Cocos sahnii Kaul: A *Cocos nucifera* L.-like fruit from the Early Eocene rainforest of Rajasthan, western India

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Cocos sahnii Kaul, a fossil palm fruit, is validated and described from the Fuller's earth deposits of Kapurdi village of Rajasthan considered as Early Eocene in age. The fossil best resembles the genus *Cocos*, particularly *Cocos nucifera* L., which is now a common coastal element thriving in highly moist conditions. The recovery of this coconut-like fruit, along with earlier described evergreen taxa from the same formation, suggests the existence of typical tropical, warm and humid coastal conditions during the depositional period. The present arid to semi-arid climatic conditions occurring in Rajasthan indicate drastic climate change in the region during the Cenozoic. The possible time for the onset of aridity in the region which caused the total eradication of semi-evergreen to evergreen forests is discussed, as well as the palaeobiogeography of coconuts.

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1. Introduction

In view of the meagre work done on the fossil flora of Rajasthan (Lakhanpal and Bose 1951; Guleria 1984, 1990, 1992, 1996) the authors organized a field trip to collect plant megafossil remains in order to reconstruct the palaeoenvironment of the region. A fossil fruit was collected from the Kapurdi Formation, which is the youngest Tertiary deposit of the Barmer Basin. The generalized stratigraphy of this basin is given in table 1. The lower boundary of the Kapurdi Formation overlies the Mataji-Ka-Dungar Formation unconformably, while a pronounced unconformity makes the upper contact of the formation with the post-Tertiary Uttarlai Formation. Lithologically, it comprises Fuller's earth with carbonaceous streaks and gypseous clay in the lower part, while dull white argillaceous limestone and bioclastic marl occurs in the upper part of the formation (Rana *et al*. 2006). Common fossils recorded in the formation include foraminifera, ostracods, echinoids and lamellibranches (DasGupta 1977), and a few plant megafossils belonging to the families Calophyllaceae and Clusiaceae were also described by Lakhanpal and Bose (1951) from the same formation. An Early Eocene age was assigned to the formation on the presence of *Assilina daviesi*, *A. granulosa* and *Nummatilites actacicus* (DasGupta 1977).

Kaul (1951) reported an impression of a fruit (endocarp) that he named '*Cocos sahnii*', resembling *Cocos nucifera* L. from the same deposits, but he did not provide any diagnosis, description or holotype number of the fossil. As per the rules of nomenclature (ICBN Article no. 42) the name of the fruit described by Kaul is not valid (McNeill *et al*. 2006). While describing our fossil fruit (mesocarp) we got the opportunity to reinvestigate the fossil endocarp reported by Kaul and describe it in detail along with our fossil. We have retained the specific name of the fossil reported by Kaul as it has been used by subsequent workers and we have validated it here by providing the description and holotype number to the specimen. Both Kaul's and our specimens are considered to be conspecific.

The family Arecaceae (palms) is monophylectic, consisting of 183 genera and 2364 species (Govaerts and Dransfield 2005; Dransfield *et al.* 2008). Palms are mostly distributed in the tropics with a few species in warm subtropics and are less prominent in the warm temperate region (Henderson *et al.* 1995; Lötschert 2006). The family is placed within the comelinid clade of monocotyledons (Chase *et al.* 2006; Davis *et al.* 2006) and consists of five subfamilies: Arecoideae,

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Table 1. Generalized stratigraphic sequence of the Tertiary sediments of Barmer Basin, Rajasthan (after DasGupta 1977)

