

## The Palms

Guest edited by William J. Baker and Scott Zona

# The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia

AARON D. PAN<sup>1\*</sup>, BONNIE F. JACOBS<sup>2</sup>, JOHN DRANSFIELD<sup>3</sup> and WILLIAM J. BAKER<sup>3</sup>

<sup>1</sup>Department of Geological Sciences, Southern Methodist University, PO Box 750395, Dallas, Texas 75275–0395, USA

<sup>2</sup>Environmental Science Program, Southern Methodist University, PO Box 750395, Dallas, Texas 75275–0395, USA

<sup>3</sup>Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

Received June 2005; accepted for publication November 2005

The African palm fossil record is limited but the data provide an outline of palm evolution from the Late Cretaceous through the Neogene. Pollen attributed to palms is reported from the Aptian (125–112 Mya), but the earliest unequivocal record in Africa is Campanian (83.5–70.6 Mya). Palms diversified 83.5–65.5 Mya and became widespread, although most records are from the west and north African coasts. Many taxa were shared between Africa and northern South America at that time, but a few were pantropical. Extirpations occurred throughout the Palaeogene, including a notable species turnover and decline at the Eocene–Oligocene boundary (33.9 Mya), a change that resulted in the elimination of nypoid palms from Africa. The Neogene plant macrofossil record is better sampled than the Palaeogene, although few palms are documented. Thus, the low diversity of African palms today is more likely the result of Palaeogene, rather than Neogene extinctions. Newly discovered palm fossils of leaves, petioles and flowers from the Late Oligocene (27–28 Mya) of north-western Ethiopia document the abundance and dominance of palms in some communities at that time. The fossils represent the earliest records of the extant genera *Hyphaene* (Coryphoideae) and *Eremospatha* (Calamoideae). © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 151, 69–81.

ADDITIONAL KEYWORDS: Campanian – Chilga – East Africa – *Eremospatha* – evolution – extinction – fossils – *Hyphaene* – Palmae – West Africa.

## INTRODUCTION

Modern African palm diversity (excluding Madagascar) is low compared with the New and the Old World tropics outside of Africa (Uhl & Dransfield, 1987; Dransfield, 1988; Henderson, Galeano & Bernal, 1995). While modern palm diversity in Africa consists of about 65 species in 14 genera, the New World tropical palm flora has about 550 species in 67 genera, and

the Old World (excluding Africa) has about 1400 species in 100 genera (Uhl & Dransfield, 1987; Henderson *et al.*, 1995; Govaerts & Dransfield, 2005). Also, palm abundance and richness in extra-African tropical forests are far greater, excluding the occurrence of monotypic *Raphia* stand communities (in Africa). Palms are usually absent from the African forest canopy and are species-poor or uncommon in the understorey. How did this marked contrast in palm richness and diversity between Africa and other tropical regions come about? Moore (1973) attributed these differences to Neogene, primarily Pleistocene, climate change. More recently,

\*Corresponding author. E-mail: apan@mail.smu.edu

Morley (2000: 276–277) noted a greater number of extinctions in African pollen taxa compared with tropical South America at the Eocene–Oligocene boundary, but concluded that it was greater Neogene desiccation in the African tropics that caused the modern disparity in palm diversity between Africa and other tropical regions (i.e. South America and south-east Asia). Other authors have emphasized Neogene climatic changes as having caused significant loss in tropical African floral diversity, thus strengthening the impression that Palaeogene changes may not have played as important a role (e.g. Axelrod & Raven, 1978; Coetzee, 1993; Richards, 1996).

Palynological data document a similarity during the Late Cretaceous between African and South American palm floras. Herngreen (1980) and Herngreen & Chlova (1981) designated this floristic complex the *Palmae Province*, which Morley (2000) extended to south-east Asia. Since palm richness was approximately uniform in Africa, South America and, to a lesser extent, south-east Asia during the Late Cretaceous, the depauperate nature of the modern African palm flora can be attributed to higher extinction rates during the Late Cretaceous or Cenozoic (Palaeogene, Neogene or both), lower origination rates during the Cenozoic, or a combination of both, compared with other tropical regions. In this paper, we review the fossil record of African palms to document their evolution and extinction (or extirpation) from the Late Cretaceous through the Cenozoic, and provide a framework into which additional fossil data can be incorporated.

Any review of the fossil record must contend with its geographical and temporal incompleteness. Tropical West Africa is sampled most consistently as a result of pollen from drill cores, which represent continuous (or nearly continuous) deposition. Temporal coverage is excellent from the Late Cretaceous through the Early Miocene, although the cores are concentrated in coastal areas. East Africa is relatively well sampled by macrofossils found in depositional basins associated with rift development, but this record is limited to the Neogene and, unlike pollen core samples, is discontinuous and palms are scarcely present. The remainder of the African palm fossil record is spatially and temporally more sporadic, consisting of either limited collections of macrofossils (with the exception of new finds reported herein) or occasional presence in pollen samples.

Taxonomic precision varies depending on more than just the quality of fossil preservation. For example, the majority of palynological studies cited here were for biostratigraphic purposes to aid petroleum exploration, and pollen types were named using morphotypes, which do not necessarily correspond to particular botanical taxa. Furthermore, the taxonomic precision possible for pollen varies, sometimes even at the

subfamily level in Arecaceae (Harley & Baker, 2001). We addressed these issues by confirming the affinity of pollen to Arecaceae, based on published literature (Morley, 2000; Harley & Baker, 2001) or indicated in the text, where affinity remains questionable. Once affinity with Arecaceae was evaluated we assumed that variation in species (or morphotype) number through time reflected changes in palm pollen richness. Almost all of the continuous pollen records are from West Africa and limited to the reports of a few palynologists, making variations in species number likely to be internally consistent and unlikely to be the result of disparate taxonomic philosophies or geographical sampling.

