–3 rows; fibres absent. Endodermis present, about 35 μm thick; cells thick walled. Vascular bundles radial and exarch. Xylem strands 25–28; protoxylem 15–30 μm in diameter; metaxylem arranged in 1 or 2 rows, 40–90 μm in diameter. Ground mass or conjunctive tissue made up of thin walled, radially elongated parenchymatous cells. Pith present, about 375 μm in diameter, mostly represented by a cavity.

Repository: Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Holotype: Specimen No. BSIP40974.

Horizon: Deccan Intertrappean beds of India.

Locality: Mothi, Sagar district, Madhya Pradesh, India.

Figure 2. *Rhizopalamoxylon nypoides* Kathal *et al.*, sp. nov. (a) A palm rhizome with root mat. (b) Transverse section of a root showing exodermis, aerenchymatous cortex and central stelar region. (c) Same section magnified to show cortical air chambers and radial vascular bundles in the stelar region.

Figure 3. *Rhizopalmoxylon nypoides* Kathal *et al.*, sp. nov. (a) A part of the section showing exodermis and outer cortex. (b) Magnified view of the stele showing endodermis and exarch xylem bundles. (c) Cross section of another root showing conjunctive tissue and parenchymatous pith. (d) Cross section of the root showing well developed radially elongated air chambers. (e) Showing an enlarged air cavity with narrow partition.

Age: Late Maastrichtian–early Danian.

Etymology: The specific epithet indicating its close resemblance with *Nypa*.

Description: The description is based on a chert piece comprising a rhizome having a large number of irregularly oriented roots forming the root mat.

There are more than 15 roots ranging about 2–3.5 mm in thickness. Each root is divisible mainly into extrastelar and stelar regions. The extrastelar region consists of rhizodermis, exodermis, cortex and endodermis, while the stelar region comprises

vascular bundles and pith. The rhizodermis is single layered measuring about 283 µm in thickness. Its cells are poorly preserved. The exodermis measures about 62 µm in thickness and is made up of 2–3 layers of horizontally elongated thick walled cells. The outer cortex is homogeneous and about 350–450 µm thick; its cells are thick walled and polygonal in shape. The inner cortex, ranging 1.8–2.2 mm in thickness, is aerenchymatous with well developed radially elongated air chambers or cavities in 1–3 rows. The air cavities are separated from each other by usually one cell wide narrow

partitions which often collapse. Fibres are absent in the inner cortex. The endodermis is present and measures about 35 μm in thickness; its cells are thick walled. Vascular bundles are radial and exarch near the periphery. Xylem strands are 25–28 in number where protoxylem vary 15–28 μm in diameter and metaxylem ranging 46–85 μm in diameter are arranged in 1 or 2 rows. The phloem alternates with xylem strands, however, its cells are poorly preserved. A ground mass or conjunctive tissue is made up of thin walled, radially elongated parenchymatous cells which are about 13–23 μm in size. The pith measures about 378 μm in diameter and is mostly represented by a cavity except in one root which is probably immature; its cells are poorly preserved, thin walled and 173–205 μm in size.

Affinities: Palm roots anatomically show a generalized pattern found in monocotyledons in having polyarch vascular tissue and absence of secondary thickening but unlike other monocots, are generally devoid of root hairs (Mahabale and Udawadia 1960; Tomlinson 1990). In order to find out nearest modern counterpart of the palm family Arecaceae, the fossil was compared with its various subfamilies (Dransfield *et al.* 2008), namely Arecoideae, Calamoideae, Ceroxyloideae, Coryphoideae and Nypoideae through the published description and photographs (Cormack 1896; Drabble 1904; Mahabale and Udawadia 1960; Tomlinson 1990; Seubert 1996a, b, 1997, 1998a, b; Chomicki *et al.* 2014). Arecoideae can be differentiated from our fossil in having lobed vascular cylinder, mechanical elements in the inner cortex and medullary bundles in the pith, while Calamoideae is distinct in possessing mucilage cells or fibres in the inner cortex with the occasional occurrence of medullary bundles. Both Ceroxyloideae and Coryphoideae differ from the present fossil in having medullary bundles, moreover, the former possesses fibres in the inner cortex. The present roots show nearest resemblance with the monotypic subfamily Nypoideae (*Nypa fruticans* Wurmb) in having large air chambers separated from each other by irregular vertical thin walled diaphragms/partitions, very small stelar region and absence of fibrous bundles in the cortex and medullary bundles in the pith. The fossil also differs from the modern *Nypa* in the absence of pericycle and in having slightly greater number of xylem strands which are up to 25 in the modern species (Mahabale and Udawadia 1960).