Age	Formation	Facies and gross lithology
Recent	Sand dune and sediments	Alluvium sands, river alluvium and gravel wash
Sub-Recent and (?) older	Uttarlai	Thin gypseous limestone and salt sequence with unconsolidated sands, kankar and gravel beds
		…..………….Unconformity……………………..
Early Eocene	Kapurdi	Lacustrine Fuller's earth deposits interbedded with marine bioclastic limestone
	Mataji-Ka Dungar	Shallow marine orthoquartzite and hard sandstone with pisolites and ball clay and impure bentonitic clay bands at the base
		…………………Unconformity……………………
	Akli (Akli Bentonite Member, Thumbli Member)	Volcanogenic bentonite sequence at the top and sandstone lignite sequence in the basal part
		……………………..Unconformity……………………
	Barmer Mandai Barmer Hill	Shallow marine sandstone with rare plant fossils and orthoquartzite bands grading into conglomerate, sandstone with plant fossils and volcanogenic clays
Palaeocene	Fatehgarh	Sandstone layer with mixed bivalve and gastropod casts at the top
	(Fatehgarh scarp Member Vijori Member)	Dominantly of ochreous clay bands, variegated sandy siltstone and sandstone sequence with coquina bends
		……………………..Unconformity…………………….
	Volcani	Acid to basic volcanic rocks mainly in form of sills and dykes and local intrusive porphyrites
		…………………..Unconformity……………………
Cretaceous	Sarnu	Intuated, terrestrial sandstone and siltstone with plant fossils

Calamoideae, Ceroxyloideae, Coryphoideae and Nypoideae. The genus *Cocos* L. belongs to the subfamily Arecoideae and *Cocos nucifera* L. (the only accepted species) is found throughout the tropics and is a life-supporting species in fragile island and coastal ecosystems. It is particularly important in the low islands of the Pacific where, in the absence of land-based natural resources, it provides almost all the necessities of life, earning it the name the 'tree of life'. It generally thrives under warm and humid conditions, but can tolerate periods of temperatures below 21°C. Based on the morphological diversity of its fruit, a diversification model was proposed for coconuts (Harries 1978). The wild-type coconut (*Niu kafa*-type) has long angular fruits with a thick husk and little liquid endosperm, evolved naturally and disseminated by ocean currents, while the domesticated coconut (*Niu vai*-type) has a high content of liquid endosperm and thin husk. The latter was evolved as a result of selection from *Niu kafa* under cultivation and dissemination by humans. Further selection and dissemination of these two types produced a wide range of varieties and pan-tropical distribution of coconut (Harries 1978). Perera *et al*. (2000) tried to evaluate the level of genetic diversity, distribution of genetic variation and genetic relatedness in coconut genotypes by using microsatellites.

2. Materials and methods

The material described here includes both the mesocarp and endocarp of the fruit in the form of impressions. The fossil specimens were collected from the Kapurdi village (25° 54′ 30′′ N; 70° 22′ 33′′ E), about 19 km north of Barmer in Rajasthan (figure 1). The endocarp was reported originally by Kaul (1951) as *Cocos sahnii*, but not thoroughly described, while the mesocarp (husk) was collected by two of us (AS and JSG). The specimens are preserved well enough to reveal diagnostic morphological features. The fossil specimens were photographed under reflected light using a Canon SX 100 digital camera. The terms used to describe the specimens are taken from Blatter (1926). The holotype and paratype are housed in the museum of the Birbal Sahni Institute of Palaeobotany, Lucknow (India).

3. Systematic description

Family: Arecaceae
Sub-family: Arecoideae
Tribe: Cocoseae
Sub-tribe: Attaleinae

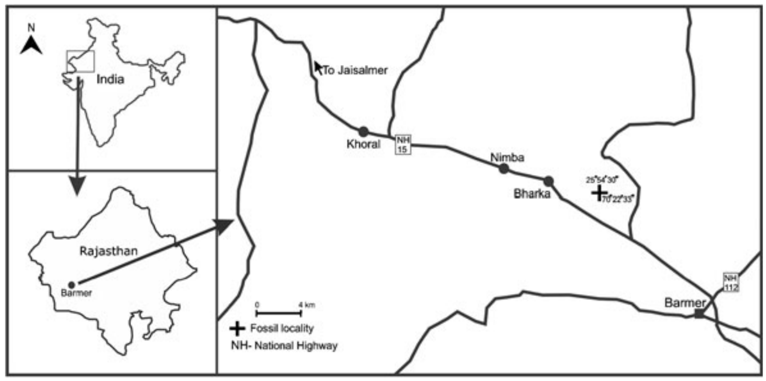

Figure 1. A map of the Barmer District of Rajasthan showing the fossil locality.

