

## The Palms

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# A summary of fossil records for Arecaceae

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Of all monocotyledons the Arecaceae displays by far the richest fossil record, and there is an extensive literature. The earliest unequivocal fossil palm material probably dates from the early to mid Late Cretaceous (Turonian > Coniacian > Santonian). The records are geographically widespread and comprise a wide range of organs: leaves, cuticles, stems, rhizomes, roots, fruits, seeds, endocarps, rachillae, peduncles, inflorescences, individual flowers and pollen. For some of these organs records are rare while for others, such as leaves, stems and pollen, records are abundant. However, fossil material often lacks sufficient diagnostic detail to allow reasonable association with living palm taxa beyond, or even to, subfamilial level. Nevertheless, many fossil genera and numerous species have been described. A brief survey of palm fossil records is presented, and their taxonomy and morphological limitations are considered. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 151, 39–67.

**ADDITIONAL KEYWORDS:** Coniacian – global cooling events – palaeogeographical distribution – Santonian – Turonian.

## INTRODUCTION

The fossil record of Arecaceae is both rich and widespread. Chronologically, the expanding and retracting distribution of fossil palm records in higher latitudes has been an important indicator of global change, particularly cooling events during the early Miocene. Fossil records also show that the continent of Africa and the subcontinent of India once possessed much richer palm floras than at present. Leaves, stems and pollen are particularly abundant in the fossil record, but there are also numerous records of fruits and seeds, rhizomes and roots. Rarely, rachillae, inflorescences or individual flowers are recovered.

The earliest unequivocal fossils are from the late mid-Cretaceous to early Upper Cretaceous. These consist of costapalmate leaves: *Sabalites carolinensis* Berry (Berry, 1914a) from the late Coniacian–early Santonian of South Carolina to the Santonian of New Jersey (USA); *S. magothiensis* (Berry) Berry (Berry,

1905, 1911) and *Sabalites longirhachis* (Unger) J. Kvaček et Herman (Kvaček & Herman, 2004) from the Lower Campanian of Austria. Pinnate leaves are first described from the Lower Campanian of northern Montana (*Phoenicites* Brongniart; Crabtree, 1987). The earliest record of fossil stems, *Palmoxylon andegavense* Crié and *P. ligerinum* Crié (Crié, 1892), is purportedly from the Turonian of France while there is a slightly later record, *Palmoxylon cliffwoodensis* Berry, from the Coniacian–Santonian of New Jersey (Berry, 1916a). Fruits are first recorded from the Upper Cretaceous of Brazil (*Palmocarpon luisii*; Maury, 1930) and from the Early Palaeocene of Greenland (Koch, 1972). Records of *Nypa* fruits (*Nipadites*) are first found in the Palaeocene of the US Gulf Coast states, eastern Brazil (Dolianiti, 1955) and north-east Africa [for example, Chandler (1954); Gregor & Hagn (1982)]. Upper Cretaceous–Palaeocene rhizomes (*Rhizopalmoxylon huepaciense* Cevallos Ferriz & Ricalde-Moreno and *R. teguachachiense* Cevallos Ferriz & Ricalde-Moreno; Cevallos Ferriz & Ricalde-Moreno, 1995) are described from northern Mexico, while an inflorescence from the lower

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Maastrichtian of north-eastern Mexico is possibly the earliest record of an inflorescence structure so far described (Weber, 1978). *Spinizonocolpites*, widespread from the Maastrichtian (Gee, 1990; Morley, 2000), represents the earliest undisputed palm pollen, but by the Maastrichtian, other palm-like pollen types also appeared, notably *Mauritiidites* and *Longaperites* (Schrank, 1994).

By the late Cretaceous all major palm fossil categories are present, and from the earliest Tertiary (Palaeocene) up until the cooling events of the Miocene, fossil records for the Areaceae are extraordinarily rich and diverse. Nevertheless, for the majority of palm fossils, the lack of distinctive morphological variation in organs frequently limits the possibility of inferring affinity to taxonomic units below the family level. Pollen records are exceptionally numerous and problematic. There are over 50 fossil pollen genera with a clear or suspected affinity to palms. At the other end of the scale, almost all described fossil palm stems are included in the single genus *Palmoxylon*. In this paper, the main palm fossil categories and their genera are reviewed, and the extent to which relationships can be attributed is considered.

## THE FOSSIL GENERA (SEE ALSO APPENDICES 1 & 2)

### LEAVES, LEAF AXES, PETIOLES, ETC.

*Leaves:* *Amesoneuron* Goeppert, *Bactrites* Berry, \**Calamopsis* Heer, *Costapalma* Daghljan, \**Eolirion* Schenk, *Flabellaria* Sternberg, *Geonomites* Visiani, *Hemiphoenicites* Visiani, *Iriartites* Berry, *Kentites* Boureau, *Latanites* Massalongo, *Manicarites* Boureau, *Palmacites* Brongniart, \**Palmophyllum* Conwentz, \**Paloreodoxites* Knowlton, *Palustrapalma* Daghljan, *Phoenicites* Brongniart (also used for fruits), *Pritchardites* Boureau, \**Propalmophyllum* Lignier, *Sabalites* Saporta (also used for fruits), *Sabalophyllum* Bonde, \**Sanmiguelia* Brown, \**Serenopsis* Hollick [\* = doubtfully from a palm (Read & Hickey, 1972)].

*Leaf axes, petioles, etc.:* *Palmocaulon* (Deshpande) Menon, *Parapalmocaulon* Bonde, *Phoenicicaulon* Bonde, Kumbhojkar & Aher, *Sabalocaulon* Trivedi & Verma.

### Level of affinity possible between fossils and extant taxa

Read & Hickey (1972) defined five basic characteristics of extant palm leaves that can be used alone or in various combinations to recognize fossil palm leaves: (1) leaf blade and segments plicate (not always evident in fossil fragments of individual segments); (2) leaf blades pinnately veined and either simple or pinnately

compound in form, or palmately veined and palmatifid in form; (3) leaf segments with a strong, uniform mid-vein bounded on either side by two orders of parallel veins; (4) a ligule-like structure (hastula) at the apex of the petiole (usually only on the adaxial surface, rarely on both surfaces) where the radiating segments are inserted on the palmate blade; and (5) a well-organized primary costa (the attenuated continuation of the petiole into the blade of costapalmate and simple blades).

On the basis of the above characteristics Read & Hickey (1972) reviewed a considerable number of palm leaf fossil genera, and many were sunk into synonymy in their revised concept of acceptable genera. They maintained six genera for fossil leaves: *Amesoneuron*, *Bactrites*, *Sabalites*, *Palmacites*, *Phoenicites* and the modern genus *Phoenix*.

Features of the leaves of the modern genera *Phoenix* [induplicate plication, pinnate, lowermost (proximal) pinnae modified as spines (acanthophylls)] and *Sabal* (induplicate plication, shortly to prominently costapalmate) are probably the most distinctive characteristics encountered within the fossil palm leaf record. Consequently, these modern generic names, particularly *Phoenix*, are often applied to fossils. Therefore, Read & Hickey (1972) redefined the fossil genus *Phoenicites* as pinnate with reduplicate plication and lowermost pinnae not spine-like. Their taxonomic recommendation that *Phoenicites* should, henceforth, be reserved or applied to non-*Phoenix*-like pinnate leaves is, perhaps, more than a little confusing to the unwary. Almost as confusing is the case of *Sabalites* and *Sabal*. Read & Hickey (1972) did not propose the use of the modern genus *Sabal* for *Sabal*-like fossil palm leaves but later Daghljan (1978) described a new species of costapalmate fossil leaf as *Sabal dortchii* because 'on the basis of its gross form and cuticular anatomy . . . it is almost indistinguishable from those [leaves] of other species of . . . this extant genus.'

Preliminary studies in palm leaf fossils by Dilcher (1968) and Daghljan & Dilcher (1971) showed that further morphological distinction can be achieved by studying venation characteristics and, in organically intact leaves, cuticular material.

### Earliest records

Costapalmate leaves are known from the late Coniacian–early Santonian of South Carolina, USA [*Sabalites carolinensis* Berry (Berry, 1914a)], the Santonian of New Jersey, USA [*S. magothiensis* (Berry) Berry (Berry, 1905, 1911)] and the Lower Campanian of Austria [*Sabalites longirhachis* (Unger) J. Kvaček et Herman (Kvaček & Herman, 2004)].

Pinnate leaves, *Phoenicites* sp., are known from the Lower Campanian of northern Montana (Crabtree, 1987).

Two types of palm leaves, *Sabalites* sp. and *Phoenicites* sp., are reported from the lower Maastrichtian of north-eastern Mexico (Weber, 1978).

The fossil palm leaf, *Eolirion primigenium* Schenk, from the Cretaceous (Urgonian) of Austria (Schenk, 1869) was reported to be the earliest palm fossil record (Collinson, Boulter & Holmes, 1993). However, Read & Hickey (1972) expressed doubts that this leaf is from a palm. Furthermore, the Urgonian (which is not a chronostratigraphic time stage) set in the Barremian to earliest Aptian of south-eastern France, is a coral limestone facies ([http://www.cretaceousfossils.com/geological\\_time\\_scale.htm](http://www.cretaceousfossils.com/geological_time_scale.htm)).

