Diversity of *Nypa* in the Indian subcontinent : Late Cretaceous to Recent

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ABSTRACT

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Nypa, a monotypic genus of the family Arecaceae, is restricted to the mangrove ecosystem in the tropical coasts of south-east Asia and Australia. In the Indian subcontinent, it grows in Gangetic delta. Andamans and Sri Lanka. The fossil remains including fruits, roots, cuticles and pollen assigned to this genus are well-documented since Late Cretaceous to Pliocene having pantropical distribution. Fruits cf. Nypa, described under several species on the basis of size and shape variations, are now considered as a single species because of wide variations in the living plants. Similarly, the roots and cuticle described show affinity with modern Nypa fruticans. Fossil pollen attributed to the pollen of Nypa are referred to Spinizonocolpites Muller 1968 which is represented by 13 species in India. Out of them, 8 species and two specimens are found to be distinct by virtue of their morphological differences in exine and its sculptural type. Only one fossil species is similar, if not identical, with the pollen of Nypa fruitcans; other fossil pollen show considerable morphological variations but the pollen of extant Nypa do not show such variations. This suggests that Nypa fruticans is a relict species of a large group of early Nypa-complex prevalent in India during Late Cretaceous to Eccene but more diverse during Palaeocene. In the Palaeocene sediments of north-eastern India Spinizonocolpites is an important element both in terms of diversity and preservation and probably the richest record of the world. After Eocene, the fossil pollen records are represented by only one species — S. prominatus showing similarity with the pollen of Nypa fruticans. Thus it seems that the early Nypa-complex may have experimented with the various habitats and due to other successful competitors may have perished except its living counterpart which occupied only mangrove habitat.

Key-words—Palynology, Nypa, Spinizonocolpites, Diversity, Late Cretaceous-Palaeocene, India.

सारांश

अन्तिम क्रिटेशस से अद्यतन युग के बीच भारतीय उपमहाद्वीप में नाइपा की विविधता रमा शंकर सिंह

नाइपा, जो एरिकेसी वंश का एक एकलप्ररूपी है, दक्षिणी पूर्व एशिया तथा आस्ट्रेलिया के उष्णकिटबन्धीय समुद्र तट में मैग्रोव पारिस्थितिक तंत्र में विशेष रूप से प्रतिवन्धित है। भारतीय उपमहाद्वीप में यह गंगा के डेल्टा, अण्डमान तथा श्रीलंका में पाया जाता है। इस वंश के पादपाश्म, जिनके अन्तर्गत फल, मूल, उपचर्म तथा परागकण आते हैं, उत्तर क्रिटेशस में प्लायोसीन युग तक भली-भाँति प्रलेखित हैं तथा इनका सार्वउष्णकिटबन्धीय वितरण है। यद्यि अपने आकार तथा आमापन के कारण नाइपा के समतुल्य फलों को अनेक प्रजातियों के अन्तर्गत रखा गया है, परन्तु इनके जीवित पादपों में पाए जाने वाले परिवर्तनों के कारण ये अब एक एकल प्रजाति के रूप में जाने जाते हैं। इसी प्रकार वर्णित मूल एवं उपचर्म आधुनिक नाइपा फूटिकन्स के साथ सजातीयता प्रदर्शित करते हैं। नाइपा के परागकणों से सूचित पादपाश्म परागकण 'स्फीनीज़ोनोकॉल्पाइटीज' मुलर 1968 को संदर्भित है, जिसे भारत में 13 प्रादर्श अपने वास्यचोल तथा इसके तक्षित रूप की आकृतिक असमानताओं के कारण सुस्पष्ट रूप में प्राप्त हुए हैं। यह मात्र एक