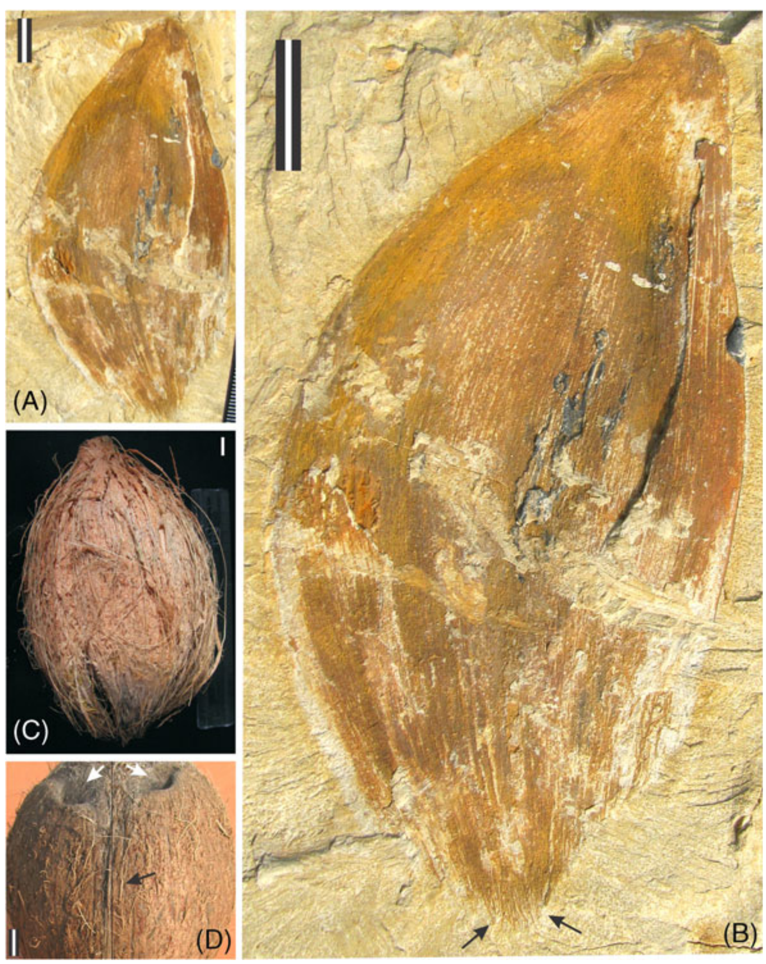

Figure 2. (**A**) Mesocarp of fossil fruit of *Cocos sahnii* in natural size. (**B**) Close up of the fossil fruit of *Cocos sahnii* showing shape and longitudinal fibres (marked by arrows). (**C**) Fruit of *Cocos nucifera*, showing resemblance to the fossil fruit in shape, size and having longitudinal fibres on the surface. (**D**) Endocarp of *Cocos nucifera* showing two eyes (marked by white arrows) and longitudinal ridge (marked by a black arrow). (Scale bar=1 cm)