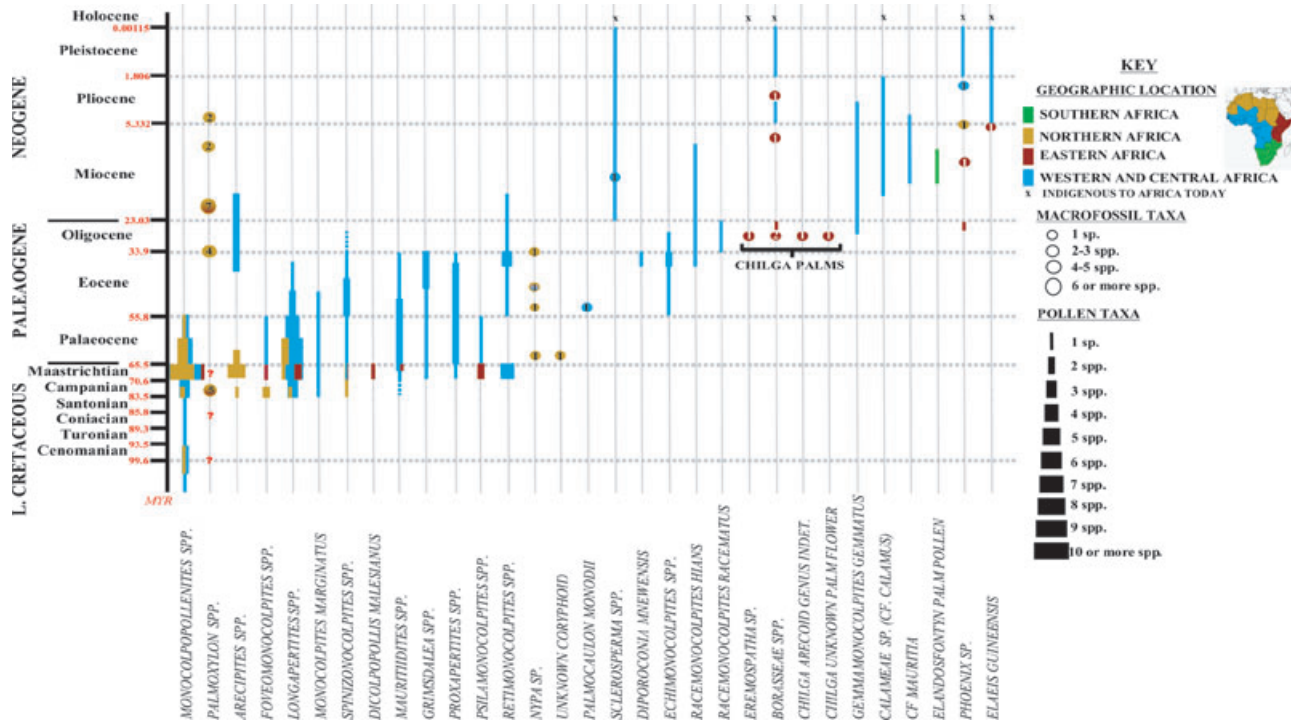
In addition to reviewing the record, we report new discoveries of palm fossils found in angiosperm dominated assemblages representing several plant communities from Late Oligocene (28–27 Mya) deposits of north-western Ethiopia. These fossils have direct bearing on the issues of African palm origins and extirpations (or extinctions), and provide information for East Africa which fills a gap that spanned the time interval from Late Cretaceous to the Early Miocene.

## THE AFRICAN PALM FOSSIL RECORD

### CRETACEOUS

The earliest purported African palms are Aptian (125–112 Mya); they include a fruit, *Hyphaeocarpon aegyptiacum* Vaudois-Miéja & Lejal-Nicol, from the Abu Ballas Formation of Egypt (Vaudois-Miéja & Lejal-Nicol, 1987; Schrank, 1992) and a palynomorph, *Monocolpopollenites spheroidites* Jardiné & Magloire, from West Africa (Salard-Chebodaeff, 1990). Both fossils are of uncertain botanical affinity and *M. spheroidites* may even be a cycad (Nichols, Ames & Traverse, 1973; Tiffney, 2004). Chiarugi (1933) suggested that fossil palm wood from Somalia might be Albian (112–99.6 Mya), but he provided no evidence for age determination. *Monocolpopollenites* species (some of which may be palms) are known from the Albian and Cenomanian (99.6–93.5 Mya) Omdurman Formation of Sudan (Fig. 1; Schrank & Awad, 1990). They occur throughout the Cretaceous and Palaeocene in West Africa (Jardiné & Magloire, 1965; Schrank & Awad, 1990), and reappear in the Campanian (83.5–70.6 Mya) in North Africa (Jardiné & Magloire, 1965; Meon, 1990; Mahmoud, 2003; Fig. 1).

By the Campanian Age there remains little doubt about the presence of palms in Africa, based upon abundant pollen with clear affinities to the family. Palm pollen diversified, became abundant, and was represented by at least 11 Campanian and 34 Maastrichtian (70.6–65 Mya) palm or palm-like taxa (Hoeken-Klinkenberg, 1966; Meon, 1990; Schrank, 1994; Morley, 2000; Mahmoud, 2003; Fig. 1). The majority of these records are



**Figure 1.** Fossil African palms from the Late Cretaceous through the Pleistocene, modified from Morley (2000) and Salard-Cheboldaëff (1990). Colours correspond to particular regions of Africa: blue, western and central Africa; tan, northern Africa; red, eastern Africa; green, southern Africa. Bars denote pollen records and circles/ovals indicate macrofossils. The width (bars) and size/number within the circles/ovals correspond to the number of species indicated at any particular time.

from coastal regions of western, northern and eastern Africa (Somalia). Many of the taxa present during these Ages, for example *Psilamonocolpites*, *Retimonocolpites*, *Spinizonocolpites*, *Proxapertites*, *Longapertites* and *Mauritiidites* (Herngreen *et al.*, 1996), also occurred in tropical South America and, to a lesser extent, in south-east Asia, forming the core of the Late Cretaceous Palmae Province (Herngreen, 1980; Herngreen & Chlonova, 1981; Morley, 2000). Late Cretaceous palms were abundant and often dominant in what can be interpreted as coastal swamp and mangrove vegetation (Morley, 2000; Jacobs, 2004). Structurally closed-canopy lowland rainforest was probably absent in equatorial Africa during the Late Cretaceous (Morley, 2000; Jacobs, 2004).