पादपाश्म प्रजाति नाइपा फ्रूटिकन्स के कारण परागकण के साथ यदि समरूप नहीं है, तो अभिन्न अवश्य है। अन्य पादपाश्म परागकण आकारिकी में पर्याप्त परिवर्तन प्रदर्शित करते हैं, परन्तु विद्यमान नाइपा के परागकण इस प्रकार के परिवर्तन प्रदर्शित नहीं करते। इससे प्रस्तावित होता है कि अन्तिम क्रिटेशस से इओसीन युग के दौरान भारत में नाइपा फ्रूटिकन्स आरंभिक संकुल नाइपा के वृहद समूह में अविशिष्ट प्रजाति के रूप में विद्यमान हैं, किन्तु यह पेलियोसीन युग के दौरान अधिक बहुविध है। उत्तर पूर्वी भारत के पेलियोसीन अवसादों में स्पीनीजोनोकालपाइटीज़ विविधता एवं संरक्षण दोनों ही दृष्टिकोण से एक महत्वपूर्ण तत्व है तथा यह सम्भवतः विश्व का सम्पन्नतम अभिलेख है। इओसीन युग के पश्चात पादपाश्म परागकण अभिलेखों का प्रतिनिधित्व मात्र एक प्रजाति स्पीनीजोनोलपाइटीज़ प्रामिनेटस करती है, जो नाइपा फ्रूटिकन्स के परागकणों के साथ अभिन्नता प्रदर्शित करती है। ऐसा प्रतीत होता है कि आरम्भ्कि संकुल नाइपा ने विभिन्न आवासियों के साथ प्रयोग किये होंगे तथा अन्य प्रतिस्पर्धियों के कारण अपने जीवित सहभागियों के अतिरिक्त अन्य सभी नष्ट हो गए होंगे, जिन्होने मात्र मेंग्रोव आवास प्राप्त कर लिया होगा।

INTRODUCTION

TYPA fruticans van Wurmberg — It is an interesting L V to note that prior to the recognition of living *Nypa* from Asia by van Wurmberg in 1779, its fossil fruits were described from the Eocene deposits of London Clay by Parsons (1758). Nypa fruticans van Wurmberg is the only species of this genus possessing a distinct vegetative and reproductive system. It differs from other palms by lacking an upright stem and having dichotomously branched creeping stem, and its large pinnate leaves reaching up to nine meters in length. The fruits are large, woody drupes borne on a compact fruiting head. Despite its characteristic morphological features which make it easily identifiable there have been several systematic positions proposed for it. It is treated within the family Palmae (Arecaceae) by Endlicher (1837), Drude (1887), Hutchinson (1959), Beccari and Hooker in Hooker (1894). A subfamily of its own, Nypoideae, is advocated by Engler and Gilg (1924) which is followed by modern taxonomists, viz., Burret (1953), Potztal (1964), Dransfield and Uhl (1986) and Uhl (1972). A family status was proposed much earlier by Brongniart (1843) which was also followed by Tralau (1964) and Muller (1964).

Nypa fruticans occurs in a narrow restricted tropical area of south-east Asia (including India in Sunderbans and Andamans Island, Bangla Desh) to Australia in the mangrove ecosystem. The plant forms sometimes pure stands be-

cause of its rhizomatous branching habit and favours quite estuarine or shallow lagoons in which fresh water runs. It does not grow on the shores with much wave action and in hypersaline conditions (Tomlinson, 1986).

The present day ecology of *Nypa* is taken to deduce the palaeoenvironment of the past on the basis of occurrence of fossil remains of cf. *Nypa*. Such deductions should be worked out cautiously with the help of other parameters of sedimentology primarily because this does not consider the evolution of the species over such a large span of time and also probable adaptability of the plant in the different habitats.

Nypa fruiticans (Pl. 2, figs 2-4) — Pollen grain elliptic, 60-80 x 33-50 μm. Sulcus meridional. Exine tectate, spinose: spine 4-10 μm long, 5-6 μm wide at the base, 2-5 μm apart, base swollen with gradually tapering apices, tips pointed, thin, flexible, sometime curved forming hook-like structure. Spine attachment supraexinal. Interspinal area microreticulate, lumina about I μm wide, uniform, polygonal; muri I μm thick, tectum with 1-2 μm high bacula and a fine sole.

Fruits of *Nypa fruticans* are large, woody drupes produced in a compact fruiting head showing variations in its shape and size; interestingly the differences or variations are also connected by transitional forms even on the same plant.

PLATE 1

England Finder reading and magnification are given for each figure. The photographs illustrated are from the Palaeocene of Langrin Coalfield.

Meghalaya and the extant pollen are from the Sunderbans, West Bengal.