#### STEMS, RHIZOMES AND ROOTS

*Stem 'wood':* *Palmoxylon* Schenk.

*Rhizomes:* *Rhizopalmoxylon* Felix.

*Bark and thorns:* *Spinophyllum* Huard.

#### *Level of affinity possible between fossils and extant taxa*

The limited number of genera for palm stems and rhizomes highlights the problem of defining differences in palm stem anatomy which support taxonomic or systematic definition. The problem of the artificial genus *Palmoxylon* was addressed by Mahabale (1958) and by Kaul (1960), but little resolution was achieved. Kaul (1960) commented that the comparative anatomy of living palm stems remained little understood and, furthermore, that the situation was becoming more and more problematic because of the increasingly large number of different palm fossils that were being discovered which, '... unfortunately ... are never found in organic connection [with one another] to give us some clue to their systematic position ...'. More recently, Tomlinson (1990) offered a concise explanation of the underlying problem: '... developmental features peculiar to the biology of the palm stem tend to transcend systematic differences. This is unfortunate because it means that the numerous fossil palm stems that have been discovered and described are difficult to relate to the modern knowledge of palm systematics.'

There are innumerable records of fossil palm stems, including many from the 19th century that were monographed in 'Fossil Palm Woods of the World' (Stenzel, 1904), in which the 43 species of *Palmoxylon* were divided into four groups: (A) *Mauritia*-like (four species) (B) *Corypha*-like (19 species) (C) *Cocos*-like (18 species) (D) 'Radices Palmarum' (roots; two species) plus a fifth group, *incertae sedis*, of four species. At that time, with the exception of *P. astrocaryoides* and *P. iriarteum* (Stenzel, 1904), none of the species names reflected any comparison to extant genera. One

hundred years later, the situation is much the same. Only occasionally is a new species of fossil palm wood described with an epithet suggesting generic affinity, for example, *P. livistonoides* (Prakash & Ambwani, 1980). Even more unusually, an affinity with the living species *Borassus aethiopicum* Mart. was suggested for *P. aschersoni* Schenk, from the lower Miocene of Libya (Louvet & Magnier, 1971).

#### *Earliest records*

The earliest records of fossil stems [*Palmoxylon andegavense* Crié and *P. ligerinum* Crié (Crié, 1892)] are, purportedly, from the Turonian of France and a later Coniacian–Santonian record from New Jersey (*Palmoxylon cliffwoodensis* Berry; Berry, 1916a). Upper Cretaceous–Palaeocene rhizomes (*Rhizopalmoxylon huepaciense* Cevallos Ferriz & Ricalde-Moreno and *R. teguachachiense* Cevallos Ferriz & Ricalde-Moreno; Cevallos Ferriz & Ricalde-Moreno, 1995) were described from northern Mexico.

#### FRUITS, ENDOCARPS AND SEEDS

*Fruits:* *Arecoideocarpon* Bonde, *Arecopsis* Fritel, *Astrocaryopsis* Fliche, *Attaleinites* Tuzson, *Burtinia* Endlicher, *Caryotispermum* Reid & Chandler, *Castellinia* Massalongo, *Fracastoria* Massalongo, *Hyphaeneocarpon* Bande, Prakash & Ambwani, *Nipa* Thunberg, *Nipadites* Bowerbank, *Palmocarpon* Miquel, *Palmospermum* Reid & Chandler, *Phoenicites* Brongniart (also used for leaves), *Sabalites* Saporta (also used for leaves).

#### *Level of affinity possible between fossils and extant taxa*

Among the more distinctive fossil fruits, endocarps or seeds are those comparable with *Nypa*, variously called *Burtinia*, *Castellinia*, *Fracastoria*, *Nipa*, *Nipadites* and *Nypa*. Today most records are referred to *Nypa* or *Nipadites*. Rendle (1894) included *Burtinia* in his revised circumscription of *Nipadites* (*N. burtini*), while Tralau (1964), in his revision of the fossil fruits, re-examined many specimens of *Castellinia* and *Fracastoria* and included them in *Nypa burtini* (Brongniart) Ettinghausen. Both Rendle (1894) and Tralau (1964) recognized that the plethora of species described for fossil *Nypa* fruits (cf. Bowerbank, 1840) was largely due to variability in size and form that they believed fell within the range of variation observed within a single infructescence of extant *Nypa fruticans* Wurmb.

*Phoenix* seeds (date 'stones') have been recorded from the Tertiary of eastern Texas as *Phoenicites occidentalis* (Berry, 1914b, 1924); from the middle Eocene of Germany (Geiseltal) as *Phoenix hercynica* (Mai,

1976) and from the lower Miocene of Central Europe as *Phoenix bohemica* (Bůžek, 1977). *Calamus daemonorops* fruits are recorded in Oligocene lignite deposits in the UK (Chandler, 1957).

Endocarps of *Cocos* were described as *C. zeylanica* from the Pliocene of New Zealand (Berry, 1926), as *C. sahnii* from the Miocene of India (Kaul, 1951) as *C. zeylanica* Berry from the Miocene of New Zealand (Balance, Gregory & Gibson, 1981) and as *C. intertrappea* from the Eocene of India (Patil & Upadhye, 1984). *Cocos nucifera* fruits are known from the Pliocene of Australia (Rigby, 1995), and *C. nucifera*-like fruits are known from the Tertiary of India (Tripathi, Mishra & Sharma, 1999).

Other 'coconuts' include *Palmocarpon acrocomioides* Hollick, *P. cetera* Hollick, *P. exemplare* Hollick and *Bactris pseudocuesco* Hollick from the Oligocene of Puerto Rico (Hollick, 1928), *Attalea* from the Upper Eocene of Florida (Berry, 1929) and possibly *Attaleinites* from the Oligocene of Hungary (Tuzson, 1913 – not seen). *Astrocaryopsis sanctae-manchildae* from the Cenomanian of France was described as having endocarps notably similar to those of some species of *Astrocaryum* (Fliche, 1894).

The unilocular ovoid fossil fruit *Hyphaeneocarpon indicum*, described by Bande, Prakash & Ambwani (1982), was considered by the authors definitely to belong with the 'Hyphaene alliance of the Borassoid group of palms'. *Hyphaeneocarpon aegyptiacum* (Vaudois-Miéja & Lejal-Nicol, 1987) was reported from the Aptian of Egypt. The fruit shape is more ovoid than pyriform, but fruits of modern *Hyphaene* are frequently very variable in shape, and modern fruits should be studied for careful comparison with the fossil (R. Bayton, pers. comm.). Furthermore, given the very early age for this material, it is not known whether this record has been thoroughly checked for accuracy of dating.

Many species of palm fruits and seeds have been described from the Lower Eocene London Clay flora: *Caryotispermum cantiense*, *Livistona* (?) *minima*, *Oncosperma* (?) *anglica*, *Sabal grandisperma*, *Serenoa eocenica*, *Corypha wilkinsonii*, ?*Trachycarpus* (Chandler, 1978). Also documented were five new species of *Palmospermum* (*P. excavatum*, *P. jenkinsi*; *P. parvum*, *P. minimum* and *P. pusillum*; Reid & Chandler, 1933); nine new species of *Palmospermum*, as well as a number of un-named species, were included in Chandler (1961). *Caryota* was considered by Reid & Chandler (1933) to be the 'nearest living ally' to *Caryotispermum* but distinct from it. Characters important for taxonomic separation of palm seeds recovered from the London Clay are shape and size, form and position of the ventral depression, hilum and chalaza; position of embryo; surface ornamentation and testa structure (Collinson, 1983).

#### Earliest records

The record of *Hyphaeneocarpon aegyptiacum* (Vaudois-Miéja & Lejal-Nicol, 1987) from the Aptian of Egypt is the oldest record of palm fruit. The deposits from which *Astrocaryopsis sanctae-manchildae* was extracted were dated as late Cenomanian (Fliche, 1894), which is considerably older than Aptian. *Palmocarpon luisii* (Maury, 1930) fossils are first recorded from the Upper Cretaceous of Brazil, and coryphoid fruits and seeds are described from the Early Palaeocene of Greenland (Koch, 1972). Records of *Nypa*-like fruits are first found in the Palaeocene of Brazil (Dolianiti, 1955) and north-east Africa (Chandler, 1954; Gregor & Hagn, 1982).

#### RACHILLAE, PEDUNCLES, INFLORESCENCES AND FLOWERS

*Flowers, inflorescences or rachillae: Arecoideostrobus* Bonde, *Palaeophoenix* Saporta, *Palaeorachis* Saporta, *Palaeospathe* Unger, *Palmanthium* Schimper, *Palmostrobus* Mahabálé, *Tuzsonia* Andreánszky.

*Peduncle(s): Palmostroboxylon arengoidum* Ambwani.

