



A juvenile *Nypa burtini* (Brongniart) Ettingshausen from the early Eocene of Southern Egypt

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Abstract

This study reports the first confirmed occurrence of *Nypa* Steck fruits and a leaf fragment from the early Eocene Dungul Formation in southwestern Aswan, Egypt. The fossils, assigned to *Nypa burtini* (Brongniart) Ettingshausen, extend the known distribution and morphological variation of the genus in North Africa, adding to the limited fossil record of mangrove palms in the region. The fruits exhibit notable size variation, a trait also observed in modern and fossil *Nypa*, which is influenced by biological, environmental, and geological factors and often leads to taxonomic misinterpretations. The geographic pattern of early *Nypa* fossils suggests a stronger Laurasian affinity, with the oldest and most abundant records concentrated in areas bordering the Tethys Ocean, such as Southeast Asia, India, and parts of Africa. This supports the view that *Nypa* originated in tropical coastal settings of Laurasia and dispersed globally during the Paleocene–Eocene. This finding provides new insights into the paleoecology and paleobiogeography of *Nypa* in North Africa, with the modern Southeast Asian distribution of *Nypa fruticans* representing the last remnant of a once-widespread lineage.

Key Words: Dungul Formation; Egypt; Mangrove; *Nypa*; Nypoideae; Paleogeography

Introduction

Nypa Steck is a monospecific genus of palm (Pole & Macphail, 1996). Being distinct from all the members of family Arecaceae, it has been set aside on its own in subfamily Nypoideae (Uhl & Dransfield, 1987). The single extant species, *Nypa fruticans* Wurmb, is the only mangrove palm in the world (Pole & Macphail, 1996; Wu *et al.*, 2024). It grows in estuarine or swampy waters, with a subterranean stem and large pinnate leaves reaching nine meters in length. It produces large woody drupes in a compact fruiting head. Its pollen is assigned to the genus *Spinizonocolpites* Muller (Collinson, 1993). Extant *Nypa* are restricted to Sri Lanka, Southeast Asia, the Philippines, Australia, and New Guinea (Dransfield *et al.*, 2008). It tends to thrive in brackish water environments, frequently forming broad zones beyond the edges of nearby mangroves or swamp forests. However, it is typically

absent from shorelines that experience strong wave action or hypersaline conditions (Tomlinson, 1986).

Nypa is represented in the fossil record by its fruits, frequently by its pollen, and only rarely by its leaves, rhizomes, and cuticle fragments (Pole & Macphail, 1996; Mehrotra *et al.*, 2003; Harley, 2006; Moreno-Dominguez *et al.*, 2016; Kathal *et al.*, 2017). Phylogenetically, the *Nypa* lineage represents one of the most ancient groups within the Arecaceae (Dransfield *et al.*, 2008), with its earliest pollen occurrence recorded from the Early Cretaceous (Martínez *et al.*, 2016). The genus attained its greatest diversity and abundance during the Eocene and subsequently experienced a progressive decline through the middle Miocene, likely as a consequence of global climatic deterioration (Gee, 2001; Dransfield *et al.*, 2008; Gómez-Navarro *et al.*, 2009; Kathal *et al.*, 2017). Fossil evidence of *Nypa* has been documented from both tropical and temperate regions across Africa, America, Asia, Australia, and several European localities (Moreno-Dominguez *et al.*, 2016), suggesting a pantropical distribution during the Paleogene and implying that the genus once extended far beyond its modern geographical range. The fossil record of *Nypa* provides critical insights into paleoclimatic reconstruction, particularly indicating deposition under warm, humid, and tidally influenced environmental conditions (Gee, 2001).

After numerous investigations, fossil fruits are now synonymized into a single species under the name *Nypa burtini* (Brongniart) Ettingshausen (Collinson, 1993). Only *N. australis* Pole & Macphail, described from the Eocene of Tasmania (Pole & Macphail, 1996), is peculiar from the other *Nypa* fossils and living species by the cuticle structure of the frond.