- Spinizonocolpites bulbospinosus Singh, Slide no. BSIP 9946. O44/ 0 x 1000.
- 2-4. SEM photomicrographs of the above species showing the gross morphology and detail exinal characters. 2 = x 750, 3 = x 1200 & 4 = x 1400.
- 5.6.8.9. S. indicus Singh, SEM photomicrographs showing the gross morphology and details of the exinc. 5 = x 750, 6 = x 1200, 8 = x 1500, 9 = x 700.
- S. indicus under light microscope. Slide no. BSIP 9979, U33/O v
- 10. Spinizonocolpites sp. Singh, Slide no. BSIP 9986, X 47/4 x 1000.
- 5. prominatus a part of the pollen showing the spinal morphology under SEM. x 750.
- Spinizonocolpites sp. (=Pollen type 2, in Singh 1990) showing the gemmae and the annulocolpate aperture. Slide no. BSIP 9949, R59/1, x 1000.

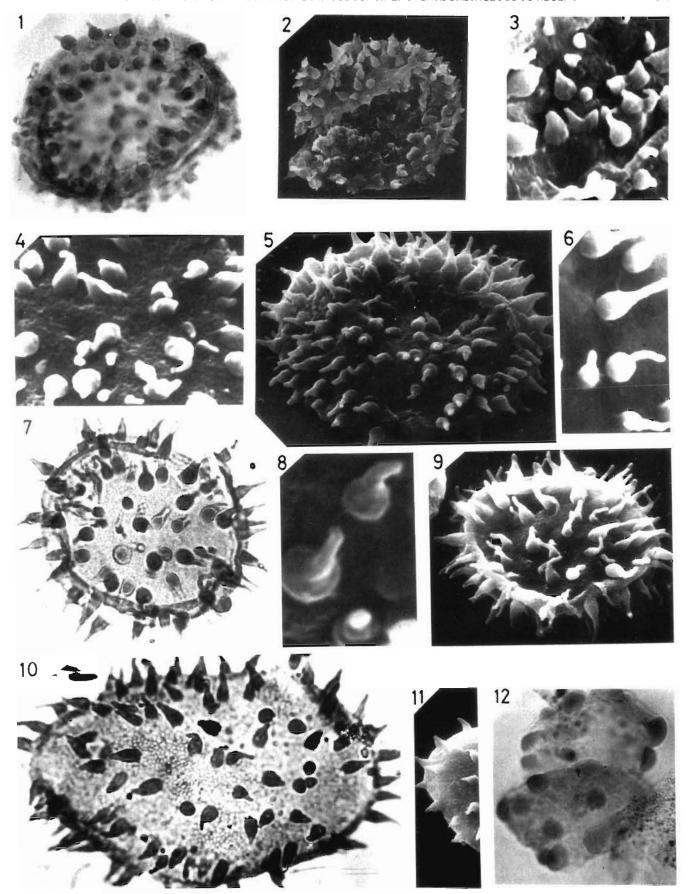


PLATE 1

FOSSIL RECORDS

Fossil cf. *Nypa* is well documented by fruits, pollen, roots and cuticles.

Fruits — Parsons (1758) described fossil fruits from the Eocene deposits of London Clay and since then numerous fossil fruits have been recorded from the Eocene deposits in Europe, Africa, America and Asia including India. A large number of species fossil fruits are instituted by various workers on the basis of minor variations in shape and size. In the Indian subcontinent fossil fruits cf. Nypa is recorded from the Deccan Intertrappean sediments exposed in Madhya Pradesh as Nipadites hindi Rode 1933, Nipa hindi (Rode) Sahni in Sahni & Rode 1937, Nipa Chitaley 1960, Nypa Nambudiri 1966 and from Maharashtra as Nipadites sp. Carter 1854. The Deccan Intertrappean beds were earlier considered to be Early Eocene but now most of the beds are considered to be Late Cretaceous (Sahni, 1990). From north-eastern India it is known from Tura Sandstone (Palaeocene but earlier considered as Eocene) of Garo Hills as Nipa Lakhanpal 1948, Sylhet Limestone (Eocene) of Khasi Hills as Nipadites sp. (Bhattacharyya, 1967) and from the Miocene sediments of Garo Hills as Nipa sahnii Lakhanpal 1952 (Table 1). In other parts of the world, all fossil fruits described are now being considered under a single species, viz., Nipa burtini (Brongniart) Ettingshausen (see Tralau, 1964), because of the fact that Nypa fruticans produces fruits with wide variations in shape and size even on the same plant. Thus, recognisation of diversity on the basis of fossil fruits of Nypa is rather impossible unless a finer morphological work is done.