#### Level of affinity possible between fossils and extant taxa

The paucity of fossil flowers and inflorescences (or infructescences) has resulted in only a few form genera. Occasionally fossils can be assigned with some confidence to modern genera. For example, fossil palm flowers in mid to late Tertiary Dominican and Mexican amber were assigned to *Trithrinax* (*T. dominicana*) and *Socratea* (*S. brownii*) (Poinar, 2002).

A fossil flower from the Tertiary of Germany was assigned to *Phoenix* as *P. eichleri* (Conwentz, 1886), and le Marquis de Saporta (1889) described *Palaeorachis gracilis*, an inflorescence 'Peut-être mâle', as presumably being related to the leaf fossil *Sabal major* Unger.

It seems extraordinary that palm flowers, which are usually very small and often have tough 'woody' petals, are rarely recovered, especially given the huge production of flowers in many palms. Corner (1966) observed that male flowers '... are so cheap that they are discarded in enormous numbers to make a mulch round the base of the trunk.' Male palm flowers tend to abscise rapidly following anthesis and therefore fossil rachillae rarely have male flowers attached (Andreánszky, 1949). A rare exception is the recovery from the Eocene Messel oil shales of numerous (several thousands) compression fossils of palm flowers. Five types were identified, two of which were associated in inflorescences. Small fruits, infructescences and, less frequently, leaves have also been recovered at the site (Schaarschmidt & Wilde, 1986), which is probably the

largest single find of fossil palm flowers and flower-related fossils. Several palm taxa seem to be represented. The flowers are usually male or female; hermaphrodite flowers are less evident. Affinities are difficult to establish because of the rather generalized flower morphology. Furthermore, due to compression it is difficult or almost impossible to study the female organs. However, many of the male flowers have pollen-rich anthers from which it has been possible to establish differences in the morphology of the monosulcate grains (Harley, 1997). One type seems to be *Phoenix*-like, although the floral morphology does not strongly support this (J. Dransfield, pers. comm.); while the exine of the other type is similar to that of pollen in some species of two arecoid genera, *Dictyocaryum* and *Dypsis*.

#### Earliest records

A fruiting palm inflorescence compared with *Manicaria* (Weber, 1978) from the lower Maastrichtian of north-eastern Mexico is possibly the earliest record of a floral structure so far described. However, Weber (1978) stated that 'The fossil inflorescence will be described elsewhere as a new genus.' The publication of the new genus has not yet been traced. The record of *Palmstrobus* (Mahabalé, 1950) from the flood basalts of the Deccan Intertrappean, which are probably Maastrichtian in age (Vandamme *et al.*, 1991), is possibly of similar age. All other records appear to be Eocene.

#### MIXED ORGANS

##### *Calamus daemnorops* (Unger) Chandler

This modern generic name, with another modern generic name as a species epithet published by Chandler (1957), has been applied to a variety of calamoid-like structures including: fragments of fruiting axes, fruits, seeds, flowers, spines and spine bases and pollen (Chandler, 1957, 1963).

#### POLLEN

*Aglaoreidia* Erdtman, *Arecipites* Wodehouse, *Arengapollenites* Kar, *Calamipollenites* Sun Mengrong, *Calamuspollenites* Elsik, *Clavamonocolpites* González Guzmán, *Clavapalmaedites* Rao & Ramanujam, *Constantinsporis* Belsky, Boltenhagen & Potonié, *Couperipollis* Venkatachala & Kar, *Dicolpopollis* Pflanzl, *Disulcipollis* Krutsch, *Disulcites* Erdtman ex Potonié, *Dorreenipites* Biswas, *Echimonocolpites* van der Hammen & Garcia de Mutis, *Echimonoporopollis* Saxena, Khare & Misra, *Echimonoporopollis* Saxena, Khare & Misra, *Echimonoporopollis* Saxena, Khare & Misra, *Gemmamonocolpites* van der Hammen & Garcia Mutis, *Grimsdalea* Gemeraad, Hopping & Muller, *Jacobipollenites* Ramanujam, *Jusingipollis*

*Jansonius* & Hills, *Longapertites* Van Hoeken Klinkenberg, *Luminidites* Pocknall & Mildenhall, *Mauritiidites* Van Hoeken-Klinkenberg, *Monocolpites* Erdtman ex van der Hammen, *Monocolpopollenites* Pflug & Thomson, *Monosulcipollenites* Levet-Carette, *Monosulcites* Cookson ex Couper, *Neocouperipollis* Kar & Kumar, *Palmidites* Couper, *Palmaemargopollenites* Harley, *Palmaepites* Biswas, *Palmaepollenites* Potonié ex Potonié, *Paravuripollis* Rao & Ramanujam, *Piladiporocolpites* Kar, *Proxapertites* van der Hammen, *Psiladiporocolpites* Kar, *Psilamonocolpites* van der Hammen & Garcia de Mutis, *Quilonipollenites* Rao & Ramanujam, *Racemonocolpites* González Guzmán, *Retidiporocolpites* Kar *Retimonocolpites* Pierce, *Retitrilatiporites* Misra, Singh & Ramanujam, *Sabalpollenites* Thiergart, *Spinizonocolpites* Muller, *Spinomonosulcites* A. Singh & Misra, *Trichotomocolpites* van der Hammen, *Trichotomosulcites* Couper, *Trilatiporites* Ramanujam ex Potonié, *Victorisporis* Belsky, Boltenhagen & Potonié.

#### Level of affinity possible between fossils and extant taxa – selected examples (see Appendix 2 for more detail)

Most palms have simple tectate, monosulcate pollen (Harley, 1990). Nevertheless, there are some very distinctive exine and aperture types in the family (Harley & Baker, 2001), many of which are also found in fossil palm pollen.

*Arengapollenites* Kar (1985) from the Lower Eocene of India is monosulcate, ellipsoid (long axis *c.* 60 µm), with a sulcus the length of the long axis, intectate and sparsely spinose except along colpus margins where the spines are arranged so that they interlock on invagination of the sulcus. An affinity with *Arenga* pollen is widely accepted.

*Dicolpopollis* Pflanzl (1956), including *Disulcites*, *Disulcipollenites* and *Disulcipollis*, is a fossil pollen form highly comparable with some extant, equatorially disulcate palm pollen. Equatorially disulcate pollen occurs in eight extant calamoid genera: *Metroxylon*, *Plectocomia*, *Myrialepis*, *Plectocomiopsis*, *Calamus*, *Retispatha*, *Daemnorops* and *Ceratolobus*. The collective distribution of the extant genera includes South-east Asia, India, Burma, south China, Africa (humid tropics), New Guinea, Queensland and the Philippines. *Dicolpopollis* (Ediger, Bati & Alisan, 1990) has been recorded from the Palaeocene of Malaysia and has been widely recorded from the Eocene of northern India and Burma, France, Hungary and Germany. There are records from the Oligocene-Miocene of northern India, Turkey and England.

*Jacobipollis* Ramanujam (1966) has been described from the Indian Miocene. According to the revised description, based on additional material, the longest

axis is 40–100 µm, the pore is circular to slightly elongate 10–25 µm, and it has a ‘rugged’ tectate margo (Ramanujam, Reddy & Ramakrishna, 1998). The authors make convincing comparisons with *Borassodendron*; the only alternative in the palms would be *Ammandra* with closely similar pollen. *Borassodendron machadonis* pollen has been reported from the Pliocene-early Quaternary of the Mahakam Delta, Kalimantan by Caratini & Tissot (1985).

*Longapertites* Van Hoeken-Klinkenberg (1964) was originally described from the Maastrichtian of Nigeria. There are isolated examples of species with extended sulcate pollen among recent palms: Calamoidae (*Eugeissona*, *Eremospatha*), Coryphoideae (*Licuala* all spp.), and Arecoideae (*Areca*, *Pinanga* and *Hydriastele*). In the fossil literature records of *Longapertites* are numerous, and it is likely that a proportion of these are from palms. However, some *Longapertites* probably represent equatorial disulcate (disulculate) pollen with a broken distal ‘bridge’, as frequently happens in extant disulcate palm pollen. Extended sulcate pollen may have arisen via loss of the distal bridge (Harley & Baker, 2001) or, alternatively, via the extended sulcate model by development of a distal bridge.

*Mauritiidites* Van Hoeken-Klinkenberg (1964), like *Longapertites*, was originally described from the Maastrichtian of Nigeria. Spiny palm pollen is sporadic but widespread in the family, and the spines take many forms. Nowhere are the spines more bizarre than in the tropical South American subtribe Mauritiinae (*sensu* Dransfield *et al.*, 2005), where they are ‘rooted’ into depressions in the ectexine (for example, Ferguson & Harley, 1993; Jaramillo & Dilcher, 2001; Rull, 2001). However, only in *Mauritia* are there distinct swellings of the inner margin of the foot layer beneath each spine. The pollen grains are large, and the swellings are clearly visible in light microscopy. The fossil counterparts are easily recognizable, and the association with *Mauritia* is widely accepted. The palaeo-distribution in Africa (Salard-Cheboudeff, 1978, 1981; Schrank, 1994) and South America (Rull, 1998, 2001; Jaramillo & Dilcher, 2001), as opposed to its current restriction to South America, is of particular interest.

