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Fossil fruit of *Cocos* L. (Arecaceae) from Maastrichtian-Danian sediments of central India and its phytogeographical significance

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ABSTRACT. A fossilised palm fruit of *Cocos* L. (*C. binoriensis* sp. nov.) is reported from the Binori Reserve Forest, Ghansor, Seoni District, Madhya Pradesh, India. The fruit is a 3-dimensionally preserved drupe, ovoid with clearly visible longitudinal ridges. The husk is made up of a thin smooth exocarp and fibrous mesocarp, with vertical and horizontal fibres present on the inner surface of the endocarp. The fruit is Maastrichtian-Danian in age and is the world's oldest fossil record of *Cocos*. The genus *Cocos* is now distributed in coastal areas of pantropical regions. The occurrence of *Cocos* along with coastal and mangrove remains such as *Acrostichum*, *Barringtonia*, *Nypa*, *Sonneratia* and marine algae *Distichoplax* and *Peyssonellia* previously recorded from Deccan Intertrappean beds further confirms the proximity of sea in the area in central India and indicates warm and humid conditions. The presence of *Cocos* and previously recorded palaeoflora supports the existence of tropical wet evergreen to semi-evergreen forests at the time of deposition in the area, in contrast to the dry to moist deciduous forests existing today in central India. The probable reasons for the change in climatic conditions are withdrawal of an arm of the sea from central India, the change in latitude, and a significant uplift of the Western Ghats during post-trappean times.

KEYWORDS: Cocos, Arecaceae, Maastrichtian-Danian, coastal, climate, pantropical

INTRODUCTION

The Deccan Volcanic Province of India is one of the largest continental flood basalts in the history of the Earth. It was formed by volcanic eruption and the outpouring of lava in peninsular India, associated with the movement of the Indian Plate over the Reunion Hotspot (Chatterjee et al. 2013). Radiometric dating and magnetostratigraphic studies (Keller et al. 2009a, b, Chenet et al. 2009 and references therein) indicate that volcanism extended from ca 67.5 ±1 to 63 Ma, with a bulk eruption (ca 80% of the total volume of Deccan basalts) in chron 29R (II phase) at 65 ±1 Ma (Chenet et al. 2009). It has been observed that Deccan volcanism and the accompanying global climate change at the K-T boundary led to the extinction of dinosaurs and decline of planktic foraminifera and other biota (Khosla & Sahni 2003, Keller et al. 2009a, b). According to Cripps et al. (2005), however, Deccan volcanism had hardly any effect on animal and floral productivity. Couvreur et al. (2011) also suggested constant diversification of palms (Yule Process/Museum Model) in tropical rain forest ecosystems until the Neogene. Our observations also suggest that palms along with other terrestrial angiosperms continued and diversified throughout the K–T mass extinction event, as a large number of fossil palms along with eudicots are reported from intertrappean beds of central India (Srivastava 2011).

Deccan Intertrappean sediments were deposited in lacustrine and fluviatile environments during quiescent phases between intervals of

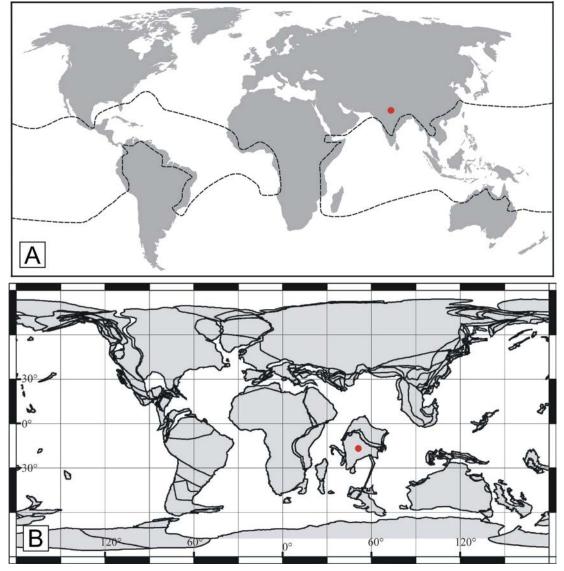


Fig. 1. A. World map showing the modern distribution of *Cocos nucifera* (dashed line) (after Shukla et al. 2012) and present fossil locality (red dot); **B**. Palaeocontinental map showing the area of the fossil locality (red dot) at 65 Ma (ODSN)