This study aims to report the first record of *Nypa* fruits and leaves from the early Eocene Dungul Formation in southwestern Aswan, Egypt. These fruits are the smallest *Nypa* fossil specimens recorded from Egypt so far, compared to previous records from the Danian to Eocene strata. Its unusually small size—comparable to that of the extant *Nypa fruticans*, which is typically smaller than fossil specimens—adds valuable insight into the morphological variation within *Nypa* fruits. The study also aims to integrate global *Nypa* macro- and microfossil records to understand better its stratigraphic range, past distribution, and the ancient environments where *Nypa* once grew as part of early mangrove ecosystems.

Materials and Methods

The present study is based on a single specimen consisting of a brownish-reddish quartz sandstone slab (measuring 26 × 18 cm in size) that was collected from the Eocene Dungul Formation in southwestern Aswan, Egypt (Fig. 1). It contains a mold and several casts of fruits that are highly attached to the rock matrix, together

with a poorly preserved part of a leaf impression lacking any organic matter. The specimen was examined macroscopically and photographed using a Nikon D7000 digital camera. The slab has been assigned a repository number (SE-RO.P01) and is stored in Prof. El-Saadawi's Paleobotany and Paleopalynology Lab., Botany Department, Faculty of Science, Ain Shams University.

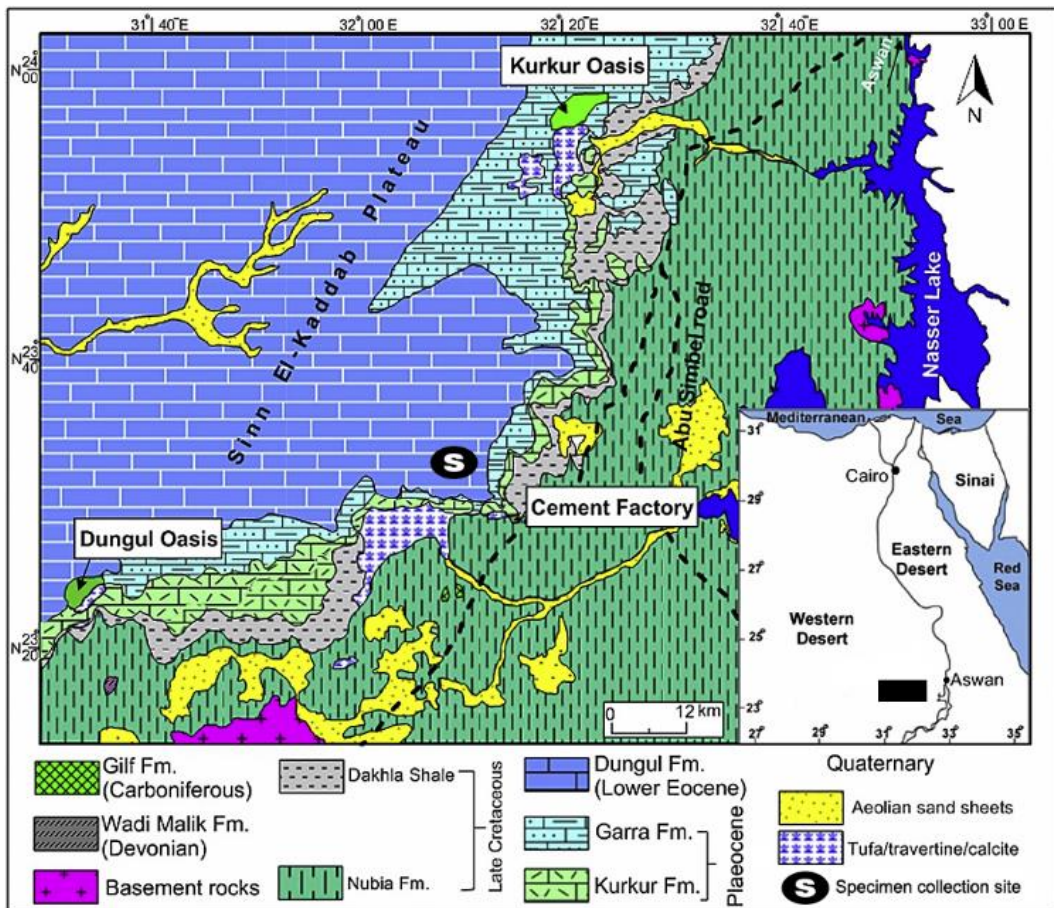


Fig. 1 Geological Map of Southern Egypt (Kurkur-Dungul area) showing the site from which the present specimen was collected (after Sallam *et al.*, 2018).

Geological setting

The Dungul Formation is a geological unit widely exposed in the Western Desert of Egypt, particularly in the Sinn El-Kaddab Plateau, Wadi Abu Ghurra, Naqb Dungul, and west of Kurkur Oasis. Its type locality is at Dungul Well in the Western Desert, where it was first described by Issawi (1969). The formation conformably overlies the Garra Formation and consists of two main lithological members. The lower Abu Ghurra Member is composed mainly of calcareous shale and siliceous claystone, reflecting deposition in relatively deeper marine settings (Ouda &

Tantawy, 1996; Abou Elmagd *et al.*, 2014, 2015). The upper Naqb Dungul Member is composed of fossil-rich reefal limestone with flinty shale, deposited in a warm, shallow, well-lit marine environment (Ouda & Tantawy, 1996). The age of the Dungul Formation has been assigned to the early Eocene based on foraminiferal markers, including *Nummulites deserti*, *N. irregularis*, and the oyster species *Spondylus alexandrae* (Issawi, 1969; Ouda & Tantawy, 1996).