The subfamily Nypoideae, represented by *Spinizonocolpites* spp. and possibly *Proxapertites cursus* van Hoeken-Klinkenberg, which may not be a palm (e.g. Zetter, Hesse & Frosch-Radivo, 2001), was present in Africa by the Late Cretaceous. Subfamily Calamoideae is represented in the Maastrichtian by pollen taxa *Mauritiidites* spp. (Lepidocaryeae: Mauritiinae; Herngreen *et al.*, 1996; Dransfield *et al.*, 2005) and *Dicolpopollis malesianus* Muller (Schränk, 1994). *Dicolpopollis malesianus* is of particular interest because it is the earliest occurrence in Africa of the

otherwise Asian calamoid tribe, Calameae (Table 1; Dransfield *et al.*, 2005). There is a gap in the record of Calameae fossils in Africa from its Maastrichtian occurrence until the Early Miocene when pollen with distinctly calamoid characters, including two elongate apertures, appear in West Africa (Morley, 2000). Morley (2000: 141) referred to this pollen as "*Calamus (deerratus-type)*". Today, *Calamus deerratus* G. Mann & H. Wendl is the sole representative of the Calameae in Africa.

The pollen genus *Longapertites*, present in Africa by the Late Cretaceous, is thought by Morley (2000) to be ancestral to the calamoid *Eugeissona* (subtribe Eugeissoneae; Dransfield *et al.*, 2005). However, based on coarse sculpturing features of the exine, Harley & Baker (2001) noted that the pollen from Pakistan identified as *Longapertites*, and compared with *Eugeissona* by Morley (1978), could actually represent Asparagalean or Lilialean species or, among the palms, *Ceroxylon* (Ceroxyleae, Dransfield *et al.*, 2005) or perhaps *Pinanga* (Arecoideae). As these issues have not been resolved and have not been addressed specifically with regard to the African record, we assume that most of the African *Longapertites* species referenced in Figure 1 are of arecaceous affinity. Several are not coarsely reticulate (and coarsely reticulate

exine does not preclude affinity outside of the palms), nor do any show preservational problems that, in some cases, could result in misidentification (Harley & Baker, 2001).

Monteillet & Lappartient (1981) identified a Late Cretaceous fossil fruit as cf. *Borassus* from the Paki Quarry of Senegal. However, this specimen is almost certainly not a palm (Uhl & Dransfield, 1987; B. H. Tiffney pers. comm.; R.P. Bayton, pers. comm.).

#### THE CRETACEOUS–PALAEOGENE (K–P) BOUNDARY AND PALAEOCENE EPOCH

The Cretaceous–Palaeogene global extinction event saw the disappearance of 47% (16 of 34) palm (or palm-like) pollen species among fossil genera in West Africa, where the record spans this time interval (Fig. 1). Although *Dicolpopollis* is the only genus to disappear at the boundary (Morley, 2000), two others are gone by the end of the Palaeocene. In addition, only six of the 12 remaining genera, *Mauritiidites*, *Grimsdalea*, *Longapertites*, *Spinizonocolpites* and *Proxapertites*, maintain or increase species richness after the K–P boundary (Fig. 1). Therefore, the last occurrences at the Cretaceous–Palaeogene (K–P) boundary document an impoverishment of the genetic diversity which, in turn, could have contributed ultimately to the limited palm flora in Africa today.

Changes to note in West Africa during the Palaeocene include the first appearance of the species *Proxapertites operculatus* van der Hammen at the beginning of the epoch and the last occurrences of the genera *Monocolpopollenites*, *Foveomonocolpites* and *Psilamonocolpites* at the Palaeocene–Eocene boundary (Fig. 1).

Records from North Africa include a core from El Kef, Tunisia, which spans the Maastrichtian through the Palaeocene and shares the pollen genera *Monocolpopollenites* and *Longapertites* with West Africa (Meon, 1990). Two macrofossils from the early Palaeocene Bir Abu Munqar Formation of Egypt (65.5–61.7 Mya) include the earliest African *Nypa* fruit and a seed representing the oldest evidence in Africa of the subfamily Coryphoideae (Gregor & Hagn, 1982). Gregor & Hagn (1982) suggested that this seed, which has a small 'sulcus' along its length on one side interpreted as the raphe canal, shares similarities with the extant Corypheae genera *Livistona*, *Corypha*, *Thrinax* and *Brahea*.

#### THE EOCENE AND OLIGOCENE EPOCHS

Extinctions and appearances at or near the Eocene–Oligocene boundary indicate a significant change in the African palm flora. Between about 36 and 34 Mya, six pollen genera disappeared from the African fossil

record: *Spinizonocolpites*, *Proxapertites*, *Mauritiidites* (Lepidocaryeae: Mauritiinae Dransfield *et al.*, 2005), *Grimsdalea*, *Longapertites* and *Diporoconia*. All but *Diporoconia*, which may not be of arecaceous affinity according to Harley & Baker (2001), had been present since the Late Cretaceous (Fig. 1). At the species level, Early and Middle Eocene last occurrences in West Africa include *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg, *Longapertites marginatus* van Hoeken-Klinkenberg, *Spinizonocolpites baculatus* Muller and *Monocolpites marginatus* Hammen (Hoeken-Klinkenberg, 1966; Salarid-Cheboldaeff, 1990; Morley, 2000; Fig. 1).

During the Eocene the mangrove palm *Nypa* was globally widespread. In West and North Africa it is represented by the pollen genus *Spinizonocolpites* as well as by *Nipadites (Nypa)* fruits that are known from Senegal and Egypt (Fritel, 1921; Kräusel, 1939; Chandler, 1954; Tralau, 1964; B. H. Tiffney, pers. comm.). However, fossil evidence indicates that palm subfamilial diversity of Africa decreased at, or soon after, the Eocene–Oligocene boundary (Fig. 1) when the Nypoideae [*Spinizonocolpites*, *Proxapertites* and *Nipadites (Nypa)*] were extirpated from the continent (Table 1). *Nypa* has recently been re-introduced into West Africa by humans in the early 20th Century (Tuley, 1995).

First appearances during the Eocene include two species of *Echimonocolpites* that disappear at the end of the Eocene (33.9 Mya) and the middle Oligocene (c. 27 Mya). *Racemonocolpites hians* Legoux appears in the Late Eocene and ranges into the Late Miocene (Jan du Chêne, Onyike & Sowunmi, 1978; Legoux, 1978; Salarid-Cheboldaeff, 1990; Morley, 2000; Fig. 1). *Echimonocolpites rarispinosus* (Hammen & Garcia) Salarid-Cheboldaeff may have affinities with the subtribe Mauritiinae (?*Lepidocaryum*) according to Morley (2000). The species *Racemonocolpites hians* has a clavate exine which is similar to that of some Oncospermatinae (Mendis, Ferguson & Dransfield, 1987), Iriarteae and Arecinae. Morley (2000) suggested that this species may be related to *Oncosperma*, although the exine differs and affinity with an extant genus cannot be confirmed (M. M. Harley, pers. comm.). *Retimonocolpites* reappeared in West Africa at the start of the Eocene, ending a hiatus that began at the Cretaceous–Palaeogene boundary (*R. irregularis* Salarid-Cheboldaeff ranged from Early Oligocene to Early Miocene; Salarid-Cheboldaeff, 1990; Morley, 2000). During the Late Eocene, two species of the monosulcate pollen genus *Arecipites* appeared in West Africa (Late Cretaceous and Early Palaeocene records are from North Africa; Legoux, 1978; Morley, 2000).