volcanic activity while the Indian Plate was still an isolated land mass moving northwards toward the Eurasian tectonic plate. The intertrappean beds sandwiched between successive lava flows are highly fossiliferous and contain diverse plant and animal fossils, mostly terrestrial and usually not age-diagnostic. Earlier the Deccan Intertrappean beds were considered to be early Tertiary due to the predominance of angiosperm remains (Sahni 1934, Bande 1992), but studies of microfloral and faunal (especially dinosaur) assemblages from several intertrappean localities have led to general acceptance of Maastrichtian age for most of the intertrappean exposures, though there are also a few Danian indicators (Sahni 1983, Kar & Srinivasan 1988, Khosla 1999, Khosla & Sahni 2003, Bajpai 2009, Keller et al. 2009a, Samant & Mohabey 2009, Srivastava 2011).

In the present communication we describe a fossil fruit resembling *Cocos* L. from Maastrichtian-Danian sediments of Deccan Intertrappean exposures of Ghansor, Seoni District, Madhya Pradesh, central India. During the period of deposition of the fossil described here, India was already separated from the rest of the Gondwanan continents but had not yet collided with Asia. The fossil locality was situated at ca 17°S palaeolatitude (ODSN) and is now at 22°40′52″N (Fig. 1A, B).

Arecaceae/Palmae, the family of *Cocos*, is monophyletic in origin and has been placed within the commelinid clade of the monocotyledons (Chase et al. 2006, Davis et al. 2006). Palms are an important and characteristic component of tropical rainforest ecosystems having a pantropical distribution (Couvreur et al. 2011). In temperate regions their diversity is

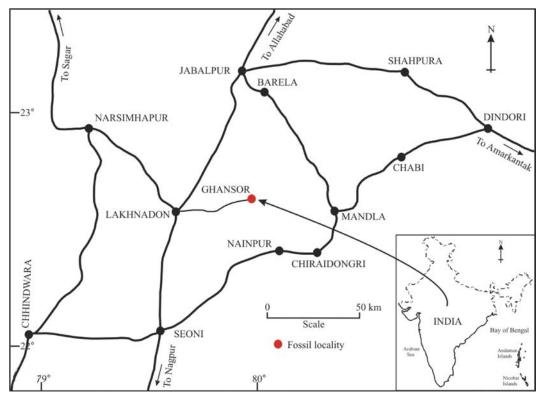


Fig. 2. Map showing the fossil locality

much lower and they have very limited frost tolerance because of their architecture (a large crown of evergreen leaves) (Tomlinson 1990, Jones 1995, Lötschert 2006). On the basis of the oldest reliable megafossil records from Europe and North America (late Coniacian to early Santonian - Berry 1914, Turonian-Campanian – Kvaček & Herman 2004, Manchester et al. 2010) and molecular phylogenetic studies (Couvreur et al. 2011), palms have been suggested to be of Laurasian origin. However, palm pollen is recorded from the Campanian of Japan (Takahashi 1964) and from the Maastrichtian onwards all over the globe (Harley 2006). The family consists of 201 genera and 2650 species distributed in five sub-families: Arecoideae, Calamoideae, Ceroxyloideae, Coryphoideae, and Nypoideae (Dransfield et al. 2005, Govaerts & Dransfield 2005, Mabberley 2005, Dransfield et al. 2008). In India, palms are represented today by 20 genera and 96 species (Kulkarni & Mulani 2004).