Result

Systematic Paleobotany

Order: Arecales Bromhead, 1840

Family: Arecaceae Berchtold & Presl, 1820, nom. cons. (=Palmae Juss., nom. cons.)

Subfamily: Nypoideae Griffith, 1850

Genus *Nypa* Steck, 1757 [= *Nipa* Thunberg, 1782; *Nipadites* Bowerbank, 1840]

Nypa burtini (Brongniart, 1828) Ettingshausen, 1880 (Fig. 2, a–c)

Synonyms:

1828 *Cocos burtini* Brongniart, p. 121, 135.

1849 *Nipadites burtini* Brongniart, p. 88.

1867 *Apeibopsis gigantea* Fraas, S. 128.

1904 *Nipadites sickenbergeri* Bonnet, p. 499, figs. on p. 500, 501.

1939 *Rubiaceocarpum markgrafi* Kräusel, p. 108, pl. 1, figs. 19–24.

Description: Eight ovoid fruit casts and one mold are preserved on the collected slab as external impressions without organic material. The casts measure 23–40 mm in length and 10–26 mm in width, showing smooth endocarp surfaces with 2–4 longitudinal ridges extending from base to apex, with truncated bases. The mold measures 41 × 24 mm.

Remarks: Some earlier records have shown fossil fruits that resemble the young *Nypa* fruits described in this study, although they were not clearly identified. Barthel & Boettcher (1978) figured a fruit cast from the Claystone of Abu Ballas (Plate 12, Fig. 4), but did not provide a definitive identification. Similarly, Klitzsch & Lejal-Nicol (1984) documented a three-lobed capsule, tentatively assigned as? *Aceraceae* sp. (Plate 5, Fig. 4), from the Middle Cretaceous Abu Agag Formation near Aswan, Egypt. Later, Lejal-Nicol (1990) reported an indeterminate *Paulliniacarpum* sp. (Plate 29.4, Fig. 2) from the Upper Cretaceous Wadi Abu Agag, which looks very similar to the juvenile *Nypa* fruit in this study. While these specimens show notable morphological similarity, they are stratigraphically older than both the current material and the typical records

of *Nypa* fruits. Interestingly, two pollen species *Spinozonocolpites baculatus* Muller and *S. echinatus* Muller, which are linked to living *Nypa*, have been found in even older strata (discussed later). This suggests that *Nypa* or *Nypa*-like plants may have existed before the currently confirmed record based on fruit fossils. However, due to the limited ability to closely examine those older specimens, it remains uncertain whether they can be definitively identified as *Nypa*.