Early Eocene plant macrofossils include *Palmocaulon monodii* Boureau & U. Prakash, a solitary palm petiole from Senegal. This specimen lacks the diagnos-

**Table 1.** Palm clades present in the African fossil record are listed with their earliest and most recent occurrences

Subfamilies	Tribes and subtribes	Earliest occurrence	Most recent occurrence in Africa
Calamoideae	Calameae	<i>Dicopolpis malesianus</i> (pollen) – Maastrichtian (~70–65 Mya; Schrank, 1994)	Present in Africa today, 1 genus ( <i>Calamus</i> )/1 species (Govaerts & Dransfield, 2005)
	Lepidocaryeae, subtribe Ancistrophyllinae	<i>Eremospatha chilgansis</i> (leaflet) – Late Oligocene (28–27 Mya; this paper)	Present in Africa today, 3 genera ( <i>Eremospatha</i> , <i>Laccosperma</i> , <i>Oncocalamus</i> )/~22 species (Sunderland, 2001, 2003; Govaerts & Dransfield, 2005)
	Lepidocaryeae, subtribe Mauritiinae	<i>Mauritiidites</i> spp. pollen – Campanian or Maastrichtian (~83–70 Mya; Morley, 2000)	cf. <i>Mauritia</i> (pollen) – Early Pliocene (~83–65 Mya; Hengreen, 1980; Morley, 2000) Morley, 2000
	Lepidocaryeae, subtribe Raphiinae	<i>Raphia</i> (wood) – Late Miocene (~6.5–5 Mya; Dechamps, 1987; Dechamps & Maes, 1987) <i>Spinizonocolpites</i> pollen – Campanian or Maastrichtian (~83–65 Mya; Salard-Cheboldaeff, 1990; Schrank, 1992, 1994; Morley, 2000)	Present in Africa today, 1 genus/20 species (Govaerts & Dransfield, 2005) <i>Spinizonocolpites echinatus</i> and <i>Nypa</i> fruit – Eocene/Oligocene boundary (33.9 Mya; Salard-Cheboldaeff, 1990; Krausel, 1939; Morley, 2000; Tiffney pers. comm.)
Coryphoideae	Livistoneae or Corypheae	aff. <i>Coryphoicarpus globoides</i> Koch – Early Palaeocene/Damian (~65–62 Mya; Gregor & Hagns, 1982)	Livistoneae – Present in Africa today 1 genus ( <i>Livistona</i> )/1 species (Govaerts & Dransfield, 2005)
	Borasseae, subtribe Hyphaeninae	<b><i>Hyphaene kappelmanii</i></b> & <i>Hyphaene</i> sp. – Late Oligocene (28–27 Mya; this paper)	Present in Africa today, 2 genera ( <i>Hyphaene</i> , <i>Medemia</i> )/8 species (Govaerts & Dransfield, 2005)
	Phoeniceae	<i>Phoenix reclinata</i> -type pollen – Late Oligocene (~25 Mya; Vincens <i>et al.</i> , in press)	Present in Africa today (Phoenix)/3 species (Govaerts & Dransfield, 2005)
Arecoideae	Sclerospermeae	<i>Sclerosperma</i> pollen – Early Miocene (~23 Mya; Medus, 1975; Morley, 2000)	Present in Africa today; ( <i>Sclerosperma</i> )/3 species (Govaerts & Dransfield, 2005)
	Cocoseae, subtribe Elaeidinae	<i>Elaeis</i> seeds – Late Miocene (6 Mya; Ergo, 1997)	Present in Africa today ( <i>Elaeis</i> )/1 species (Govaerts & Dransfield, 2005)

tic characters to determine relationships within the Arecaceae (Boureau & Prakash, 1968).

The Late Eocene–Early Oligocene macroflora from the Jebel Qatrani Formation of Egypt (Fayum) is particularly diverse in fossil palms (Fig. 1). There are at least four species of *Palmoxylon* present in the flora, as well as fruits and a seed of *Nypa* and *Palmospermum* (Krausel, 1939; Bown *et al.*, 1982; El-Saadawi, Youssef & Kamal-El-Din, 2004; B. H. Tiffney, pers. comm.). Although most of these fossils can only be identified to family, a more thorough examination of the woods may help to determine subfamilial or lower taxonomic affinities. All the fruits, seeds and wood from the Jebel Qatrani Formation, including *Cynometra* (Fabaceae), *Triplochiton* (Malvaceae *s.l.*), *Epipremnum* (Araceae), *Acrostichum* (pteridophyte), *Gynotrochoxylon* (Rhizophoraceae), *Canarium* (Burseraceae) and *Menispermaceae*, are interpreted as indicating tropical moist forest vegetation (though not necessarily rainforest) and mangroves (Krausel, 1939; Bown *et al.*, 1982; Tiffney, 1991). Therefore, while the Jebel Qatrani Formation may not help us to determine which taxonomic groups of palms were present during this time interval, the flora indicates that palms were prevalent and diverse in northern Egypt.

The Oligocene is represented primarily by records from West Africa that document a great diversification of angiosperm pollen (Salard-Cheboldaëff, 1981). Palm pollen richness remains comparatively moderate after the Eocene–Oligocene boundary, but a new pollen species, *Gemmamonocolpites gemmatus* van der Hammen & Garcia de Mutis, is documented in the mid-Oligocene and continued throughout the Miocene until the early Pliocene (Morley, 2000). Also in West Africa, *Racemonocolpites racematus* Gonzalez-Guzman, which is thought to have affinities to the New World palm genus *Iriarteia* (Arecoideae: Iriarteae; Morley, 2000), is confined to the Oligocene epoch. Apart from the Fayum Jebel Qatrani Formation, Oligocene data are rare in central and eastern Africa. A pollen record from the Lokichar Basin in northern Kenya documents a Borasseae, unknown pollen with possible affinities to Asian palms and the earliest African record of *Phoenix* (Vincens, Tiercelin & Buchet, in press; Table 1). Below, we report new data from the Late Oligocene of north-western Ethiopia where fossil-rich deposits have produced abundant palaeofloral assemblages, many of which include palms.