The fruit of *Cocos nucifera* L., commonly known as the coconut, is a very important food plant having both domestic and commercial importance. In view of the importance of coconut in culture, the environment and agriculture, the origin and dispersal of the genus is a much-discussed topic amongst biogeographers and palaeobotanists (Harries 1992, Gunn et al. 2011). Earlier, on the basis of fossil records, the genus was hypothesized to have originated in South America (Colombia) during the middle-late Palaeocene (Gomez-Navaro et al. 2009). Later, Couvreur et al. (2011) used the Colombian fossil record (Gomez-Navarro et al. 2009) in conjunction with molecular phylogenetic studies to infer an age of 54.8 Ma for the stem node of sub-tribe Attaleineae, tribe Cocoseae, to which *Cocos* belongs.

MATERIAL AND METHODS

The fossil fruit was collected from Ghansor village (22°40'28"N; 80°02'E) situated in the Binori Reserve Forest (Block No. 444-445), Seoni District, Madhya Pradesh, India (Fig. 2). The fossiliferous intertrappean bed, 1.5 m thick, is associated with basal flow of the Dhuma Formation of the Amarkantak Group of Deccan Traps comprised of chert, cherty limestone and thin shaley fragments between cherts (GSI, 2002). Petrified palm stems and leaf remains (Sahni 1934, Guleria & Mehrotra 1999) and dicotyledonous woods (Srivastava 2008, 2010) were earlier reported from the area. The associated sediments attached to the fruit specimens were removed with a fine chisel and the cleaned fruit was photographed under low-angle sunlight using a 10 mpx digital camera. The holotype is housed in the museum of the Birbal Sahni Institute of Palaeobotany. Another specimen from the same site was sectioned for examination of anatomical structure but no internal anatomy was preserved, so it seems that these specimens represent molds and casts of successive layers within the fruit, rather than having been permineralised.

RESULTS

SYSTEMATIC PALAEOBOTANY

Class Monocotyledons (Liliopsida)

Family Arecaceae Schultz Schultzenst. (nom. altern.)

Subfamily Arecoideae Griffith

Tribe Cocoseae Mart.

Subtribe Attaleineae Drude

Genus Cocos L.

Cocos binoriensis Srivastava & Srivastava sp. nov. (Pl. 1, figs 1, 3–4)

Etymology. The specific name is derived from the Binori Reserve Forest.

Holotype. Museum of Birbal Sahni Institute of Palaeobotany, No. BSIP 40107.

Diagnosis. Fruit a 3-dimensionally preserved drupe, ovoid, somewhat triangular, longitudinal ridges present, apex obtuse with depression in centre, base broad. Husk made up of exocarp and mesocarp. Exocarp preserved in places, smooth, thin; mesocarp fibrous, vertical and horizontal fibres present on inner surface of endocarp.

Type locality. Ghansor, Binori Reserve Forest, Seoni District, Madhya Pradesh, India.

Type horizon. Deccan Intertrappean Beds.

Age. Maastrichtian-Danian.

Description. Fruit a 3-dimensionally preserved drupe, shape ovoid, somewhat triangular, slightly broader at base, ca 11.7 cm long and 10.0 cm wide; apex obtuse with depression in centre, two longitudinal ridges clearly visible; base obtuse, longitudinal fibre scars converging at base (Pl. 1, figs 3, 4). Husk made up of exocarp and mesocarp. Exocarp preserved in places, smooth, thin; mesocarp fibrous, marks of longitudinal fibres seen (Pl. 1, figs 3, 4); endocarp 2–4 mm thick, vertical and longitudinal fibres present on inner surface (Pl. 1, fig. 4).

Botanical affinity. The diagnostic characters of the fossil fruit – ovoid, somewhat triangular, the presence of longitudinal ridges, a fibrous mesocarp surrounding a smooth endocarp, and relatively large size – can only be found in Arecaceae and more specifically subtribe Attaleinae. Among the modern genera of Attaleinae, only *Cocos* is similar to the present fossil in terms of the aforementioned characters (Pl. 1, fig. 2). However, due to the presence of the husk (exocarp and mesocarp) the endocarp was not fully exposed, so it was not possible to determine whether the three germination pores characteristic of *Cocos* were present in the specimen.