Indetermined Leaf Morphotype (Fig. 2, d)

Description: Linear, symmetrical lamina; 26 mm long, 5 mm wide; entire margin; apex and base not preserved; parallel venation; no additional diagnostic features, though interpreted as a monocot.

Comparisons and affinities

Fruits with an ovoid shape, prominent longitudinal ridges, and truncated bases suggest an affinity with the family Arecaceae, particularly the subfamily Nypoideae with its single monotypic genus *Nypa*, as this unique combination of features distinguishes them from other palm subfamilies. Fruit size variation in *Nypa* is extreme and arises mainly from biological factors, including carpel position within the syncarp, developmental differences, and environmental conditions in the modern species (Collinson, 1993; Mehrotra et al., 2003). In the case of fossil specimens, additional geological factors such as deformation due to the pressure of the strata or tectonic phenomena can greatly influence the morphological variations of these fossil fruits. These variations cause significant morphological diversity, making it difficult to establish consistent diagnostic traits (Collinson, 1993). Consequently, many researchers have misinterpreted this natural variation as evidence of separate species, resulting in the creation of numerous invalid names and increasing taxonomic confusion (Biosca & Via, 1987). The morphological characters of the fossil fruits under study are indicative of the subfamily Nypoideae. A small variance in size between the casts under study is observed, where the length and width vary from 23–40 mm and 10–26 mm respectively, (Table 1). Collectively, the fossil fruit casts described show a close affinity to the fruits of the extant *Nypa fruticans*.

The fossil records of *Nypa* leaves are meagre as they are not easily differentiated from other palm foliage (Mehrotra et al., 2003); however, the occurrence of the leaf fragment along with several *Nypa* fruit casts increases the probability that the leaf belongs to the same genus.