#### THE MIOCENE EPOCH

The Early Miocene palm macrofossil record includes several wood taxa from the Western Desert of Egypt, Algeria and the Omo Region of Ethiopia (Aubreville, 1970; Lemoigne, 1978; El-Saadawi *et al.*, 2004). The palynomorphs *Arecipites* (two species) and *Retimono-*

*colpites* (Fig. 1), known since the Late Cretaceous, disappeared from the West African fossil record during the Early Miocene (Legoux, 1978; Salard-Cheboldaëff, 1990; Morley, 2000). The Early Miocene saw the appearance of the unusual triporate pollen of the African endemic *Sclerosperma* (Medus, 1975; Morley, 2000; Table 1). *Gemmamonocolpites* and *Racemonocolpites hians*, first recorded from the Oligocene, were present in the early Miocene. Disulcate palm pollen (tribe Calameae) appeared in the Early Miocene of West Africa and was designated by Morley (2000) as *Calamus (deeratus-type)*. This fossil is the first indication of the Calameae in Africa since the apparent extinction of the related *Dicolpopollis malesianus* at the Cretaceous–Palaeocene boundary in Somalia.

The Middle Miocene saw the appearance in West Africa of pollen identified by Morley (2000) as *cf. Mauritia*. In South Africa, Coetzee & Rogers (1982) reported an abundant, unknown, nonextant, southern African, palm pollen taxon from the Elandsfontein Formation, where pollen assemblages occur in an approximately 13 m stratigraphic section. Interestingly, their figure 9 appears to be an asymmetrical monosulcate pollen grain that could be of arecoid affinity based on the morphological descriptions provided by Harley & Baker (2001: fig. 6). Today, the arecoid genera *Jubaeopsis* and *Elaeis* occur in South Africa, but their pollen morphology does not match that of the fossil (Harley & Hall, 1991). The South African palm pollen occurred in a flora dominated by *Podocarpus* and was interpreted as a subtropical mixed conifer or gallery forest. In the overlying sediments, the flora changed to a palm-dominated environment (Coetzee & Rogers, 1982). Coetzee (1993) also reported Miocene palm pollen from lignites found in Knysna, South Africa.

Other Middle Miocene palm fossils include a possible Phoeniceae (Coryphoideae; Dransfield *et al.*, 2005) seed from the Rusinga Flora of Kenya (M. E. Collinson, pers. comm.), which is interpreted as a tropical moist (perhaps gallery) forest (Chesters, 1957). A leaf compression and cuticle of an extinct species of *Sclerosperma* (considered to be Middle Tertiary) was described from the Kivu region of the Democratic Republic of Congo (Lakhanpal, 1966). *Sclerosperma*, which is today limited to the wetter regions of Ghana, Togo, eastern Nigeria, Cameroon, Equatorial Guinea, Gabon and Angola (Uhl & Dransfield, 1987), may have had a much wider distribution in the past.

Ergo (1997) reported seeds of the African oil palm, *Elaeis*, from the Late Miocene (6 Mya) of Uganda, which marks its earliest occurrence (Table 1). Other Late Miocene palm fossils from Uganda include *Hyphaene coriacea* Gaertn. fruits (Borasseae) from the Nkondo Formation (6.5–5 Mya), which Dechamps,

Senut & Pickford (1992) interpreted as moist forest vegetation. From the same period (Fig. 1), palm wood, which is difficult to identify within the family (Tomlinson, 1990), was documented from the Sahabi Formation, Libya and identified as *Phoenix*, *Raphia* and an unknown palm (Dechamps & Maes, 1987; Dechamps, 1987).

#### THE PLIOCENE AND PLEISTOCENE EPOCHS

The pollen taxon, cf. *Mauritia*, the only representative of the subtribe Mauritiinae in Africa at that time, and *Gemmamonocolpites gemmatus* disappeared during the Early Pliocene (Morley, 2000). *Hyphaene* or *Borassus* pollen is present in the Early Pliocene Upper Laetolil Beds of Tanzania, and fruits of *Borassus aethiopicum* Mart. are documented from the Kaiso Village Formation (2.6 Mya), Uganda (Bonnefille & Riollet, 1987; Dechamps *et al.*, 1992; Fig. 1). *Phoenix reclinata* Jacq. wood was reported from the Pliocene Lusso Beds of the Semliki Valley, Democratic Republic of the Congo (Zaire), which Dechamps & Maes (1990) interpreted as representing gallery forest, savannah or moist forest. A Neogene palm leaf (in association with a fossil tropical forest flora) is reported from Mount Cameroon by Menzel (1920).

Other taxa, including the African oil palm *Elaeis guineensis*/*Elaeis* sp., *Sclerosperma* and *Calamus* (*deerratus*-type), were present throughout the Pliocene, Pleistocene and Holocene (Dechamps *et al.*, 1992; Morley, 2000). With the exception of cf. *Mauritia* and *Gemmamonocolpites gemmatus*, both of which disappeared by the Pleistocene, Pliocene pollen taxa are all referred to extant genera or species. *Elaeis* is the most commonly cited palm in Late Pleistocene and Holocene pollen records and is known to be associated with human disturbance (Vincens, 1993; Maley & Brenac, 1998; Sowunmi, 1999). Pliocene palm wood (*Palmoxydon cossoni* Fliche) from Tunisia was reported by Aubreville (1970), but its possible botanical affinities within the palms are not suggested.