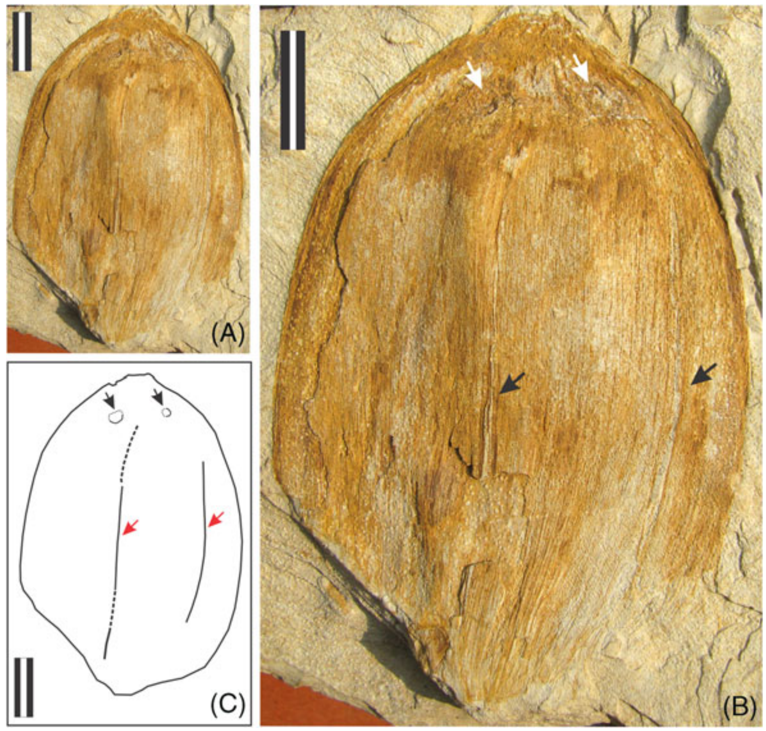

Figure 3. (**A**) Fossil endocarp of *Cocos sahnii* in natural size. (**B**) Close up of the fossil fruit showing presence of two 'eyes' (marked by white arrows) and longitudinal ridges on the surface (marked by black arrows). (**C**) Line diagram showing shape, size, presence of two 'eyes' (marked by black arrows) and longitudinal ridges (marked by red arrows) on the surface. (Scale bar=1 cm)

Genus: *Cocos* L.
Species: *Cocos sahnii* Kaul (figures 2 and 3)
Description: The study is based on two specimens, of which one consists of a mesocarp impression and the other an endocarp. Fruit a fibrous drupe (figure 2A–B), measuring 11.7 cm long and 5.8 cm wide, ovoid (figure 2A–B), asymmetrical; apex acute; mesocarp consisting of parallel, longitudinally oriented fibres (figure 2A–B); endocarp (shell) hard (figure 3A–B), 6 cm long and 4 cm wide, oval (figure 3A–B), two micropyles or 'eyes' visible at the apex (figure 3B–C), two longitudinally oriented ridges present on the surface (figure 3B–C); endosperm not preserved.
Holotype: Specimen no. BSIP 35466.
Paratype: Specimen no. BSIP 39951.
Horizon: Kapurdi Formation (Fuller's earth).
Locality: Kapurdi village, Barmer, Rajasthan.
Age: Early Eocene.
Material: Two well preserved specimens.
Affinities: The diagnostic features of the fossil such as ovoid shape, fibrous mesocarp, two micropyles or 'eyes' at the top and longitudinal ridges on the surface of endocarp show its close resemblance to the fruit of the modern Arecaceae genus *Cocos* (figure 2C, D) containing the single species *C. nucifera* (coconut) (Dransfield *et al.* 2005; Asmussen *et al.* 2006). The other genera of the subtribe Attaleinae are different from the fossil by having smaller fruit size. The modern species of *Cocos* has about 20 varieties which differ mainly in the size of the fruits (Mahabale 1978; Bourdeix *et al.* 2005).

The fossil record of coconuts includes reports from many parts of the world; the earliest record of *Cocos*-like fruits is from the lower Cenomanian of Argonne, France (Fliché 1896). From India, the oldest fossil is a stem described by Sahni (1946) as *Palmoxylon sundaram* from the Deccan Intertrappean beds of Madhya Pradesh. The age of the Intertrappean beds is now considered as late Maaschtrictian–Danian (Shukla *et al*. 1997). Palm fruits resembling *Cocos* were also described as *Palmocarpon cocoides* Mehrotra (1987) and *Cocos intertrappeansis* Patil and Upadhye (1984) from various Deccan Intertrappean localities of Madhya Pradesh. Tripathi *et al.* (1999) also described a *Cocos*-like fruit from Amarkantak, Madhya Pradesh, but the exact locality, horizon and age of the fossil were not mentioned. Later on, from the same area Mishra (2004) also described a fruit resembling *Cocos nucifera* as *Cocos pantii*. Apart from India, *Cocos*-like fruits have also been described from New Zealand, Australia and South America (table 2). Berry (1926) described *C. zeylandica* from the Pliocene of New

Table 2. Comparison of *Cocos sahnii* (Kaul) with the previously described fossil fruits of *Cocos*