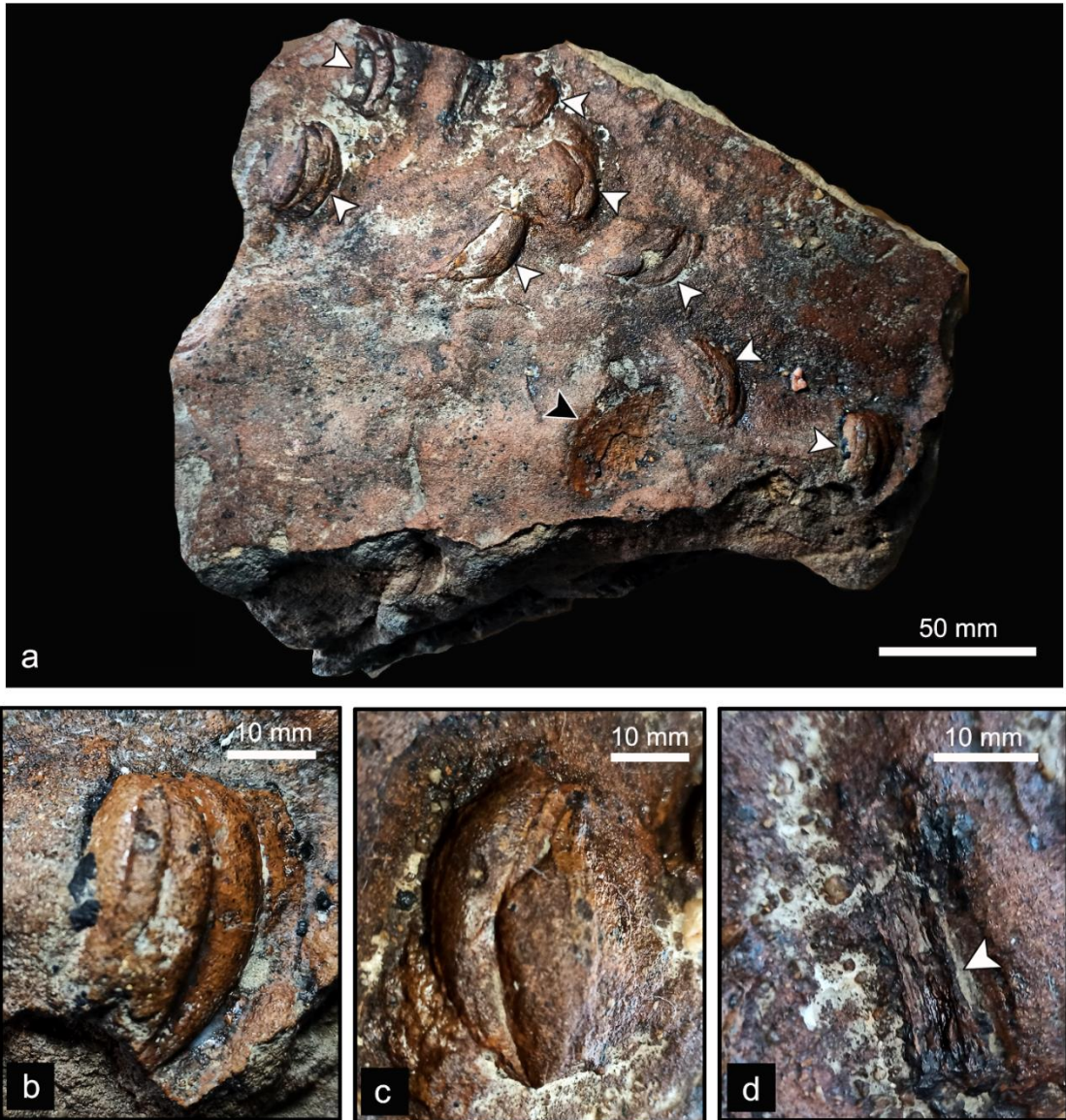


Fig. 2 a) Fossiliferous slab (SE-RO.P01) of reddish-brown quartz sandstone from the Dungul Formation (lower Eocene), containing eight casts of *Nypa burtini* fruits (white arrowheads), and one fruit mold (black arrowhead), all tightly embedded in the rock matrix. **b)** Close-up view of one ovoid fruit cast, showing a smooth endocarp surface with four prominent longitudinal ridges. **c)** Close-up view of a fruit mold, showing a single central furrow and two longitudinal ridges. **d)** A linear leaf fragment impression with entire margin and parallel venation (white arrowhead).

Table 1 Comparative measurements of fossil and extant *Nypa* fruit from various global localities.

Continent	Country	Reference	Age	Fruit length	Fruit width
Africa	Egypt	Bonnet 1904	Eocene	100 mm	80–90 mm
		Gregor & Hagn 1982	Eocene	26–113 mm	18–74 mm
		El-Soughier <i>et al.</i> 2011	Maastrichtian-Danian	31–97 mm	13–86 mm
		Current study	early Eocene	23–40 mm	10–26 mm
	Morocco	Herbig & Gregor 1990	Paleocene-Eocene	120–150 mm	100 mm
Asia	India	Lakhanpal 1952	Miocene	110 mm	65 mm
		Mehrotra <i>et al.</i> 2003	Oligocene-early Miocene	30–95 mm	25–58 mm
		Kaur 2022	Late Cretaceous	0.9–1.38 mm	0.6–0.86 mm
	Indonesia and Thailand	Collinson 1993	Modern (Extant)	50–120 mm	20–85 mm
Australia	Tasmania	Pole & Macphail 1996	Eocene	40–110 mm	10–50 mm
Europe	England	Bowerbank 1840	Eocene	10–180 mm	13–120 mm
	Spain	Moreno-Dominguez <i>et al.</i> 2016	Eocene	90–140 mm	45–90 mm
	Unknown	Tralau 1964	Eocene	40–150 mm	35–145 mm
South America	Colombia	Gómez-Navarro <i>et al.</i> 2009	Paleocene	84–119 mm	45–92 mm