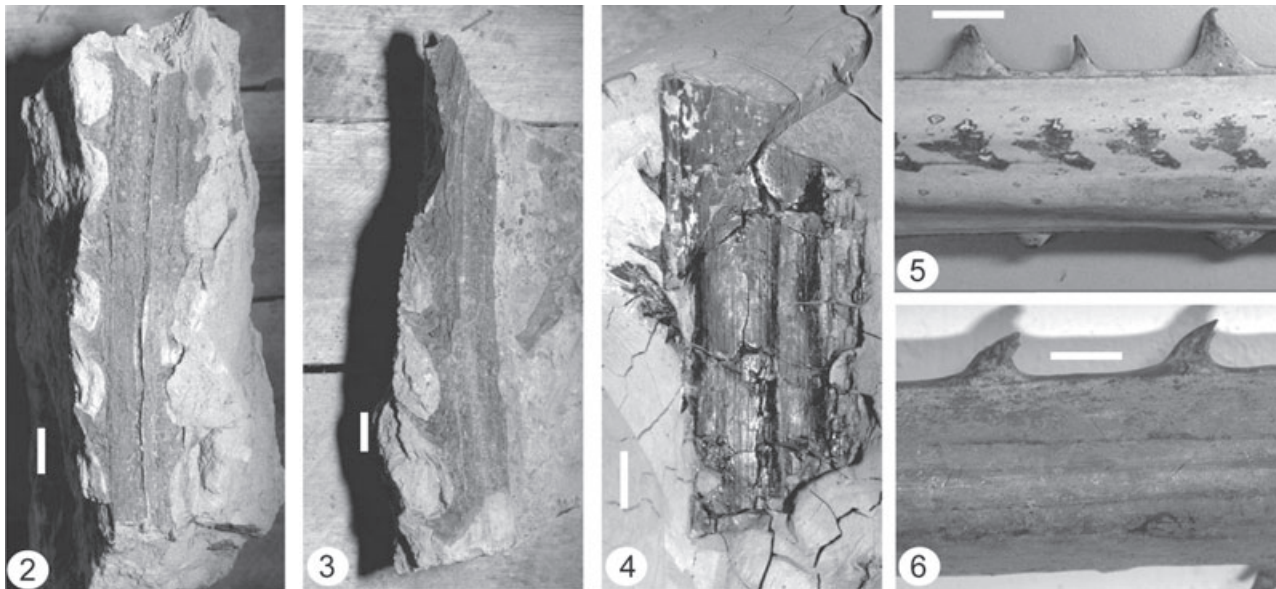
#### LATE OLIGOCENE PALM FOSSILS – CHILGA WOREDA, ETHIOPIA

Plant fossils, which crop out in Chilga Woreda ('Chilga') about 60 km west of Gondar, were dated to the Late Oligocene and occur in a structural basin within plateau flood basalts of Early Oligocene age. A tuff (indurated volcanic ash) near the top of a 150 m section provided an  $^{40}\text{Ar}/^{39}\text{Ar}$  age of  $27.36 \pm 0.11$  Mya, a basalt conformably underlying the sediments is dated by K/Ar at  $32.4 \pm 1.6$  Mya, and this entire sedimentary package is correlated with the Geomagnetic Polarity Timescale, further constraining the age to between 28 and 27 Mya, the limits of Chron C9n (Cande & Kent, 1995; Kappelman *et al.*, 2003).

The Chilga area of the Ethiopian Plateau was a mostly flat upland with variations in vegetation dependent upon the local water table and influx of volcanic ash. This variation was preserved laterally across the basin and also vertically through the approximately 1 Myr time interval represented by the fossiliferous strata (Jacobs *et al.*, 2005). Across the approximately 100 km<sup>2</sup> of fossiliferous strata at Chilga, palms are common, occurring at all levels and in all sediment types including tuff, tuffaceous ironstone, and volcanoclastic channel and overbank (or pond) deposits (Jacobs *et al.*, 2005). Unidentified coryphoid palm fronds and stumps occur in the tuff deposits. One site where no palms are present preserves large *in situ* silicified trunks, many of which are buttressed and are estimated to represent trees up to 20–35 m tall (Jacobs *et al.*, 2005). Another ash-fall locality is dominated by ferns (*Acrostichum*), suggesting edaphically wet and perhaps saline- or nutrient-limited habitat (J. L. Garcia Massini, B. Jacobs and A. Pan, unpubl.; Jacobs *et al.*, 2005). The numerous tuff deposits probably represent a variety of environments, but they all indicate mesic settings, some of which would have supported forest vegetation.

The tuffaceous ironstone deposits include *Hyphaene* petioles or petiole fragments (described below; Figs 4, 5) that represent the earliest definitive occurrence of the genus in Africa (Table 1). These are documented at the north end of the basin in association with dicotyledonous fruits and seeds, and large mammals (Kappelman *et al.*, 2003; Sanders, Kappelman & Rasmussen, 2004).

A well studied example of the Chilga overbank (or pond) deposits occurs along a stream cut of the Guang River where a deposit is continuously exposed laterally for about 80 m. This mudstone is approximately 22 cm thick and preserves the organic compressions of about 40 angiosperm leaf and floral taxa. The Guang River flora represents a tropical moist forest, a hypothesis based on the occurrence of numerous species bearing leaves with entire margins (> 90%), many leaf species of mesophyll size and laterally heterogeneous composition across distances as small as 10 m within the same bed (Jacobs *et al.*, 2005). The presence of taxa such as *Sorindeia*, *Dioscorea* and cf. *Mimusops* is consistent with a forest community. There are also at least four species of palm in the subfamilies Calamoideae, Coryphoideae and (probably) Arecoideae (unarmed, pinnate, multifolded, reduplicate leaflets), two of which are described below. These fossils include the earliest record of *Eremospatha* (Fig. 2; Table 1), a heavily armed, endemic, African rattan genus found today in tropical moist forest formations, swamps and forest margins (Tuley, 1995). The deposit also includes a petiole of *Hyphaene* (Fig. 3), almost certainly a dif-



**Figures 2–6.** *Hyphaene* petioles. Scale bars : 10 mm. Figs 2, 3. *Hyphaene kappelmanii* Pan *et al.* **sp. nov.** Tuffaceous ironstone deposit. Fig. 2. *H. kappelmanii* Holotype CH8- 6. Fig. 3. *H. kappelmanii* CH8-E. Fig. 4. *Hyphaene* sp. Guang River flora, an overbank deposit. Figs 5, 6. Extant *Hyphaene* species. Fig. 5. *H. compressa*. Fig. 6. *H. coriacea*.

ferent species from that of the tuffaceous ironstone deposit discussed above (formally described below). All specimens will be permanently housed at the National Museum of Ethiopia, Addis Ababa.