*Monocolpopollenites* Pflug & Thomson (Thomson & Pflug, 1953) was originally described from the Eocene of Germany. This genus has been widely adopted for fossil monosulcate pollen grains, and records are extensive and geographically widespread in the Tertiary. However, this taxon was erected strictly for distinctly asymmetric monosulcate monocot-like fossil pollen (e.g. Harley & Morley, 1995). Asymmetric monosulcate pollen is very common in the palms, especially in the Arecoideae but also, to a lesser extent, in the Coryphoideae. Unfortunately, the genus

has been over-used for dispersed fossil monosulcate pollen whether symmetric or asymmetric; therefore, records have to be checked carefully for palm-like qualities.

*Quilonipollenites* (Rao & Ramanujam, 1978) was originally described from the Neogene Quilon Beds of Kerala, southern India. The large (long axis: 50–55 µm) extended sulcate pollen, with a thick, semi tectate exine, and coarse reticulum with smaller lumina around the aperture margo, is now widely accepted as having an affinity with some extant species of *Eugeissona* (*E. tristis*, *E. utilis*) (Phadtare & Kulkarni, 1984). The palaeodistribution is of particular interest in view of the Early Tertiary collision of the Indian plate with Asia. Based on the fossil pollen records, the West Malesian genus *Eugeissona* is thought to be Indian in origin. In India, *Quilonipollenites* is recorded from the Neyveli lignites (Phadtare & Kulkarni, 1984) which are considered to be Early to middle Eocene in age (Saxena, 1992; Morley, 2000).

*Spinizonocolpites* Muller (1968) includes a considerable number of described species, but the most frequently encountered morphology is that of *S. echinatus* and *S. baculatus* Muller (1968), which were originally known from the Late Cretaceous (or Late Palaeocene; Morley, 2000) of Sarawak. The spiny zonosulcate pollen is usually found as one half of the original spheroidal grain, due to breakdown of the aperture membrane during fossilization. Pollen records are globally widespread from the Maastrichtian, reaching a crescendo in the Eocene, after which records gradually reduce until, by the Early Miocene, records are more or less restricted to South-east Asia; presumably in response to continental movement, and also to less favourable climate changes. *Spinizonocolpites* is widely accepted as ancestral to the modern genus *Nypa*, with a South-east Asian distribution. *Spinizonocolpites* fossils appear to represent more than one species, but extant *Nypa* is monotypic.

*Trichotomosulcites* Couper (1953) was originally described from the Cretaceous of New Zealand. The pollen was compared with *Phormium* (Phormiaceae), and given its type locality, this association is accepted. However, this pollen form is very common in the palms, especially in the arecoid palms, and also in the Asparagales, where there is a large clade of genera (Chase, Rudall & Conran, 1996) including *Phormium*, with trichomosulcate pollen. It may be time to consider the re-circumscription of *Trichotomosulcites* to embrace a wider application for fossil monocot pollen. In retrospect, it is amusing to reconsider the comment that, ‘many monosulcate pollen (Liliaceae, Palmae) contain abnormal trichotomosulcate pollen . . . a form genus for such atavistic, teratological forms is superfluous.’ (Kruttsch, 1970).

*Earliest records*

*Spinizonocolpites*, widespread from the Maastrichtian (Gee, 1990; Morley, 2000), represents the earliest undisputed palm pollen but, by the Maastrichtian, other palm-like pollen types had also appeared, notably *Mauritiidites* and *Longapertites* (Schrank, 1994).

## CONCLUSIONS

The Arecaceae are extremely well represented in the fossil record. Nevertheless, it is reasonable to suppose that, for any one geological epoch, the fossil record represents no more than a tantalizingly small proportion of the species which comprised the family during that time. By the Late Cretaceous, leaves, stems, fruits, inflorescences and pollen, unequivocally representing the Arecaceae, are present. By this time, within each organ category, there is a range of variation denoting a well established lineage, rather than a recently emerged family. Earliest unequivocal fossil records disallow speculation, and yet the earliest fossils, for example for pollen, *Spinizonocolpites* and *Mauritiidites* – both spiny but with strikingly different ultrastructure – cannot represent the most ancient palms. Therefore, if forms like these were already in place by the Maastrichtian, an earlier origin for Arecaceae is surely more likely.

The pollen of *Nenga gajah* J. Dransf. has a very unusual spinulose reticulum which is more or less detached from the underlying foot layer (Kessler & Harley, 2004). This phenomenon is intriguing, as it is reminiscent of similar reticulate ectexine pollen encountered in the earlier Cretaceous, such as the monosulcate *Brenneripollis* from the Albian of the North American Atlantic Coastal Plain and Northern Europe (Juhász & Góczán, 1985) and the inaperturate *Afropollis* from Africa (Doyle, Jardiné & Doerenkamp, 1982). Some records from the English Barremian–Aptian are of loosely reticulate, spinulose monosulcate pollen (Hughes, 1994) and are particularly reminiscent of *Nenga* pollen. Although an unequivocal association with *Nenga* or any other palm is ruled out, it would appear that pollen with a coarse, loosely attached, reticulum was more common in some early evolving angiosperm groups than in extant angiosperms.

Finally, the serendipitous nature of fossil recovery and the limits it imposes on the range and quantity of recovered fossils have to be considered. Cretaceous and Tertiary palaeobotany relies mainly on working with cores and bedding planes made available by natural events, or drilling, mining and quarrying. Pollen is less affected by these limitations than macro fossil organs but also shares a richer Northern than Southern Hemisphere record, a reflection of the more extensive drilling and mining activity of the Northern Hemisphere. Nevertheless, it is probably only a mat-

ter of time before unequivocal palm fossils predating the Turonian are discovered. Emberger (1960) suggested that there are palm stem fossils in the Upper Jurassic, but this may be a step too far.

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## APPENDIX 1

Fossil genera frequently encountered in the literature, excluding pollen.

## 1. Leaves, petioles &amp; cuticles

<i>Amesoneuron</i>	Goeppert, 1852	leaf (fragmentary) – overall leaf form unclear – fragments overlain in part by a dico
<i>Bactrites</i>	Berry, 1924	leaf fragments armed with small teeth on one margin.
<i>Calamopsis</i>	Heer, 1859	'Probably a cycad.' (Read & Hickey, 1972)
<i>Costapalma</i>	Daghlian, 1978	leaf (costapalmate)
<i>Eolirion</i>	Schenk, 1869	'pinnate leaves with no midveins. Not a palm.' (Read & Hickey, 1972). NB. Misspelled as <i>Elolirion</i> – p. 20 of original description in Schenk (1869)
<i>Flabellaria</i>	von Sternberg, 1820	leaf (palmate – no costa or extension of petiole into blade)
<i>Geonomites</i>	de Visiani, 1864	leaf – in synonymy of <i>Sabalites</i> (Read & Hickey, 1972)
<i>Haemiphoenicites</i>	de Visiani, 1864	leaf (pinnate)
<i>Iriartites</i>	Berry, 1919b	leaf fragments (pinnate) – 'a convenient form-genus for the remains of fossil palms that appear to belong to tribe Iriarteae, but whose exact generic identity is uncertain.'
<i>Kentites</i>	Bureau, 1896	leaf (pinnate)
<i>Latanites</i>	Massalongo, 1858	leaves sharing similarities with those of subtribe <i>Lataninae</i>
<i>Manicarites</i>	Bureau, 1896	leaf (pinnate)
<i>Palmacites</i>	Brongniart, 1822	leaf (palmate – no costa or extension of petiole into blade). NB. this generic name also used for palm stems – mostly pre <i>Palmoxyton</i> .
<i>Palmophyllum</i>	Conwentz 1886	leaf – questionable affinity to true palms (Read & Hickey, 1972)
<i>Paloreodoxites</i>	Knowlton 1930	leaf – questionable affinity to true palms (Read & Hickey, 1972)
<i>Palustrapalma</i>	Daghlian, 1978	leaf (palmate)
<i>Phoenicites</i>	Brongniart, 1828	leaf (pinnae reduplicate on adaxial surface – lowermost (proximal) pinnae not spine-like – Read & Hickey, 1972) NB. this generic name has also used for fruit – e.g. <i>Phoenicites occidentalis</i> (Berry, 1914a)
<i>Pritchardites</i>	Bureau, 1896	leaf (palmate)
<i>Propalmophyllum</i>	Lignier, 1895	leaf – questionable affinity to true palms (Read & Hickey, 1972)
<i>Sabalites</i>	le Marquis de Saporta, 1865	leaf (costapalmate). NB. this generic name has also been used for fruit
<i>Sabalophyllum</i>	Bonde, 1986	leaf segment
<i>Sanmiguelia</i>	Brown, 1956	leaf – questionable affinity to true palms (Read & Hickey, 1972)
<i>Serenopsis</i>	Hollick, 1893	'Probably a cone of <i>Williamsonia</i> .' (Read & Hickey, 1972)
<i>Palmocaulon</i>	(Deshpande) Menon, 1964	leaf petiole
<i>Parapalmocaulon</i>	Bonde, 1987	leaf petiole
<i>Phoenicicaulon</i>	Bonde, Kumbhojkar & Aher, 2000	'a sheathing leaf base'
<i>Sabalocaulon</i>	Trivedi & Verma, 1981	leaf petiole