Characters	*Cocos zeylandica*, Berry (1926)	*Cocos intertrappeansis* Patil and Upadhye (1984)	*Cocos nucifera* Rigby (1995)	*Cocos nucifera*-like fruit Tripathi *et al.* (1999)	*Cocos pantii*, Mishra (2004)	cf. *Cocos* sp., Gomez-Navarro *et al.* (2009)	*Cocos sahnii* (present fossil)
Epicarp	Not preserved	Present, 135 μm thick	Not preserved	Present, .5–2 mm wide	Present with fine longitudinal striations	Not preserved	Not preserved
Mesocarp	Fibrous	Fibrous, 1–2 mm thick	Not preserved	Fibrous, 2–5 mm thick	Fibrous, 2–5 mm thick	Not preserved	Fibrous
Shape	Prolate spheroid	Oval	?	Ovoid	Oval	Ovoid, asymmetric	Ovoid, asymmetric
Apex	?	?	?	?	?	Acute with stigmatic remains	Acute
Maximum width (mm)	25–30	50	95	60–100	80–130	150	58
Maximum length (mm)	3–5 cm	30	100	130	100–150	250	117
Endocarp	Preserved	Preserved	Preserved	Preserved	Preserved	Not preserved	Preserved
Longitudinal ridges	?	?	?	Preserved	3	1 preserved	2 preserved
Eyes	3	3 (?)	3	?	?	Not preserved	2

Zealand, but Couper (1952) dated them as Miocene and Balance *et al*. (1981) suggested they were associated with tsunami derived turbidities. Hayward *et al*. (1990) also reported late Oligocene New Zealand specimens, using them as evidence for warm conditions there. Rigby (1995) also described a fossil fruit resembling *Cocos nucifera* from the Pliocene of Australia, while Gomez-Navarro *et al.* (2009) described a *Cocos* fruit from the Palaeocene of Colombia. A comparative chart of these fossils and their characteristics is provided in table 2.

4. Palaeoclimatic implications

To reconstruct the past climate the best and reliable method for qualitative study is nearest living relative (NLR), which assumes that the climatic requirements of the fossils are generally similar to those of their modern counterparts (Feng *et al.* 2010; Bamford 2011; Mehrotra *et al*. 2011). Here we followed the same concept and found a drastic change in the environmental conditions of Rajasthan since the Palaeogene. The present-day climate of Rajasthan is characterized by low and erratic rainfall with extreme variation in the diurnal and annual temperature, low humidity and high wind velocity. The annual rainfall in the west of Aravalli Range varies from <10 cm to >40 cm and the vegetation is sparse in the desert region (Puri *et al.* 1964; Bhandari 1990; Sharma 2002).

The coconut palm is native to coastal areas (the littoral zone) of Southeast Asia (Malaysia, Indonesia, Philippines) and Melanesia, and has wide pantropical distribution, much of which is possibly anthropogenic (Harries 1990, 1992). It is a ubiquitous sight in all the tropical and subtropical regions occurring 23° north and south of the equator (figure 4) and thrives in areas with a mean annual rainfall of 1500–2500 mm and mean annual temperature 21–30°C (Chan and Elevitch 2006). This supports the hypothesis that the environmental conditions of the fossil locality were much better and favourable to support the growth of coconut trees. Moreover, the presence of evergreen taxa such as *Calophyllum* L., *Mesua ferrea* L. (Calophyllaceae) and *Garcinia* L. (Clusiaceae), which were described by Lakhanpal and Bose (1951) from the same formation, further supports the existence of warm and humid, possibly coastal conditions, during the Palaeogene, as compared to the present-day dry, desertic conditions in the region. The evergreen plant taxa (*Mesua ferrea*, *Garcinia*, *Calophyllum*, *Cocos*), along with crabs, fish, turtles and gastropods from the Kapurdi Formation suggest a lacustrine, or more probably lagoonal environments, as well as tropical conditions (DasGupta 1977; Rana *et al*. 2006).