## DESCRIPTIONS OF THE PALM FOSSILS

ARECACEAE SCHULTZ SCH. 1832; CORYPHOIDEAE

BURNETT 1835; BORASSEAE MART. 1837

HYPHAENINAE BECC. 1924

*HYPHAENE* GAERTN. 1788

***HYPHAENE KAPPELMAII* SP. NOV.** A. D. PAN, B. F. JACOBS, J. DRANSF. & W. J. BAKER

**Diagnosis:** The petiole (holotype) is 102 mm in length and 14.17–17.74 mm in width (Fig. 2). The petiole spines in both specimens (CH8-6 and CH8-E) are 8–20.19 mm in length, averaging 13 mm (Figs 2, 3). The spines are spaced 12–19 mm apart along the petiole and are large, flattened, curved and may occasionally be paired (Figs 2, 3). The bases of the spines are broad and form extended, arcuate connections with adjacent spines (Figs 2, 3).

**Holotype:** CH8-6 (Fig. 2).

**Paratype:** CH8-E (Fig. 3).

**Etymology:** The epithet honours Dr John Kappelman, who found the fossil petioles and was leader of fieldwork at Chilga in 1997, 2001 and 2003.

**Locality:** These fossils were found in a tuffaceous ironstone deposit of Late Oligocene age (28–27 Mya) located at N 12°29', E 37°12'.

**Comments:** The petiole is referred to the genus *Hyphaene* (tribe Borasseae) based on the presence of the following characteristics of the spines: (1) robust, curved and generally uniform in size, shape and spacing; (2) the bases are broad, flattened and not noticeably bulbous. The fossil differs from other genera within subtribe Hyphaeninae, including *Bismarkia* and *Medemia*, which have unarmed petioles, and *Satranala*, which has armed petioles with minute irregular teeth (Uhl & Dransfield, 1987; Dransfield & Beentje, 1995a). The fossil also differs from genera of subtribe Lataniinae, including *Borassus* (coarse, irregular teeth along the petiole margin), *Borassodendron*, which has sharp, nonspinose margins, and *Latania* and *Lodoicea*, which have unarmed margins (Uhl & Dransfield, 1987). Petiole spines in *Hyphaene* differ from those in *Livistona* (Coryphoideae: Corypheeae, Livistoninae), which are typically bulbous at the base and can vary significantly in size, large spines alternating with one or two small ones.

*Hyphaene kappelmanii* petioles can be identified readily based on the large (mainly longer than 10 mm), upturned, robust spines (sometimes paired), flattened, broad spine bases and the distinctive arcuate shape of the petiole edge between the spines, characteristics which, taken together, distinguish this fossil from living species of *Hyphaene* and from the Guang River *Hyphaene* described below.

Extant *Hyphaene* occur from Africa to India and Sri Lanka in arid and semiarid environments. They are usually associated with seasonal water courses, coastal sand dunes and flats, and oases. Less frequently they are found in gallery and coastal forests (Uhl & Dransfield, 1987; Dransfield & Beentje, 1995b). *Hyphaene* still occurs in Ethiopia and may have been present continuously in the region since the Oligocene.

ARECACEAE SCHULTZ SCH. 1832; CORYPHOIDEAE  
BURNETT 1835; BORASSEAE MART. 1837

HYPHAENINAE BECC. 1924

*HYPHAENE* GAERTN. 1788

*HYPHAENE* SP.

**Diagnosis:** An incomplete petiole is 72 mm in length and 32.45 mm in width (Fig. 4). Two petiole spines are 6.76–7.44 mm in length and are spaced 5.07 mm apart from each other (Fig. 4). The spines are flattened, curved and broad at the base, measuring 4.32–6.72 mm (Fig. 4).

**Specimen:** CH54-2 (Fig. 4).

**Locality:** The fossil is from an overbank or pond deposit consisting of volcanoclastic mudstone located at N 12°30', E 37°07', and is from an assemblage named here as the Guang River flora. The flora and the fossil are Late Oligocene (28–27 Mya) in age.

**Comments:** The fossil *Hyphaene* has spines that are most similar in size and shape to those of *Hyphaene compressa* H. Wendl. (Fig. 5) and, to a lesser extent, *H. coriacea* (Fig. 6). *Hyphaene compressa* inhabits coastal forest, floodplains and palm savannahs in Kenya and Tanzania, while *H. coriacea* is commonly found on sand dunes and along creeks behind mangroves from Somalia to Mozambique, South Africa and Madagascar (Dransfield, 1986).

ARECACEAE SCHULTZ SCH. 1832; CALAMOIDEAE  
BEILSCHM. 1833 ; LEPIDOCARYEAE MART.  
EX DUMORT. 1829

ANCISTROPHYLLINAE BECC. 1918

*EREMOSPETHA* (G. MANN & H. WENDL.)

H. WENDL. 1878

***EREMOSPETHA CHILGAENSIS* SP. NOV.** A. D. PAN,  
B. F. JACOBS, J. DRANSF. & W. J. BAKER

**Diagnosis:** A single incomplete leaflet is 25 mm in length and widens towards the apex from 1.10 to 6.80 mm (Fig. 7A). The base is acute and robust. The margin is thickened compared with the rest of the

laminar surface and is 1.15–1.61 mm in width (Fig. 7B). A single spine near the base is 3.69 mm in length and robust, upturned and rounded at the tip (Fig. 7). The base of the spine is nonbulbous and has distinctive wrinkles approximately parallel to the leaflet (Fig. 7B). The spine is angled at 43° from the leaf margin. The leaflet has a single primary vein extending the length of the fossil, and secondary veins diverge from the base towards the apex (Fig. 7A).

**Holotype:** CH54-33 (Figs 7A, B).

**Etymology:** The specific epithet refers to the locality, Chilga Woreda, Ethiopia.

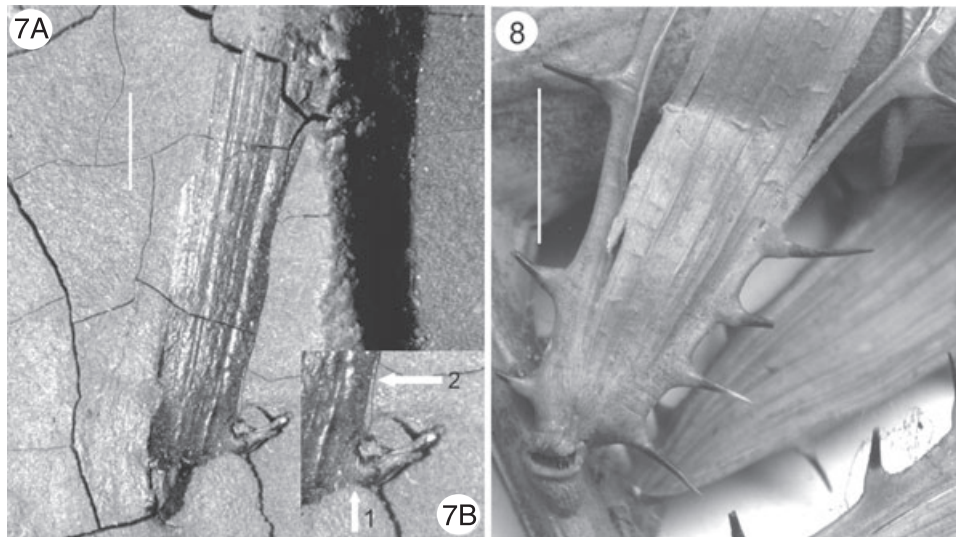
**Locality:** Located at N 12°30', E 37°07', within the Late Oligocene (28–27 Mya) Guang River flora.