Comparison with fossil species: The genus *Rhizopalmoxylon* was informally instituted by Felix (1883) for fossil roots referable to the family

Arecaceae (Palmae) without any description/diagnosis. Later on, Gothan (1942) validated the genus by providing description/diagnosis and described two species under *Rhizopalmoxylon*. However, later workers ignorant of Gothan's work referred their species to *Rhizopalmoxylon* Felix (1883). Many palm roots have also been assigned to the genus *Palmoxylon* Schenk (Stenzel 1904; Stockmans and Williere 1943; Shukla 1946; Lakhanpal 1955; Ogura 1962; Rao and Menon 1965; Menon 1968; Tidwell *et al.* 1971; Bonde *et al.* 2004), while some have been described without assigning any name (Verma 1974; Ambwani 1981).

So far, about 14 species of *Rhizopalmoxylon* Gothan (1942) are reported, viz., *R. glaseli* Gothan (1942), *R. bohlenianum* Gothan (1942), *R. pilosum* van der Burgh and Meulenkamp (1966), *R. libycum* Koeniguer (1970), *R. behuninii* Tidwell *et al.* (1972), *R. blackii* Tidwell *et al.* (1972), *R. scottii* Tidwell *et al.* (1972), *R. sundaram* Mahabale and Rao (1973), *R. huepaciense* Cevallos-Ferriz and Ricalde-Moreno (1995), *R. teguachiense* Cevallos-Ferriz and Ricalde-Moreno (1995), *R. borassoides* Awasthi *et al.* (1996), *R. singularis* Bonde *et al.* (2009), *R. angiorhizon* (= *Palmoxylon angiorhizon* Stenzel 1904) Bonde *et al.* (2009) and *R. macrorhizon* (= *Palmoxylon macrorhizon* Stenzel 1904) Bonde *et al.* (2009).

Rhizopalmoxylon glaseli Gothan, *R. bohlenianum* Gothan and *R. singularis* Bonde *et al.* differ from the present roots in having medullary bundles in the pith and distribution of air cavities in the cortical region. In *R. behuninii* Tidwell *et al.*, *R. blackii* Tidwell *et al.*, *R. scottii* Tidwell *et al.* rhizodermis and exodermis are not preserved. In *R. behuninii* and *R. blackii*, stele is bigger and metaxylem is arranged in three rows. *R. scottii* markedly differs in having fewer and smaller air cavities. In *R. sundaram* Mahabale and Rao endodermis is indistinct and larger number of vascular bundles (up to 45) are present. In *R. huepaciense* Cevallos-Ferriz and Ricalde Moreno, *R. teguachiense* Cevallos-Ferriz and Ricalde Moreno, and *R. singularis*, fibrous tissue is interspersed in the cortex. Borassoid palm roots (Ambwani 1981) differ in having larger number of vascular bundles (50–55) and presence of medullary bundles in the pith. *R. borassoides* Awasthi *et al.* can be differentiated in having sclerenchymatous outer cortex (hypodermis), 2–3 seriate partition walls and vascular strand in three rows. The root showing resemblance with *Nypa* reported by Verma (1974) compares well with the present specimen in having large air spaces separated by 1–2 celled thick septa or diaphragm, but differs also in possessing only 12–15 vascular bundles. Since the present roots are different from the earlier reported fossilized

palm roots, a new species of *Rhizopalmoxylon*, *Rhizopalmoxylon nypoides* is established; the specific name is after the extant genus *Nypa*.

4. Discussion

Amongst monocotyledons, Arecaceae/Palmae is one of the largest families having monophyletic origin and has been placed within the Commelinid clade (Chase *et al.* 2006; Davis *et al.* 2006). Palms are pantropical in distribution and considered as an important and characteristic component of tropical rainforest ecosystem (Couvreur *et al.* 2011). Arecaceae consists of 201 genera and 2650 species distributed in five sub-families (Govaerts and Dransfield 2005; Mabberley 2005; Dransfield *et al.* 2008). The subfamily Nypoideae consists of a single monotypic genus *Nypa* Steud. On the basis of molecular phylogenetic analysis, subfamily Nypoideae is resolved as sister to all palms except Calamoideae by Asmussen *et al.* (2006), while other studies made by Uhl *et al.* (1995) and Lewis and Doyle (2001) consider Nypoideae as sister to all palms, including Calamoideae. In India, palms are represented today by about 20 genera, including *Nypa* comprising 96 species (Kulkarni and Mulani 2004).