Fossil records of Cocos have been reported from all of the Gondwana continents (e.g. India, Australia, New Zealand, South America) except Africa and Antarctica. Fossils of Cocoslike fruits, especially fossilised endocarps, are numerous. They are recorded from the Pliocene of Australia as Cocos nucifera (Rigby 1995) and from Miocene and Pliocene sediments of New Zealand, for example C. zeylandica Berry (1926) and Cocos fruit (Ballance et al. 1981). A middle-late Palaeocene occurrence was recently reported from northern South America as cf. Cocos sp. (Gomez-Navaro et al. 2009). A few fruits resembling coconut have been described from various Deccan Intertrappean localities of central India under various morphotaxa such as Palmocarpon cocoides (Mehrotra 1987), Cocos intertrappeansis (Patil & Upadhye 1984), Cocos nucifera-like fruit (Tripathi et al. 1999) and Cocos pantii (Mishra 2004), while Cocos sahnii was reported from the early Eocene of Rajasthan (Kaul 1951, Shukla et al. 2012). Besides fruits, Sahni (1946) reported a petrified palm stem of Palmoxylon (Cocos) sundaram, and Bonde et al. (2004) reported a basal portion of a stem with roots closely resembling modern Cocos from the Deccan Intertrappean sediments of central India.

The fossil fruit *Palmocarpon cocoides* (Mehrotra 1987) cannot be compared with the present specimen because of its different shape and insufficient details, while *Cocos intertrappeansis* $(3.0 \times 5.0 \text{ cm}, \text{Patil & Upadhye 1984})$ and *C. zeylandica* $(2.5 \times 5.0 \text{ cm}; \text{Berry 1926})$ differ in being smaller. *Cocos pantii* is larger $(10.0-15.0 \times 8.0-13.0 \text{ cm}, \text{Mishra 2004})$, and

the Cocos nucifera-like fruit and the above species are based on anatomical characters. Cocos sahnii from the Eocene of Rajasthan is based on impressions of the endocarp and mesocarp and differs in shape from the present fossil. The compressed fruit cf. Cocos sp. from Colombia shows similar external morphology but is larger $(15 \times 25 \text{ cm})$. Therefore a new species, Cocos binoriensis sp. nov., has been established. The specific epithet refers to the locality of the fossil.

DISCUSSION

The origin and dispersal of the coconut palm are still a matter of debate and interest in view of its dispersal by sea currents (Mahabale 1978, Ward & Brookfield 1992) and its ability to germinate even after floating in sea water for 110 days (Edmondson 1941). Some authors believe that it originated in western Pacific islands of tropical Asia, Polynesia or Melanesia (Beccari 1963, Corner 1966, Moore 1973, Harries 1978), from where it was dispersed, mainly via oceanic currents, to sandy and coralline tropical coasts, but this is not supported by the fossil record. Others suggest a South American origin (Gomez-Navaro et al. 2009) and a later range extension to the Indo-Pacific region (Guppy 1906, Cook 1910, Gunn 2004).

The available records of Cocos known from Australia, New Zealand and South America indicate its distribution in different stratigraphic successions of Cenozoic sediments (from Palaeocene to Miocene-Pliocene), whereas records of Cocos fruit from Maastrichtian-Danian sediments of Deccan Intertrappean beds indicate the earliest occurrence of Cocos on the Indian Peninsula. The oldest fossils of Cocos may well be of late Cretaceous origin in the Deccan Intertrappean period, later dispersing into Southeast Asia and other parts of the world, rafting northwards on the Indian plate, supporting the "Out of India" dispersal hypothesis. Three well-supported subtribes (Bactridinae, Elaeidinae, Attaleinae) are recognised, with the groups Bactridinae and Elaeidinae resolved as sister clades on the basis of molecular phylogenetic analysis of the tribe Cocoseae (Dransfield et al. 2005, 2008, Govaerts & Dransfield 2005). Gunn (2004) suggests that sub-tribes Bactridinae-Elaeidinae diverged from Attaleinae between 50 and

60 Ma ago. The present fossil record of *Cocos* from a well-dated horizon (65.5–61.7 Ma; Gradstein et al. 2004) of Deccan Intertrappean sediments suggests that sub-tribe Attaleinae must have diverged earlier than 60 Ma. Phylogenetic analyses of palms from Colombia, South America, also support the hypothesis (Gomez-Navarro 2009, Futey et al. 2012).