The main cause of these marked environmental changes in the region was probably the uplift of the

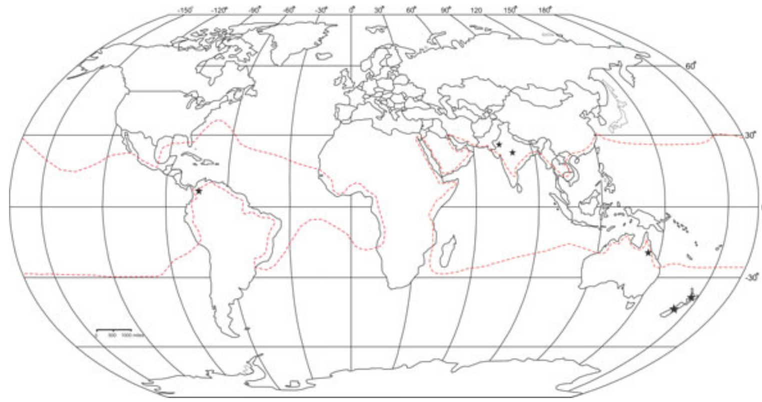

Figure 4. Present distribution of *Cocos nucifera* (dotted line) and fossil records showing resemblance to *Cocos* (stars).

Himalayas and formation of the Tibetan Plateau during the Cenozoic. The uplift of the Tibetan Plateau began in the Palaeogene about 50 Ma when the Indian subcontinent made initial contact with southern Asia (Chatterjee and Scotese 1999). This uplift was the cause of the general global cooling trend that has continued since that time. It has also been suggested that the monsoon system was initiated about 20 Ma once the uplift of the Tibetan Plateau exceeded a critical height (Harrison *et al.* 1992; Prell and Kutzbach 1992; Molnar *et al.* 1993). However, the main uplift only occurred about 8 Ma (Morley 2000), creating the fundamental changes in circulation patterns that resulted in the present-day Asian monsoons (Prell *et al.* 1992; Zhisheng *et al.* 2001). The Thar Desert in Rajasthan is the most populated desert of the world and is an easternmost extension of mid-latitude desert belts of Africa and western Asia (Deotare *et al.* 2004), but stable isotope data from a few ESR dates on calcretes indicate initiation of a monsoonal climate in the Thar during the Neogene at around 0.8 Ma (Deotare *et al.* 2004).

5. Origin and phytogeographical history of *Cocos nucifera*

The origin of coconut has always been a matter of interest, as it is a very common and ubiquitous tree in the tropical coastal regions, and there are two schools of thoughts about its origin. According to one school it was supposed to have an origin in the western Pacific islands including tropical Asia, Polynesia or Melanesia (Beccari 1963; Corner 1966; Moore 1973; Harries 1978), while the other school proposed a South American origin and a later range extension to the Indo-Pacific region (Guppy 1906; Cook 1910; Hahn 2002; Gunn 2004), based on its ability to disperse long distances over water. In prehistoric times, wild forms (*Niu kafa*) are believed to have been carried eastward on ocean currents to the tropical Pacific islands (Melanesia, Polynesia and Micronesia) and westward to coastal India, Sri Lanka, East Africa and tropical islands (e.g. Seychelles, Andaman, Mauritius) in the Indian Ocean.

The dispersal as well as cultivation of coconut is basically related with human history in the tropics, which is responsible for the geographical distribution of *C. nucifera* and its phenotypic diversity. However, this represents domestication and diversity rather than the origin (Harries 1990, 1992). The best argument put forward for the Melanesian origin is by Lepesme (1947), who drew attention to the high proportion of insects in the region that use coconuts as their primary host. It was further supported by the close biological association of *Birgos latro* L. (coconut crab) with coconut (Harries 1992). Although the fossil records of the genus cover almost all the continents that were once a part of the southern supercontinent Gondwana (i.e. India, Australia, New Zealand and South America) (figure 4) (Chatterjee and Scotese 1999), there is a need for more study to confirm if this represents the place of origin or centre of diversity for the genus.

6. Conclusions

The fossil fruit specimens collected from Early Eocene sediments of the Barmer District of Rajasthan show a resemblance to *Cocos nucifera* of the family Arecaceae, which has strong palaeoecological and palaeoclimatological significance as this palm now thrives only in coastal regions. Its presence indicates warm, humid, possibly coastal conditions during the Early Eocene in Rajasthan, in contrast to the present-day dry and desertic climatic conditions occurring there. This finding, along with earlier described evergreen taxa at the site, indicates that the climate of Rajasthan was much better and luxuriant to support the growth of these evergreen taxa. The drastic change in the climate might be the result of uplift of the Himalayas as well as the Tibetan Plateau and the onset of aridity during the late Pliocene time in the state.

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