Appendix 1 *Continued*

## 2. Stems, rhizomes &amp; roots

<i>Palmoxylon</i>	Schenk, 1882	stem
<i>Rhizopalmoxylon</i>	Felix, 1883	rhizome
<i>Spinophyllum</i>	Huard, 1967	'bark' & thorns

## 3. Fruits, endocarps &amp; seeds

<i>Arecoidocarpon</i>	Bonde, 1990	fruit
<i>Astrocaryopsis</i>	Fliche, 1894	fruit
<i>Attaleinites</i>	Tuzson, 1913	'a reproductive (?fruit)'
<i>Burtinia</i>	Endlicher, 1837	Nipa-like fruits
<i>Caryotispermum</i>	Reid & Chandler, 1933	seed – shares some similarities to <i>Caryota</i>
<i>Castellinia</i>	Massalongo, 1852	Nipa-like fruits
<i>Fracastoria</i>	Massalongo, 1858	Nipa-like fruits
<i>Hyphaeneocarpon</i>	Bande, Prakash & Ambwani, 1982	fruit
<i>Nipa</i>	Thunberg, 1782	fruits
<i>Nipadites</i>	Bowerbank, 1840	fruit
<i>Palmocarpon</i>	Miquel, 1853	carpel
<i>Palmospermum</i>	Reid & Chandler, 1933	seed
<i>Phoenicites</i>	Brongniart, 1828	this generic name also used for leaves
<i>Sabalites</i>	le Marquis de Saporta, 1865	NB. this generic name has also been used for leaves

## 4. Rhachillae, peduncles, inflorescences &amp; flowers

<i>Arecoideostrobos</i>	Bonde, 1996	rhachilla
<i>Palaeophoenix</i>	le Marquis de Saporta, 1878	inflorescence – the flowers – 'probablement mâles' not present
<i>Palaeorachis</i>	le Marquis de Saporta, 1889	rhachillae and inflorescences
<i>Palaeospatha</i>	Unger 1860	
<i>Palmanthium</i>	Schimper, 1870	flowers
<i>Palmostrobos</i>	Mahabalé, 1950	inflorescence
<i>Palmostroboxylon</i>	Ambwani, 1983–84	peduncle
<i>Tuzsonia</i>	Andreánsky, 1949	rhachilla and inflorescences

## Mixed organs

<i>Calamus daemonorops</i>	(Unger) Chandler, 1957	fragments of fruiting axes, fruits, seeds?, flowers, spines & spine bases, pollen
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## APPENDIX 2

Fossil pollen genera which have, or may have, an affinity to extant palms: column 1: genus & type species; column 2: taxonomic comments; column 3: age of type material; column 4: Original type comparison to an extant taxon; column 5: morphology of fossil & evaluation of palm affinity.

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Aglaoreidia</i> Erdtman, 1960 Type: <i>A. cyclops</i> Erdtman		Upper Eocene – Lower Oligocene, England	None	Monoporate slightly oblate-spheroidal (LA 40–55 µm), exine reticulate except in area surrounding pore. Comparable with pollen of <i>Borassodendron machadonis</i> , but smaller.
<i>Andreisporis</i> Belsky, Boltenhagen & Potonié, 1965 Type: <i>A. mariae</i> Belsky, Boltenhagen & Potonié	Named after one of the field work assistants working with the authors.	lower Senonian, Equatorial West Africa	... perhaps corresponds, in transitional terms, to ancient palms – <i>Problematicopalmites</i> (Belsky & Boltenhagen, 1963)	Subequatorial triporate, sometimes with cryptotrichotomosulcus, tectate, rounded triangular (LA 20–50 µm), planaperturate. Some similarity to <i>Constantinisporis</i> , but pores set further in from margin. No further comment on affinity.
<i>Arecipites</i> Wodehouse, 1933 Type: <i>A. punctatus</i> Wodehouse	Name reflects a general affinity with Areceaceae.	Middle Eocene, USA	<i>Phoenix dactylifera</i> L.	Small monosulcate grain (LA 23–25 µm). Possible coryphoid type palm.
<i>Arengapollenites</i> Kar, 1985 Type: <i>A. achinatus</i> Kar		Lower Eocene, India	Name reflects an affinity with <i>Arenga</i> .	Monosulcate, ellipsoid (LA c. 60 µm), sulcus length as long axis, sparsely spinose except along colpus margins where the spines are arranged so that they interlock on invagination of aperture. Affinity with <i>Arenga</i> accepted.
<i>Calamipollenites</i> Sun Mengrong, 1989 Type: <i>C. calamides</i> Sun Mengrong		Palaeocene, China	<i>Calamus</i>	Pollen in equatorial view the typical trapezium of invaginated disulcate pollen (LA 23–29 µm) distinct, finely reticulate sculpture. Most probably referable to calamoid palms, perhaps should be placed in the synonymy of <i>Dicolpopollis</i> .

<i>Calamuspollenites</i> Elsik in Stover, Elsik & Fairchild, 1966 Type: <i>C. pertusus</i> Elsik	Nichols, Tate Ames & Traverse (1973) placed this genus in synonymy with <i>Arecipites</i> and emended the type species to <i>A. pertusus</i> .	Lower Eocene, USA	<i>Calamus</i> Not disulcate, like pollen of <i>Calamus</i> .	Monosulcate, ellipsoid (LA 32–40 µm), sulcus length as long axis, tectate-punctate. A misleading name as the type specimen is monosulcate.
<i>Clavamonocolpites</i> González Guzmán, 1967 Type: <i>C. terrificus</i> González Guzmán		Eocene – Colombia	None	Monosulcate (LA 49–69 µm) with conspicuous and prominent clavate sculpture, probably intectate. Clavate monosulcate pollen occurs in <i>Caryota</i> , <i>Arenga</i> and <i>Pinanga</i> (intectate); and in <i>Pinanga</i> and <i>Oncosperma</i> (supratectate).
<i>Clavapalmaedites</i> Rao & Ramanujam, 1978 Type: <i>C. hammenii</i> Rao & Ramanujam	'closely similar to <i>Paravuripollis</i> except that this genus is zonalulcate' (Jansonius in Jansonius & Hills, 1980).	Miocene, India	Palms	Extended sulcate, ellipsoid (LA 25–31 µm), with suprareticulate clavae. Possibly a disulcate calamoid with fractured distal 'bridge', suprareticulate clavae are found in disulcate <i>Daemonorops</i> .
<i>Constantinispors</i> Belsky, Boltenhagen & Potonié, 1965 Type: <i>C. jacquei</i> Belsky, Boltenhagen & Potonié	Named after one of the field work assistants working with the authors.	lower Senonian, Equatorial West Africa	'... perhaps corresponds in transitional terms to ancient palms – <i>Problematicopalmites</i> ' Belsky & Boltenhagen (1963)	Subequatorial triporate with cryptotrichotomosulcus, circular equatorial outline (LA 20–50 µm), pores circular to oval. Some similarity to <i>Andreisporis</i> but pores closer to margin. No further comment on affinity.
<i>Couperipollis</i> Venkatachala & Kar, 1969 Type: <i>C. perspinosus</i> (Couper) Venkatachala & Kar Basionym: <i>Monosulcites perspinosus</i> Couper, 1953		Pliocene, New Zealand	None	Monosulcate (LA 34–44 µm) tectate, spinose, sulcus length as long axis. There are examples of monosulcate tectate, as well as intectate, spinose palm pollen. Spinose pollen ultrastructure is very varied in the Areaceae.

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Dicolpopollis</i> Pflanzl, 1956 Type: <i>D. kockelii</i> Pflanzl		?Miocene, Germany	<i>Calamus</i>	Equatorial disulcate, small to medium forms, reticulate, verrucate or granular exine. Widely accepted as disulcate <i>Calamus</i> type – however, there are eight palm genera which share this pollen type (see text).
<i>Disulcipollis</i> Krutzsch, 1970 Type: <i>D. cuddalorensis</i> (Ramanujam) Krutzsch Basionym: <i>Disulcites cuddalorensis</i> Ramanujam, 1966		Miocene, southern India	<i>Metroxylon</i>	Equatorial disulcate (LA 30–37 µm), smooth or finely punctate exine. Widely accepted as disulcate <i>Calamus</i> type – however, there are two other genera where equatorial psilate perforate disulcate pollen occur: <i>Calamus</i> & <i>Daemonorops</i> .
<i>Disulcites</i> Erdtman, 1947 ex Potonié, 1960 Type: <i>D. kalevensis</i> Potonié, 1960	Junior synonym of <i>Dicolpopollis</i> .	Eocene, Burma	None	In equatorial view the typical trapezium of invaginated disulcate pollen (LA 25–38 µm). Accepted as disulcate <i>Calamus</i> type – however, there are eight palm genera which share this pollen type.
<i>Dorreenipites</i> Biswas, 1962 Type: <i>D. platydesma</i> Biswas	Thanikaimoni <i>et al.</i> (1984) included <i>Dorreenipites</i> in the synonymy of <i>Trilatiporites</i> which has often been compared with <i>Sclerosperma</i> . However, Biswas (1962) does not compare <i>Dorreenipites</i> with <i>Sclerosperma</i> but with <i>Platydesma</i> (Rutaceae).	lower Middle Eocene, India	<i>Platydesma</i> (Rutaceae)	Heteropolar, triporate protrudent (LA 39 µm) suboblate, tectate. This pollen form which is closely similar to <i>Trilatiporites</i> is not considered to have an ancestral to <i>Sclerosperma</i> or any other palm (Harley & Baker 2001).