Pollen — Extinct Pollen related to Nypa are referred to Spinizonocolpites Muller 1968 which is widely recorded from Late Cretaceous to Eocene sediments. From the Late Cretaceous it is known from South America (Germeraad et al., 1968), Venezuela and Colombia (Regali et al., 1974a, b), Brazil (Jardine & Magloire, 1963), Cameroon and Borneo (Muller, 1968), South Arabia (Schrank, 1984) and India (Venkatachala & Sharma, 1974; Baksi & Deb, 1981; Nandi, 1990). Its record from the Cretaceous-Tertiary transition comes from south-east Asia (Muller, 1968; Herngreen & Chlonova, 1981). In the Eocene sediments Spinizonocolpites is widely reported from North America, Europe, Australia, Malaysia, Pakistan and India (Table 1). During Miocene Nypa disap-

peared from the most parts of the world and almost reached its present status.

Root and Cuticles — Roots cf. Nypa is described from the Late Cretaceous sediments of Deccan Intertrappean beds (Verma, 1974) and cuticle cf. Nypa is also known from the Miocene of Ratnagiri of Maharashtra (Kulkarni & Phadtare, 1980).

DISCUSSION

Nypa had a wide geographical distribution during the past but at present grows in a narrowly restricted areas of tropical coasts of south-east Asia in mangrove ecosystem. Fossil representation of this genus is also well documented (Table 1). Several species of these fruits were instituted simply on the basis of variations in their size and shape, but in living Nypa such variations may be seen even in the same plant. Thus, it is very much possible that the fossil fruits of Nypa assigned to different fossil species actually belonged to one species of Nypa. But this needs further finer morphological studies of the fruits of both living as well as fossil. Similarly, fossil roots and cuticles assigned to various species of Nypa should be studied critically. Pollen of Nypa fruticans have characteristic morphology and do not show much variations and thus provides an opportunity to compare with the extinct pollen in detail. Spinizonocolpites prominatus (MacIntyre) Stover & Evans (= S. echinatus Muller 1968; Pl. 1, fig. 11; & Pl. 2, figs 5, 8-11) is the most common species reported from various parts of the world. In India, it ranges from Late Cretaceous to Neogene (Table 1). It has more or less similar morphology of the spines as that of the pollen of Nypa but the size of the pollen grains is generally smaller (average 50 µm). Nevertheless, the smaller size of the fossil pollen may be due to the loss of moisture during the fossilization. One of the closely related species with the above fossil pollen is S. indicus Singh 1990 (Pl. 1, figs 5-9) which has comparatively much longer (7-15 µm) and bulbous base of spines (Pl. 1, figs 6, 8). It is observed that S. indicus is a dominant element in the Tura Sandstone while S. prominatus is widely distributed species in the Tertiary sediments of India and abroad. Thus, it seems that either the above two species may have been produced by two ecotypes of the same species or possibly produced by two distinct species belong-

PLATE 2

- S. wodehousei Singh, Slide no. BSIP 9965, F68/3, x 1000.
- 2-3. Pollen of *Nypa fruticans* van Wurmberg, Specimens from the Sunderbans, x 1000.
- SEM photomicrograph of the pollen of Nypa fruticans showing the detail morphology (courtesy Dr K. Ambwani, BSIP). x 850.
- 5,8-10. SEM photomicrographs of *S. prominatus* showing the various types of spines and the gross morphology. $5 = x \cdot 1500$, $8 = x \cdot 1200$, $9 = x \cdot 750 \cdot \& \cdot 10 = x \cdot 1000$.
- 6.7 SEM photomicrographs of S. baculatus Muller, 6 = x + 1500, 7 = x + 1500

- x 750.
- Spinizonocolpites prominatus (MacIntyre) Stover & Evans, Slide no. BSIP 9949, Q33/3, x 1000.
- 12 S. intrarugulatus Muller, de Di Giacomo & van Erve. Slide no. BSIP 9973, O44/2, x 1000.
- S. baculatus Muller, Slide no. BSIP 9953, W28/3, x 500 & BSIP 9959, R33/O, x 500.
- 15. S. bulbospinosus Singh, Slide no. BSIP 9947, G46/4, x 500.