Discussion

Previous records of Nypoideae in Egyptian strata

Several researchers have recorded fossil remains attributed to the subfamily Nypoideae or *Nypa* from different Egyptian strata. Fruit casts identified as *Nypa burtini* have been recovered from Cretaceous–Paleocene deposits at Bir Abu Munqar and along the Farafra–Dakhla road; Paleocene layers near Lake Nasser, and Eocene exposures at Gebel Atshan, the Quseir area, Gebel Giuschi, and Gebel Mokattam (Fraas, 1867; Bonnet, 1904; Fritel, 1922; Kräusel & Stromer, 1924; Kräusel, 1939; Chandler, 1954; Gregor & Hagn, 1982; Lejal-Nicol, 1987; El-Soughier *et al.*, 2011). In addition, El-Saadawi (2005) and El-Saadawi *et al.* (2018) reported unnamed *Nypa*-like rhizome casts resembling those of the extant mangrove palm *Nypa fruticans*, along with a *Nypa*-like leaf impression from the Eocene mangrove deposits at the Wadi Al-Hitan World Heritage site. These macrofossil records are consistent with the occurrence of two pollen species—*Spinizonocolpites echinatus* and *S. baculatus*—identical to those of extant *Nypa fruticans*, which have been reported

from subsurface Late Cretaceous Egyptian strata by several authors (e.g., Schrank, 1987; Hendriks *et al.*, 1990; Abdelkireem *et al.*, 1996), supporting the presence of Nypoideae in the region during that time.

The record of *Nypa* and Nypoideae fossils across Egyptian strata—from the Cretaceous to the Eocene—demonstrates that these mangrove palms were once widespread in ancient tropical coastlines of Egypt. The agreement between macrofossil and pollen data confirms the presence and ecological importance of *Nypa*-like palms in the region's past mangrove systems, reflecting warm, coastal, and humid paleoenvironmental conditions that later disappeared as climates cooled, and sea levels changed.

Stratigraphic range and geographic distribution of Nypoideae

Fossil evidence demonstrates that members of the subfamily Nypoideae, including the mangrove palm *Nypa*, once exhibited a broad global distribution and extensive stratigraphic range (Figs. 3, 4). Fossil remains, encompassing pollen, fruits, seeds, rhizomes, leaves, and cuticle fragments, have been documented from early Late Cretaceous to Miocene strata across Africa, Asia, Europe, the Americas, and Australia. The pollen record precedes other macrofossil evidence, with the earliest occurrence of *Spinizonocolpites echinatus*—morphologically identical to the pollen of extant *Nypa fruticans*—reported from the Barremian–Albian of Patagonia (White, 2008; Martínez *et al.*, 2016).

The genus attained its maximum global expansion during the Paleocene and Eocene, a period marked by elevated global temperatures and extensive coastal wetland systems. The co-occurrence of fruit and pollen fossils on several continents during this interval confirms that *Nypa* was once cosmopolitan. The Asian record is particularly rich, extending from the Albian to the Miocene and including significant assemblages from India, Malaysia, Indonesia, and Thailand. In Africa, notable occurrences span from the Campanian to the Miocene, while European records (Paleocene-Eocene) and those from the Americas (Cenomanian–Miocene) further demonstrate the genus's wide ecological tolerance. Although Australia yields fewer finds, its Eocene *Nypa australis* remains represent an important southern extension of the group. A pronounced decline in *Nypa* abundance toward the end of the Eocene corresponds with global climatic cooling and the contraction of tropical mangrove habitats (Gee, 1990; Baker *et al.*, 1998; Morley, 2000; Harley, 2006; Pan *et al.*, 2006).