<p><i>Echimonocolpites</i> van der Hammen &amp; Garcia de Mutis, 1965 Type: <i>E. ruedae</i> (van der Hammen &amp; Garcia de Mutis Basonym: <i>Monocolpites ruedae</i> van der Hammen, 1954b</p>	<p><i>Echimonocolpites</i> Mathur 1966 a junior homonym. NB. <i>E. scabratus</i> Mathur, compared with spiny Nymphaeaceae pollen.</p>	<p>Maastrichtian, Colombia</p>	<p>Compared with <i>Mauritiidites</i>, but spines not embedded in exine, or with a swelling of the inner foot layer margin beneath each spine.</p>	<p>Small, monosulcate (colpus not very well defined), spinose (LA 27 µm). Could have an affinity with palms – there are a number of examples of monosulcate tectate, as well as imtectate, spinose palm pollen. (Spinose pollen ultrastructure is very varied in the Arecaceae).</p>
<p><i>Echimonoporopollis</i> Saxena, Khare &amp; Misra, 1991 Type: <i>E. grandiporus</i> Saxena, Khare &amp; Misra</p>	<p>Lower to Middle Eocene, India</p>	<p>None</p>	<p>Spherical to brevi ellipsoid (LA 30–46 µm), large circular to oval pore with unthickened margo, exine thin, tectate and spinose, interspinal exine punctate to microreticulate. Superficial resemblance to <i>Ravenea</i> (Ceroxyloideae) however, pollen of this genus has a thicker exine in relation to overall pollen size.</p>	
<p><i>Echimonophomonocolpites</i> González Guzmán, 1967 Type: <i>E. solitarius</i> González Guzmán</p>	<p>Eocene, Colombia</p>	<p>Monosulcate (LA 59–65 µm), with two/three types of sculptural elements, spines being the most frequent (1–4 µm), exine thin relative to overall size (1.5 µm). Possibly an affinity with palms – there are examples of monosulcate tectate, as well as intectate, spinose palm pollen. Spinose pollen ultrastructure is very varied in the Arecaceae. However, an endexine is remarked – if this observation is correct, it is not typical of palm pollen, or monocot pollen in general.</p>		

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Foveomonocolpites</i> Juhász & Góczán, 1985 Type: <i>F. pereensis</i> Juhász & Góczán		lower Cenomanian, Hungary	'a form of Palmae'	Monosulcate, sulcus as long axis (LA 77 µm), microfoveolate with thin exine cf. to overall size. Largest palm pollen, LA 70–90 µm, foveolate exines do occur – could be from an ancestral palm.
<i>Gemmamonocolpites</i> van der Hammen & Garcia Mutis, 1965 Type: <i>G. gemmatus</i> (van der Hammen) van der Hammen & Garcia Mutis Basionym: <i>Monocolpites gemmatus</i> van der Hammen, 1954b		Maastrichtian, Colombia	'differs from <i>Sabalpollenites</i> '	Monosulcate, irregularly micro gemmate (LA 22.5 µm). Small monosulcate pollen (LA <35 µm) occur commonly in Coryphoideae, and less frequently in Arecoideae – not possible to establish any clear affinity with palms.
<i>Grimsdalea</i> Gemeraad, Hopping & Muller, 1968 Type: <i>G. magnaclavata</i> Gemeraad, Hopping & Muller		Miocene – Pliocene, Trinidad	None	Aperture absent or indistinct (LA 40–62 µm), thin walled with finely baculate scabrate surface and very long (7–10 µm) widely spaced clavae, swollen apices, and bases sunken into locally thickened 'endexine'. This fossil often considered to have some affinity to <i>Spinizonocolpites</i> . However, the inwardly bulging 'endexine' towards the spines is much more reminiscent of the situation in <i>Mauritiidites</i> – perhaps the endexine is actually foot layer, and the fossil has an affinity to <i>Mauritia</i> and its relatives.

<p><i>Jacobipollenites</i> Ramanujam, 1966 Type: <i>J. magnificus</i> Ramanujam</p>	<p><i>Borassodendron</i> (Ramanujam <i>et al.</i>, 1998)</p>	<p>Miocene, southern India</p>	<p>Spheroidal (LA 38.5–48 µm), monoporate, pore 5–10 µm, semi tectate, coarsely reticulate. Revised description based on further material (Ramanujam <i>et al.</i>, 1998) – size, LA 40–100 µm, pore, circular to slightly elongate 10–25 µm, with a rugged tectate margo. The comparisons of Ramanujam <i>et al.</i> (1998) with <i>Borassodendron</i> are convincing, the only alternative in the palms would be <i>Ammandra</i> with closely similar pollen.</p>
<p><i>Jusingipollis</i> Jansonius &amp; Hills, 1987 Type: <i>J. microreticulata</i> (Juhász &amp; Góczán) Jansonius &amp; Hills Basionym: <i>Singipollis microreticulata</i> Juhász &amp; Góczán, 1985</p>	<p>None</p>	<p>middle Albian, Hungary</p>	<p>Trichotomosulcate (LA 16 µm), tectate, microfoveolate. Attention is drawn to this fossil mainly because the angiosperm-like trichotomosulcus is a feature of the pollen of many palms. However, the small size of the pollen suggests that it is possibly from an early dicotyledonous plant.</p>
<p><i>Longaperites</i> Van Hoeken Klinkenberg, 1964 Type: <i>L. marginatus</i> Van Hoeken Klinkenberg</p>	<p>Compared with <i>Dicolpopollis</i>, but accepting that apices nearest to the distal pollen have merged (in an evolutionary sense) to form an elongated sulcus.</p>	<p>Maastrichtian, Nigeria</p>	<p>There are isolated examples of species with extended sulcate pollen in recent palms – Calamoideae (<i>Eugieissona</i>, <i>Eremospatha</i>); Coryphoideae (<i>Licuala</i> all spp.); Arecoideae (<i>Areca</i>, <i>Pinanga</i>, <i>Hydriastele</i>). In the fossil literature records of <i>Longaperites</i> are numerous and it is very likely that many of these are from ancestral palms, but are actually disulcate pollen with a broken distal 'bridge'.</p>

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Luminidites</i> Pocknall & Mildenhall, 1984 Type: <i>L. reticulatus</i> (Couper) Pocknall & Mildenhall Basionym: <i>Phormium reticulatum</i> Couper, 1960		Miocene, New Zealand	None	Trichotomosulcate, subcircular to sub triangular, coarsely reticulate, but around margo or even generally on distal side, perforate. In palms coarsely reticulate trichotomosulcate pollen grains are known for <i>Ceroxylon</i> , <i>Pinanga</i> & <i>Hydriastele</i> .
<i>Mauritiidites</i> Van Hoeken-Klinkenberg, 1964 Type: <i>M. crassibaculatus</i> Van Hoeken-Klinkenberg		Maastrichtian, Nigeria	<i>Mauritia</i>	Monosulcate, spinose, sulcus as long axis (LA 63–65 µm), spines deeply rooted in ectexine, swelling of the inner margin of the foot layer beneath each spine. Association with <i>Mauritia</i> accepted – this is the only one of the three genera in subtribe Mauritiinae (Lepidocarpaceae: Calamoideae) with embedded spines where there are also swellings of the inner face of the foot layer below the spines.
<i>Monocolpites</i> Erdtman, 1947 ex van der Hammen, 1954b Type: <i>M. longicolpatus</i> van der Hammen, 1956 (first designation)	The holotype of the type species is a recent pollen grain of <i>Orthosanthus chimboraensis</i> (HBK) Baker (Iridaceae) thus <i>Monocolpites</i> , by the designation of the type species, is made illegitimate and a later synonym of <i>Orthosanthus</i> (Jansonius & Hills 1976). In Erdtman (1947) <i>nomen nudum</i>			Monosulcate pollen.