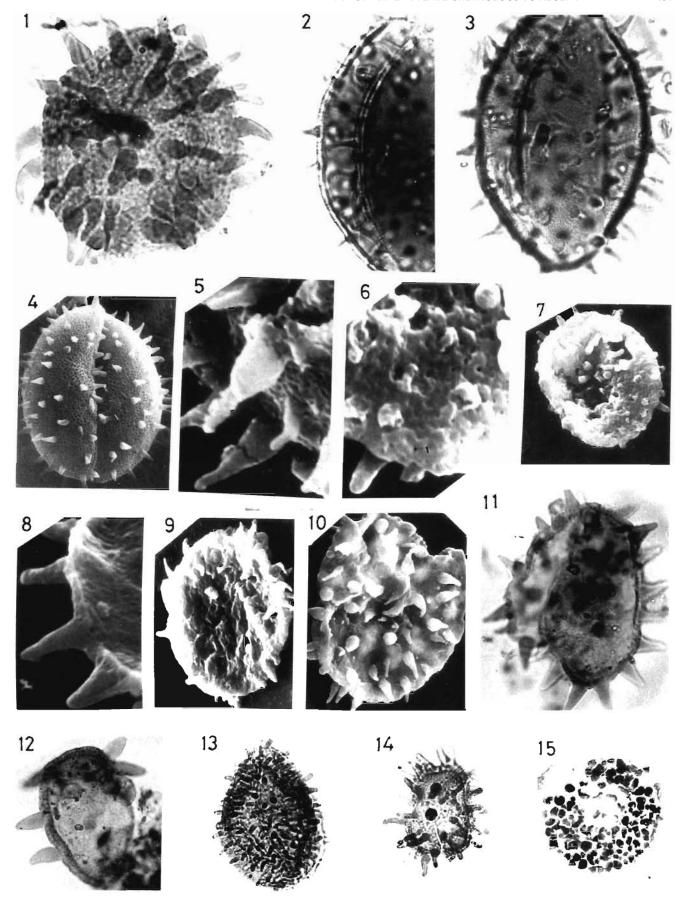


PLATE 2

Table 1 — Showing the distribution of species related to Nypa in the Indian sediments

Taxa	Late- Cretaceous	Palaeocene	Eocene	Oligocene	Neoger Miocene	Pliocene	Quaternary
POLLEN			<u> </u>				
Spinizonocolpites			_				
S. baculatus	IJ*, XII; 1, 13						
S. prominatus		27 15, 14, 7, 29, 3	30, 24, 6, 16, 8	3,12, 25, 1, 13	3, 18		
S. mulleri	II*; 1						
S. mucus	V*; 29						
S. decoris	V*; 29						
S. intrarugulatus		XII: 25					
S. bulbospinosus		XII.25					
S. indicus		XII; 25					
Spinizonocolpites sp. 1		XII; 25					
S. wodehousei		II*; 1X; 22, 1,	25				
S. brevispinous		11*; 1					
S. sahii			II*; I]			
Spinzonocolpites sp. 2			IV; 6	ĺ			
Spinizonocolpites sp. 3			I; 16	j			
S. quilonensis				,	X; 19, 20), 17, 26	
S. spinulosus					X; 17		
Spinizonocolpites sp. 4					X; 17		
FRUITS							
Nipa hindia	VII 21, 23						
Nipa sp. 1	VI; 5	Ī					
Nipadites compressure	VI; 23						
Nipadites sp.	VI; 4	7					
Nipadites sp. 3		_	XII; 2				
Nipadites sp. 4			VII; 10				
Nipa salmii		VII; 3		•	VII; 11		
ROOTS & CUTICLES			_				
Nypa (Root)	VI; 31	7					
Nypa (cuticle)		_			XI; 9		
NYPA FRUTICANS							XII, XIV

BASIN/AREAS — I= Arunachal Pradesh, II- Bengal, III= Cambay, IV= Kutch, V= Cauvery, VI= Decean interappean, VII= Garo Hills, VIII= Krishna-Godavari, IX= Neyveli (Cauvery), X= Kerla-Lakshadeep, XI= Ratnagiri (Maharashtra), XII= Khasi & Jaintia Hills XIII= Sunderbans, XIV= Andamans, * Borehole Data.