The spatial and temporal distribution of early *Nypa* fossils supports a Laurasian origin rather than a Gondwanan one. The oldest and most abundant occurrences are associated with Tethyan coastal regions, including Southeast Asia, India (prior to its collision with Asia), and northern Africa. Fossils from South America and parts of

Africa appear later or in lower abundance, suggesting subsequent dispersal events. Consequently, current evidence favors a scenario in which *Nypa* originated in tropical coastal environments of the Tethyan realm, expanding globally during the Paleocene–Eocene greenhouse intervals.

At present, the only surviving species, *Nypa fruticans*, is restricted to the Indo-Malayan region, including Southeast Asia, Sri Lanka, the Ganges Delta, northern Australia, and adjacent islands. This limited modern distribution designates *Nypa* as a paleoendemic genus, representing the last remnant of a once globally widespread lineage of mangrove palms (Uhl & Dransfield, 1987; Dransfield *et al.*, 2008).

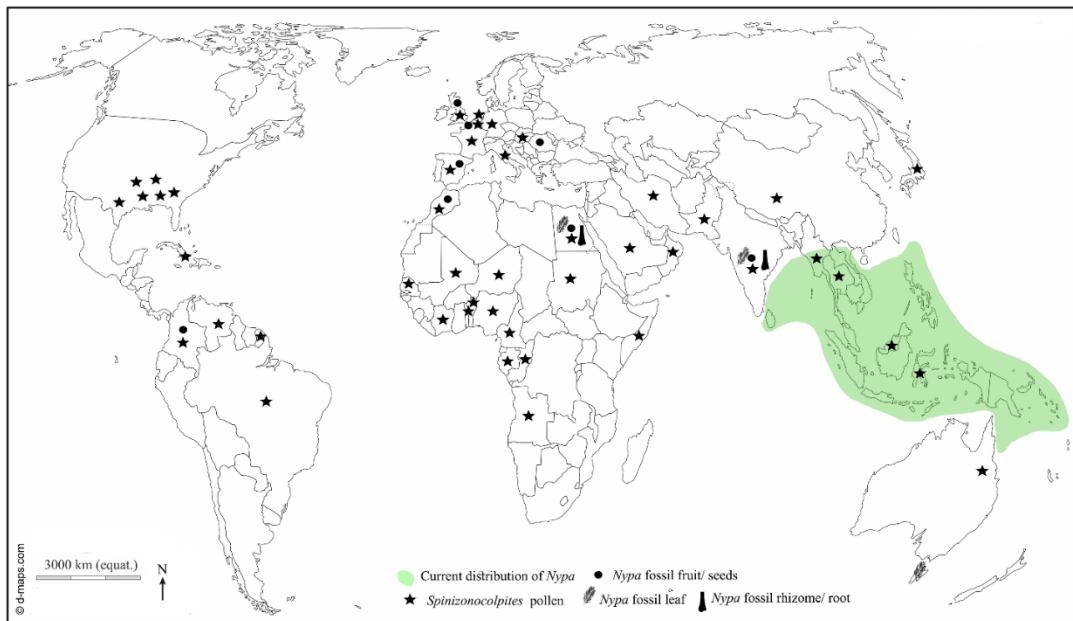


Fig. 3 Distribution of living and fossil Nypoideae (modern distribution adapted from Uhl and Dransfield, 1987).