<p><i>Monocolpopities</i> Biswas, 1962</p> <p><i>Monocolpopollenites</i> Pflug &amp; Thomson in Thomson &amp; Pflug, 1953</p> <p>Type: <i>M. tranquilus</i> (Potonié) Thomson &amp; Pflug</p> <p>Basionym: <i>Pollenites tranquilus</i> Potonié, 1934</p>	<p>No type species, no diagnosis, therefore <i>nomen nudum</i>.</p>	<p>Originally Eocene, Germany – however, a widely adopted genus for asymmetric monosulcate fossil pollen grains, and records extensive, and widespread in the Tertiary.</p>	<p>Originally none, but now widely accepted as palm-like. However, the genus has been widely used, and often misapplied, over the years for monosulcate pollen generally, with inattention to the asymmetric form of the type species.</p>	<p>Monosulcate pollen.</p>
<p><i>Monosulcipollenites</i> Levet-Carette, 1964</p> <p>Type: <i>M. minimus</i> (Cookson ex Couper) Levet-Carette</p> <p>Basionym: <i>Monosulcites minimus</i> Cookson ex Couper, 1953</p> <p><i>Monosulcites</i> Cookson ex Couper, 1953</p> <p>Type: <i>M. minimus</i> Cookson ex Couper</p>	<p>Obligate junior synonym of <i>Monosulcites</i> with which it shares the same type species.</p>	<p>?Lower Tertiary [Palaeocene], New Zealand</p>	<p>Gingkoales</p>	<p>Monosulcate pollen.</p>
<p><i>Monosulcites</i> Cookson ex Couper, 1953</p> <p>Type: <i>M. minimus</i> Cookson ex Couper</p>	<p>Monosulcate, elliptic in outline (LA 29–34 µm), strong exine. Small monosulcate pollen (LA &lt;35 µm) occur commonly in Coryphoideae, and less frequently in Arecoideae – not possible to form strong conclusions regarding affinity.</p>	<p>Monosulcate, generally asymmetric with regard to overall shape, and often also in relation to aperture shape, aperture usually slightly shorter than long axis. Tectate and, usually, psilate, perforate finely rugulate. Original size given as 24 µm, however, Nichols <i>et al.</i> (1973) suggest a range of 20–50 µm, which is more realistic. Strictly this taxon was erected for distinctly asymmetric monosulcate monocot-like fossil pollen – as such it is decidedly palm-like – especially Arecoideae or, to a lesser extent, Coryphoideae.</p>	<p>Monosulcate pollen.</p>	

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Neocouperipollis</i> Kar & Kumar, 1986 Type: <i>N. kutchensis</i> (Venkatachala & Kar) Kar & Kumar Basionym: <i>Couperipollis kutchensis</i> Venkatachala & Kar, 1969		Lower Eocene, India	Correctly compared unfavourably to spine type and density in <i>Arengapollenites</i> .	Monosulcate, sulcus length as long axis, brevi ellipsoid (LA 35–65 µm), spines strong with bulbous bases and pointed tips (up to 5 µm). Not clear whether pollen tectate or intectate. An affinity with palms not obvious, but should not be entirely ruled out.
<i>Palmaemargopollenites</i> Harley, 1997 Type: <i>P. fossperforatus</i> Harley		Eocene oil shales, Messel, Germany	Pollen from anthers <i>in situ</i> in fossil palm flowers.	Ellipsoid or broadly ellipsoid monosulcate pollen grains (LA 20–35 µm). Sulcus slightly shorter than long axis, tectate or semi tectate, tectum of sulcus margins differentiated from non-marginate tectum which may be punctate, perforate, microslits, fossulate, microfossulate, rugulate, cerebroid, insulate, foveolate, or finely reticulate.
<i>Palmaepites</i> Biswas, 1962 Type: <i>P. eocenica</i> Biswas		Lower – Middle Eocene, India	Arecaceae * <i>Jessenia bataua</i> , <i>Juania australis</i> (* <i>Jessenia</i> included in <i>Oenocarpus</i> – Dransfield <i>et al.</i> , 2005).	Monosulcate, sulcus slightly shorter than long axis, exine psilate-perforate, thin (LA 36 µm). Common and characteristic in the deposits where it is found. Could well be a palm – but particular associations with <i>Jessenia</i> or <i>Juania</i> seem unfounded.
<i>Palmaepollenites</i> Potonié, 1951 ex Potonié, 1958 Type: <i>P. tranquilus</i> (Potonié) Potonié Basionym: <i>Pollenites tranquilus</i> Potonié, 1934	Obligata junior synonym of <i>Monocolpopollenites</i> (they share same type species)	Eocene, Germany		Asymmetric monosulcate pollen (LA c. 24 µm).

<p><i>Palmidites</i> Couper, 1953 Type: <i>P. maximus</i> Couper</p>	<p>Earlier Chitaley (1951) had suggested this generic name as a <i>nomen nudum</i> section of <i>Monosulcites</i></p>	<p>Pliocene, New Zealand</p>	<p>'palmaceous'</p>	<p>Monosulcate (LA 50–88 µm) sulcus length as long axis, psilate perforate. If a palm affinity is correct then it is most likely to be with ceroxylod or arecoid palms.</p>
<p><i>Parauripollis</i> Rao &amp; Ramanujam, 1978 Type: <i>P. mulleri</i> Rao &amp; Ramanujam</p>	<p>Correctly compared unfavourably to <i>Spinizonocolpites</i>.</p>	<p>Miocene (–Pliocene?), India</p>	<p>Correctly compared unfavourably to <i>Spinizonocolpites</i>.</p>	<p>Ellipsoid and zonosulcate, the aperture divides the grain into two more or less equal halves (LA 22.5–29 µm), intectate, densely pilate-clavate. Being a dispersed grain it is not possible to know whether the zonosulcus is orientated meridionally or equatorially relative to the poles. Similar pollen occur in <i>Korthalsia</i> (Calamoideae).</p>
<p><i>Piladiporocolpites</i> Kar, 1995 Type: <i>P. caratini</i> Kar</p>	<p>One of three new fossil form genera described by Kar (1995), showing variations of 'a new type of aperture' which he called 'diporocolpis', a confusing name as the apertures are large pores, not colpi.</p>	<p>Lower Eocene, India</p>	<p>'not comparable to any known fossil or living genera in its apertural condition.'</p>	<p>Pollen ellipsoid with two large pores, one on either short axis (LA 48–55 µm), gemmate (not pilate as inferred from name), margine of pore described as 'spinose' not clear from images – probably the ragged margo of the pore, exine thick (2–4 µm). No obvious affinity in palms but, could be a modification of distal disulcate. Diporate forms are known in <i>Daemonorops</i> and <i>Korthalsia</i>, but the pores are comparatively small and discrete.</p>

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<p><i>Proxapertites</i> van der Hammen, 1956  Type: <i>P. operculatus</i> (van der Hammen) van der Hammen  Basionym: <i>Monocolpites operculatus</i> van der Hammen, 1954b</p>		Palaeocene, Colombia	<i>Astrocaryum acaule</i> Mart.	<p>More or less zonosulcate (LA c. 50 µm) – however, one half slightly larger than other, exine thin, microfoveolate to foveolate. In the original description the grains are described as having ‘a big wide aperture’ at the proximal side of the grain, the illustrations show a zonosulcate grain – possibly one half of the grain was interpreted as an operculum.</p> <p>The comparison with <i>Astrocaryum</i> pollen is erroneous – here the pollen is mono- or trichotomosulcate. In the palms pollen grains showing notable similarity to <i>Proxapertites</i> occur in a few species of <i>Areca</i>. They also occur, and much more frequently, in the Araceae where monosulcate or zonate account for the majority of aperturate genera.</p>
<p><i>Psiladiporocolpites</i> Kar, 1995  Type: <i>P. pachyexinus</i> Kar</p>	<p>One of three new fossil form genera described by Kar (1995), showing variations of ‘a new type of aperture’ which he called ‘diporocolpis’, a confusing name as the apertures are large pores, not colpi.</p>	Lower Eocene, India	<p>‘not comparable to any known fossil or living genera in its apertural condition.’</p>	<p>Pollen ellipsoid with two large pores, one on either short axis (LA 42–55 µm), psilate, margin of pore described as ‘spinose’ not clear from images – probably the ragged margo of the pore, exine thick (2–5 µm). No obvious affinity in palms but, could be a modification of distal disulcate. Diporate forms are known in <i>Daemonorops</i> and <i>Korthalsia</i>, but the pores are comparatively small and discrete.</p>