1= Baksi & Deb (1980), 2= Bhatacharyya (1967), 3= Bhattacharyya (1983), 4= Carter (1854), 5= Chitaley (1960), 6= Kar (1985), 7= Kar & Jain (1981), 8= Kar & Kumar (1986), 9= Kulkarni & Phadtare (1980), 10= Lakhanpal (1948), 11= Lakhanpal (1952), 12= Mandal (1987), 13= Mathur & Chopra (1987), 14= Nandi (1990), 15= Prakash *et al.* (1990), 16= Prasad & Dey (1986), 17= Ramanujam (1987), 18= Ramanujam & Rao (1977), 19= Rao & Ramanujam (1975), 20= Rao & Ramanujam (1978), 21= Rode (1933), 22= Dutta & Sah (1970), 23= Sahni & Rode (1937), 24= Sarma *et al.* (1984), 25= Singh (1990), 26= Srisarlam & Ramanujam (1982), 27= Venkatachala (1973), 28= Venkatachala & Rawat (1972), 29= Venkatachala & Sharma (1974), 30= Venkatachala & Sharma (1984), 31= Verma (1974).

ing to the genus Nypa. Two other fossil pollen species, viz., S. baculatus Muller 1968 (Pl. 2, figs 6-7, 13-14) and S. intrarugulatus Muller, de Di Giacomo & van Erve 1987 (Pl. 2, fig. 12) are closely related with each other in gross morphology having baculate sculptural elements but again differ in size range and exinal characters below the bacula. Though the baculate sculptural elements are absent in the pollen of Nypa, but similar general organization of the pollen as that of Nypa strongly suggests that the baculate type of the pollen were produced by plants related to Nypa. S. wodehousei Singh 1990 (Pl. 2, fig. 1) is characterised by "long beaked flask shaped" sculptural elements (8-18 µm) and wide lumina at the interspinal area, whereas S. bulbospinosus Singh 1990 (Pl. 1, figs 1-4; Pl. 2, fig. 15) also has sculptural elements but they are gemmae-like with small protruding spines. S. duplispinosus Ambwani 1993 described from the Palaeocene of north-eastern India seems as a specimen of S. bulbospinosus Singh 1990 having some fused spines. S. decoris Venkatachala & Sharma 1974 has thick exine at the base of each spine, such thickening do not occur in Nypa pollen. S. spinolosus Ramanujam 1987 is characterised with very small spines (about 1 μm long) but S. quilonensis Rao & Ramanujam 1975 can be related with the species of Salaca since the pollen have smaller sculptural elements (about 3 µm long) with psilate exine in between the spines. S. mucus Venkatachala & Sharma 1974 is characterised by curved tipped spines but in the original diagnosis the authors state that the apertural type is not clearly observed. Curving of spine may be due to artifact of compression (Babajide-Salami, 1985). Baksi and Deb (1980) illustrated S. mulleri, S. sahii and S. brevispinosus but neither provided any description nor diagnosis of any of the above species and hence all are invalid. But from the photographs it seems that S. mulleri is a specimen of S. intrarugulatus, whereas S. sahii resembles S. prominatus. The photograph of the S. brevispinosus is not clear to make any comment. Spinizonocolpites sp. described by Singh 1990 (Pl. 1, fig. 10) is exceptionally large (68-92 μm) with small spines (3-10 µm). Spinizonocolpites sp. (Kar, 1985) has spines slightly constricted at the middle and then broadened and gradually tapers towards the ends. "Pollen type 2" described in Singh 1990 from the Palaeocene possesses gemmae as sculptural element (Pl. 1, fig. 12) but the other characters are same as that of Spinizonocolpites and hence it also represents and species of early Nypa-complex. Spinizonocolpites sp. in Prasad and Dey (1986) and Spinizonocolpites sp. in Ramanujam and Rao (1977) are comparable to S. prominatus.

Thus, the fossil pollen species, viz., S. prominatus, S. baculatus, S. intrarugulatus, S. indicus, S. bulbospinosus, S. wodehousei, S. spinolosus, S. decoris, Spinizonocolpites sp., and "Pollen type 2" (Singh, 1990) instituted on the basis of morphological variations represent an early Nypa-complex comprising different species or subspecies of the genus. The highest diversity of early Nypa-complex is recorded in In-

dia during Palaeocene (Table 1) which suggests rapid evolution of this early *Nypa* complex. Most of the reports of *Nypa*complex are from the coastal areas which indicate to be the mangrove plants but their occurrence in the non-marine Deccan Intertrappean beds of central India associated with megafossils mostly belonging to other palms prompt to suggest that the early *Nypa* may have been growing in the habitats other than the mangrove, probably lacustrine environment. After Eocene it may be very much possible that due to competitive co-association of other floral elements the early *Nypa*-complex could not compete with and thus got extinct leaving the only relict species of the present in its specialized habitat. In Sunderbans, the genus *Nypa* being over exploited for its leaves used in thatching is in verge of extinction.

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