The family Arecaceae is represented globally by richest fossil records. Harley (2006) listed fossil records of this family from all over the world. The earliest unambiguous fossils of the family are from the Upper Cretaceous of Europe and USA. They are in the form of costapalmate leaves named *Sabalites*. On the basis of oldest reliable megafossil records from Europe (Dransfield *et al.* 2008) and molecular phylogenetic studies (Couvreur *et al.* 2011), palms have been suggested to be of Laurasian origin. However, recent reports of pollen grains of Arecaceae from the Lower Cretaceous (Barremian-Albian) of Patagonia (Argentina) are the oldest records (Martínez Leandro *et al.* 2016) of the palm family. These records suggest the origin of monocots and a probably initial diversification of palms during the Early Cretaceous in high latitudes of Gondwana instead of Laurasia.

Phytogeographical and palaeoecological considerations: The genus *Nypa* Steud. is monotypic with a single species *N. fruticans* Wurm. It is strictly a mangrove palm presently growing on swampy coastline and estuaries of Indian and Pacific Oceans. It was introduced in West Africa and has now spread and naturalized in Cameroon, Panama and Trinidad (Dransfield *et al.* 2008). It does not occur on shores exposed to strong wave action and in hypersaline conditions (Tralau 1964; Collinson 1993). In India, it is commonly distributed in the Sunderbans in the eastern

part of mangrove forest, on sides of tidal creeks and very often grows on intertidal flat lands and marshy places. It is also found in the Andaman and Nicobar Islands and southeast Asian countries (Naskar and Mandal 1999a, b). In addition to *Nypa*, the other important palm fossil known from the inter-trappean beds of Sagar is *Palmoxylon sundaram* (Sahni 1946; Bonde *et al.* 2004) resembling *Cocos* L., which is native to coastal areas. The presence of *Nypa*, along with *Cocos* in Sagar suggests a warm and humid climate with marine influence, similar to that found in the Sunderbans at present.

The fossil records of *Nypa* are known from both tropical and temperate zones such as Africa, America, Asia and a number of European countries, mostly in the Late Cretaceous, Paleocene and Eocene. The fossils of the genus reduced gradually during the middle Miocene due to climatic deterioration (Tralau 1964; Morley 2000; Gee 2001; Harley 2006; Dransfield *et al.* 2008; Gomez-Navarro *et al.* 2009). The oldest records are known from the late Maastrichtian–early Danian sediments of the Deccan Intertrappean of India (Sahni and Rode 1937; Lakhanpal 1952; Chitaley 1960; Nambudiri 1966; Verma 1974; Chitaley and Nambudiri 1995). The occurrence of *Nypa*, along with the known coastal and mangrove fossil records like *Acrostichum* (Bonde and Kumaran 2002), *Barringtonia* (Srivastava *et al.* 2009), *Cocos* (Srivastava and Srivastava 2014), *Sonneratia* (Srivastava 2008) and marine algae, *Distichoplax* and *Peyssonellia* (Bonde *et al.* 1981) from the same horizon indicates marine seaway (an arm of Tethys sea) up to central India. This marine seaway model in central India was proposed by Lakhanpal (1970) and was further substantiated by palaeontological evidences (Sahni 1983; Bajpai 2009; Keller *et al.* 2009a, b). In India, *Nypa* is reported from the following younger horizons also: Eocene of Meghalaya (Bhattacharyya 1983) and Nagaland (Mehrotra *et al.* 2007), Oligocene of Assam (Mehrotra *et al.* 2003) and Miocene of Meghalaya (Lakhanpal 1952), Mizoram (Mehrotra *et al.* 2003) and Maharashtra (Kulkarni and Phadtare 1980). During the Late Cretaceous, India was already separated from rest of the Gondwanan continents, but yet not collided with Asia and had southern latitudinal position. The fossil locality was situated at ~17°S palaeolatitude (ODSN), which is in contrast to its present day location, i.e., 23°40'52"N. The fossil records indicate that the continent of Africa and India possessed richer palm flora in the past (Srivastava *et al.* 2014). In their study on Araceae biogeography, Nauheimer *et al.* (2012) came to the conclusion that the ancestral area of Aroideae might have been either Asia or Africa. It appears that India played an important role in the dispersal of Arecaceae, Araceae, Connaraceae,

Dipterocarpaceae, Oleaceae, Vitaceae and many other families (Dutta *et al.* 2011; Manchester *et al.* 2013; Shukla *et al.* 2013; Shukla and Mehrotra 2014; Srivastava *et al.* 2015; Baas *et al.* 2017); this supports 'Out of India' hypothesis, according to which the dispersal of many families from India into southeast Asia took place when they came on rafting with the Indian plate from south to north (Shukla *et al.* 2016).

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