<p><i>Psilamonocolpites</i> van der Hammen &amp; Garcia de Mutis, 1965  Type: <i>P. medius</i> (van der Hammen) van der Hammen &amp; Garcia de Mutis  Basionym: <i>Monocolpites medius</i> van der Hammen, 1954b</p>	<p>Maastrichtian, Colombia</p>	<p>Compared, and seen to be different from, <i>Arecipites</i> and <i>Palmapollenites</i></p>	<p>Monosulcate, aperture length as, or slightly less than long axis (33 µm), exine thin, psilate perforate.  Illustrated pollen appears to slightly extended sulcate – could be from a palm, see comments under entry for <i>Longapertites</i>.</p>
<p><i>Quilonipollenites</i> Rao &amp; Ramanujam 1978  Type: <i>Q. sahnii</i> Rao &amp; Ramanujam</p>	<p>Neogene (Quilon Beds), Kerala, S. India</p>	<p>‘referable to Palmae’</p>	<p>Extended sulcate (LA 50–55 µm), tectate, coarsely reticulate – lumina smaller around aperture margo.  Now widely accepted as having an affinity with some extant species of <i>Eugeissona</i> (<i>E. tristis</i>, <i>E. utilis</i>) which have closely similar pollen (Phadtare &amp; Kulkarni, 1984).</p>
<p><i>Racemonocolpites</i> González Guzmán, 1967  Type: <i>R. racematus</i> (van der Hammen) ex González Guzmán  Basionym: <i>Monocolpites racematus</i> van der Hammen, 1954a</p>	<p>Upper Cretaceous – Eocene, Colombia</p>	<p>None</p>	<p>Monosulcate (LA 30–40 µm), probably intectate, gemmate, baculate or clavate sculpture. Uncertain, but could have a palm affinity.</p>
<p><i>Retidiporocolpites</i> Kar, 1995  Type: <i>R. excellens</i> Kar</p> <p>One of three new fossil form genera described by Kar (1995), showing variations of ‘a new type of aperture’ which he called ‘diporocolpis’, a confusing name as the apertures are large pores, not colpi.</p>	<p>Lower Eocene, India</p>	<p>‘not comparable to any known fossil or living genera in its apertural condition.’</p>	<p>Pollen ellipsoid with two large pores, one on either short axis (LA 33–42 µm), finely reticulate, finer around aperture margins, exine (c. 2.5 µm).  No obvious affinity in palms, could be a modification of distal disulcate. Diporate forms are known in <i>Daemonorops</i> and <i>Korthalsia</i>, and in <i>Calamus</i> there are many species with reticulate disulcate pollen, in some cases the distal exine area is wide, and the sulci short.</p>

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Retimonocolpites</i> Pierce, 1961 Type: <i>R. dividuus</i> Pierce		'lower' Upper Cretaceous	'Monocotyledoneae (?) Similar forms <i>Liliacidites</i> Couper 1953'	Monosulcate, aperture almost encircles grain, ellipsoidal to spherical (LA c. 27 µm), tectate, finely reticulate, occasionally separated from endexine; exine c. 1.5 µm. Small zonasulcate pollen grains occur in the calamoid palms ( <i>Salacca</i> & <i>Korthalsia</i> ) reticulate forms not known. If the endexine is indeed endexine and not a foot layer, it suggests that the pollen is more likely to be from an early dicot.
<i>Retitriatiporites</i> Misra, Singh & Ramanujam, 1996 Type: <i>R. kutchensis</i> (Venkatchala & Kar) Misra, Singh & Ramanujam Basionym: <i>Trilatiporites kutchensis</i> Venkatchala & Kar, 1969	A new genus introduced to distinguish the overt protrudent pore morphology of <i>Trilatiporites</i> and <i>Dorreenipites</i> from the 'feeble to imperceptible protrusions of some other triporates.	Eocene, India	'closely resembles Miocene <i>Sclerosperma</i> -type pollen (Médus, 1975) from Senegal, western Africa.'	Triporate, triangular in presumed polar view, straight or slightly convex faces (LA 24–41 µm) triangular or rounded triangular, reticulate, exine 2–4 µm thick. More <i>Sclerosperma</i> -like than <i>Dorreenipites</i> or <i>Trilatiporites</i> , but walls too thick, and pore position not quite right – altogether not as convincing as the Senegal examples.
<i>Riedelia</i> Thiergart & Frantz 1963 Type: <i>R. simplex</i> Thiergart & Frantz		Tertiary, India	'we suppose that this type of pollen grain may be associated to the Gymnospermeae of the Gingko-group or to Palmae'	Monosulcate (LA 25 µm), sulcus length as long axis. Uncertain, but could have a palm affinity.
<i>Sabaloidites</i> Potonié, Thomson & Thiergart, 1950	No generic diagnosis, not validly proposed, junior synonym of <i>Sabalpollenites</i> .			

<i>Sabaloipollenites</i> Potonié, 1951	Junior synonym of <i>Arecipites</i> – invalid no longer recognised by the author (Potonié, 1958).	<i>Sabal</i> , <i>Chamaedorea pavoniana</i>	Monosulcate (LA 36–41 µm), sulcus length as long axis, perforate to reticulate. <i>Sabalpollenites</i> is used for small to average more or less bisymmetric monosulcate coryphoid-like pollen – many of the comparisons seem convincing.
<i>Sabalpollenites</i> Thiergart in Raatz (1937–38) Type: <i>S. convexus</i> Thiergart in Raatz	Junior synonym of <i>Arecipites</i> .		
<i>Spinizonocolpites</i> Muller, 1968 Type: <i>S. echinatus</i> Muller	A considerable number of species described, but the most frequently encountered morphology is that of <i>S. echinatus</i> , and <i>S. baculatus</i> (Muller 1968).	<i>Nypa fruticans</i> , and it is also often considered to be related to the plants which produced <i>Proxaperites</i> , although this may well not be the case.	Zonasulcate, usually only found as one half of the original spheroidal grain, due to breakdown of aperture during fossilisation (LA 33–43 µm), tectate, exine perforate to finely reticulate with short to long spines. Widely accepted as ancestral to <i>Nypa</i> , and possibly once represented by a number of species.
<i>Spinomonosulcites</i> A. Singh & Misra, 1991 Type: <i>S. varispinosus</i> A. Singh & Misra	Several other species, previously assigned to <i>Neocouperipollis</i> , were also transferred to <i>Spinomonosulcites</i> .	None	Monosulcate, sulcus length as long axis (LA 70–85 µm), spinose, spines 1–7 µm long, sulcus margo smooth or spinose.
		Miocene, India	

## Appendix 2 Continued

Genus & type species	Taxonomic comments	Age of type material	Original type comparison to an extant taxon	Morphology & evaluation of palm affinity [LA = long axis]
<i>Trichotomosulcoides</i> van der Hammen, 1956 Type: <i>T. normalis</i> van der Hammen	the holotype of the type species – <i>T. normalis</i> – is a recent pollen grain of <i>Pyrenoglyphis major</i> (Jacq.) Karst (Palmae): ( <i>Pyrenoglyphis</i> syn. <i>Bactris</i> ). Thus <i>Trichotomosulcoides</i> , by designation of the type species is made illegitimate and a later synonym of <i>Pyrenoglyphis</i> (see Jansonius & Hills, 1976).		Palmae	'pollen grains with only a three-split aperture'
<i>Trichotomosulcites</i> Couper, 1953 Type: <i>T. subgranulatus</i> Couper		Cretaceous, New Zealand	<i>Phormium</i> (Phormiaceae) 'many monosulcate pollen (Liliaceae, Palmae) contain abnormal trichotomosulcate pollen ... a form genus for such atavistic, teratological forms is superfluous.' (Kruttsch, 1970)	Trichotomosulcate, sulcus 3-armed, subcircular to triangular outline (LA 27–35 µm), psilate-granular. Common in Cretaceous of New Zealand – but these probably more likely to be ancestral to Phormiaceae than Palmae. Nevertheless, asymmetric, less frequently symmetric, trichotomosulcate pollen is very common in the palms, especially in subfamily Arecoideae.
<i>Trilatiporites</i> Ramanujam, 1966 ex Potonié, 1970 Type: <i>T. noremi</i> Ramanujam ex Potonié	<i>Dorreenipites</i> may be a senior synonym.	Miocene, southern India	None	Heteropolar, triporate protrudent with thickened rim (LA 29–48 µm) suboblate, tectate. This pollen form is closely similar to <i>Dorreenipites</i> ; it is not considered to have any association with Arecaceae (Harley & Baker, 2001).

<p><i>Victoriisporis</i> Belsky, Boltenhagen &amp; Potonié, 1965 Type: <i>V. robertii</i> Belsky, Boltenhagen &amp; Potonié</p>	<p>Named for one of the field work assistants working with the authors.</p>	<p>lower Senonian, Equatorial West Africa</p>	<p><i>Sclerosperma mannii</i> H. Wendl.</p>	<p>Subequatorial poro- trichotomosulcus, tectate, rounded triangular equatorial outline (LA 20– 50 µm), pores circular to oval. Some similarity to <i>Andreisporis</i> but pores closer to margin, and set in the angles of the triangular outline.</p>
<p><i>Weylandipollis</i> Takahashi, 1964 Type: <i>W. retiformis</i> Takahashi</p>	<p>Campanian, Japan</p>	<p>'differs from <i>Liliacidites</i> mostly in the shape of the pollen and the colpus'</p>	<p>There are a number of reasons why this is unlikely to be ancestral to <i>Sclerosperma</i> (Harley &amp; Baker, 2001). Probably should also be referred to <i>Problematicopalmites</i> with <i>Andreisporis</i> &amp; <i>Constaniniisporis</i>. Monosulcate broad ellipsoidal (LA 34–46 µm), sulcus wide with broad apices, semi tectate, coarsely reticulate, sparsely columnellate, lumina reduced to perforations around sulcus margo. Closely similar grains found in some species of <i>Hydriastele</i>.</p>	