Conclusions

The genus *Nypa*, represented today by the sole species *Nypa fruticans*, is a unique mangrove palm with a long and widespread fossil history, primarily from the Early Cretaceous to the Miocene. Despite its current confinement to the Indo-Pacific region, fossil evidence indicates that *Nypa* once had a pantropical distribution. This study documents the first confirmed record of *Nypa* fruits and a leaf fragment from the early Eocene Dungul Formation in southwestern Aswan, Egypt. The fossil fruit casts, assigned to *Nypa burtini*, are notable for their small size, resembling those of extant *N. fruticans*, and expanding the known morphological range of the genus. Stratigraphically, this record contributes to our understanding of the genus's persistence in North Africa during the early Eocene. Comparisons with global fossil occurrences of *Nypa* fruits and pollen, particularly *Spinizonocolpites*, support the interpretation of a warm, humid, and low-energy tidal environment during

deposition. The findings provide new insights into the paleoecology and paleobiogeography of *Nypa*, reinforcing its role as a key proxy for reconstructing past coastal mangrove ecosystems and climatic conditions.

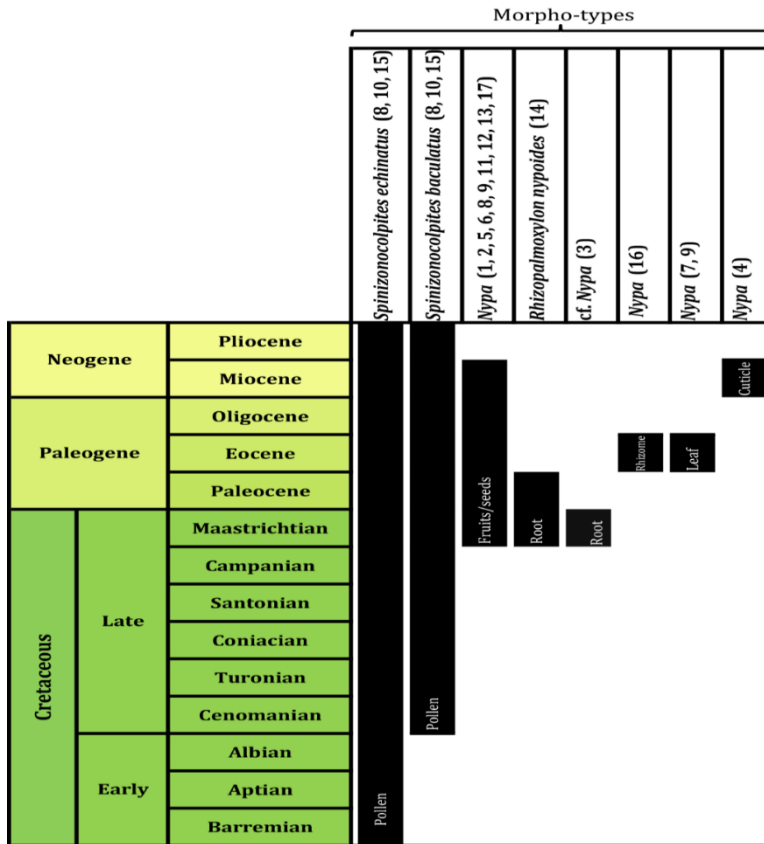


Fig. 4 Stratigraphic range of macro- and microfossil Nypoideae remains reported worldwide. 1- Lakhanpal, 1952; 2- Chandler, 1954; 3- Verma, 1974; 4- Kulkarni and Phadtare, 1980; 5- Gregor and Hagn, 1982; 6- Herbig and Gregor, 1990; 7- Pole and Macphail, 1996; 8- Gee, 2001; 9- Mehrotra *et al.*, 2003; 10- White, 2008; 11- Gómez-Navarro *et al.* 2009; 12- El-Soughier *et al.*, 2011; 13- Moreno-Dominguez *et al.*, 2016; 14- Kathal *et al.*, 2017; 15- Martínez *et al.*, 2017; 16- El-Saadawi *et al.*, 2018; 17- Kaur, 2022.

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