The coconut palm is now cultivated in coastal areas of Southeast Asia and Melanesia and has a wide pantropical distribution (Fig. 1 A). The occurrence of *Cocos* along with known coastal and mangrove fossils like Acrostichum (Bonde & Kumaran 2002), Barringtonia (Srivastava et al. 2009), Nypa (Chitaley & Nambudiri 1995), Sonneratia (Srivastava 2008) and marine algae Distichoplax and Peyssonellia (Bande et al. 1981) indicate marine incursions in central India. The idea of a marine seaway in central India was originally proposed by Lakhanpal (1970) and later substantiated by palaeontological evidence (Sahni 1983, Keller et al. 2009a, Bajpai 2009). Presently the area is dominated by dry to moist deciduous forest because of the change in the climate, which may be due to withdrawal of an arm of the sea, the change in latitude, and a significant uplift of the Western Ghats during post-trappean times (Bande & Prakash 1982, Gunell et al. 2003).

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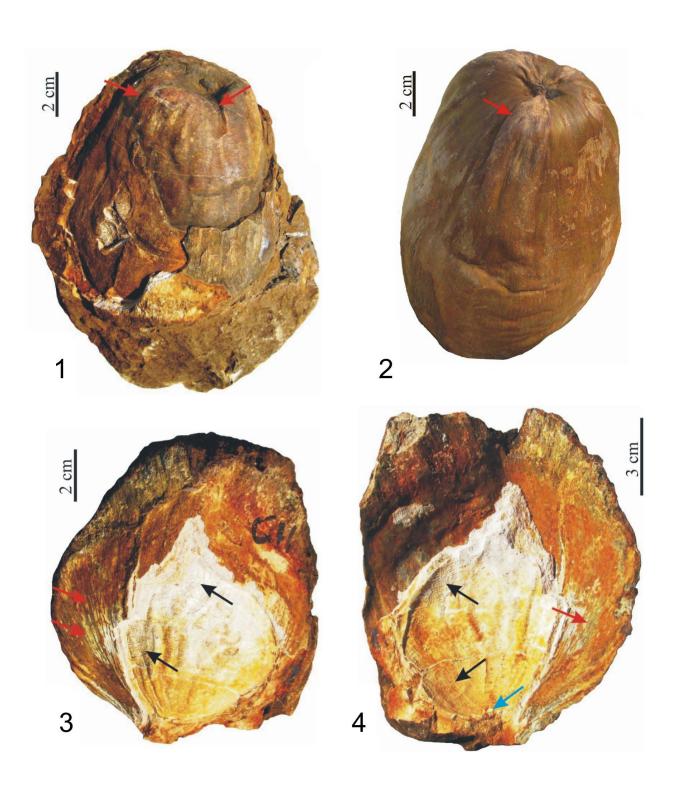
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PLATE

Plate 1

Cocos binoriensis sp. nov.

- 1 Fossil fruit showing shape, size and two longitudinal ridges (red arrows)
- 2. Modern fruit of Cocos nucifera showing its shape, size and longitudinal ridges, similar to the fossil (red arrow)
- 3. Longitudinally broken part of the fossil showing fibrous mesocarp (red arrows) and endocarp with horizontal and longitudinal fibres (black arrows)
- 4. Counterpart of the same fossil fruit showing inner surface of the endocarp having horizontal and longitudinal fibres (red arrow), fibrous mesocarp (black arrows) and basal portion (blue arrow)



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