**Comments:** Living *Eremospatha* species are distinct from the remaining genera of the endemic African rattan subtribe Ancistrophyllinae, *Laccosperma* and *Oncocalamus*, and palms in general, by having heavily armed, thickened, reduced proximal leaflets with robust spines (Tuley, 1995; Sunderland, 2001). The leaflet margins are also thickened. *Laccosperma* differs from the fossil and from *Eremospatha* in having leaflets with nonthickened margins and spines that are more slender. Some species of *Oncocalamus* have thickened lamina margins, but less pronounced than in *Eremospatha*, or a thickened margin restricted to the base of the spines. The more distantly related *Raphia* has spines that are flattened, short (usually only 1–2 mm) and more acute with respect to the petiole. The Asian calamoid genera, including *Calamus* to which the disjunct African endemic *C. deeratus* belongs, differ from *Eremospatha* in having slender spines and leaflets with nonthickened margins.

The fossil is most similar to *Eremospatha dransfieldii* Sunderland (Fig. 8) and *E. macrocarpa* H. Wendl., both of which have robust, rounded spines and thickened margins. However, these species differ from the fossil by having several primary veins and spines that are bulbous or flattened at the base (Sunderland, 2003). *Eremospatha* is distributed today in lowland forests of West Africa and the Congo Basin, with disjunct occurrences in Uganda, Tanzania and Zambia (Sunderland, 2001). Thus, *Eremospatha* was eliminated from Ethiopia some time after the Late Oligocene.

## DISCUSSION

Perhaps the most interesting aspect of African palms is their limited number and diversity when compared with other tropical regions of the world. What we see today is the result of a combination of climatic, bioge-



**Figures 7, 8.** *Eremospatha* proximal leaflets. Scale bars: 5 mm. Fig. 7. *Eremospatha chilgaensis* Pan *et al.* **sp. nov.** Holotype CH54-33 from the Guang River flora, an overbank deposit. A, Leaflet with a proximal robust spine. B, Close-up of the leaflet spine. Note the distinctive wrinkles running parallel to the leaflet (1). Note the thickened margin in comparison with the rest of the laminar surface (2). Fig. 8. *Eremospatha dransfieldii*. Note the thickened margin that is tearing away towards the apex.

graphical and evolutionary factors. These historical factors either reduced the number and diversity of palms from an original diverse stock, or limited speciation in Africa relative to other tropical regions, or both. The plant fossil record offers the best opportunity to investigate the impact of historical factors on diversity and abundance, and this same record can provide data for tests of hypothesized origination times based upon phylogenetic studies of living material. Despite the incompleteness of the fossil record, especially in Africa, changes in palm diversity through time are apparent and abundances can be estimated qualitatively.

The fossil pollen record documents similarly diverse and abundant palm floras across the tropical regions of South America, Africa and, to a lesser extent, south-east Asia during the Maastrichtian, presumably a reflection of evolutionary diversification following earlier Cretaceous *Arecaceae* origins. Although a careful comparison of South American and African palynofloras is required, the data are consistent with the hypothesis that these two continents had floristically similar palm floras during the Late Cretaceous when they were geographically close (Scotese, Gahagan & Larson, 1988; Hengreen *et al.*, 1996).

The first significant decline in African palm diversity, documented primarily by pollen records from West Africa, took place at, or soon after, the Cretaceous–Palaeogene boundary (65 Mya) or prior to the end of the Palaeocene. However, perhaps more important was the turnover and decline in fossil pollen

species at or near the Eocene–Oligocene boundary (34 Mya; Morley, 2000) documented almost entirely by West African pollen records. The Chilga palm flora serves as a test of the geographical magnitude of this change as it provides an inland assemblage from eastern tropical Africa. While Chilga fossils document the importance of palms in some Late Oligocene communities, the identified palm genera are all first occurrences and can be found in Africa today. That is, these taxa differ from those present among pre-Oligocene West African pollen assemblages, indicating that changes in species number and composition at or near the boundary were not limited to West Africa.

The fossil record has something to contribute to understanding the depauperate nature of *Arecaceae* in Africa today in comparison with South America and south-east Asia, but pinpointing whether these differences are due to relatively greater numbers of extinctions, fewer originations or both is difficult to tease apart. The data show that when palms experienced a significant turnover and decline at or near the Eocene–Oligocene boundary, there was a tremendous diversification of angiosperm pollen in West Africa (Salard-Cheboldaëff, 1979, 1981; Salard-Cheboldaëff & DeJax, 1991). Salard-Cheboldaëff (1979, 1981) and Salard-Cheboldaëff & DeJax (1991) interpreted this as representing the evolution and expansion of West African lowland forest. We would expect palms to play a significant role in that evolutionary diversification or occupy an important ecological position in such lowland forests. However, the African plant fossil record

documents little evidence for forest palm diversification following the boundary event. We favour the view that as extinctions and extirpations occurred, originations of palms in Africa were relatively limited while other angiosperms diversified, perhaps due to a declining Areaceae gene pool and generally limited immigration to an isolated continent.

#### ACKNOWLEDGEMENTS

We thank the Authority for Research and Conservation of Cultural Heritage, the Ministry of Culture and Sports Affairs, Ethiopia, particularly Ato Jara, for permission to conduct our ongoing research at Chilga, the director and staff of the National Museum, Addis Ababa and the Royal Botanic Gardens Kew for their assistance with collections, and the Gondar ARCCH and Chilga Ministry of Culture and Sports Affairs for logistical support. This project was funded by grants from the National Science Foundation EAR-0001259 and EAR-0240251, the National Geographic Society, and the Institute for the Study of Earth and Man at Southern Methodist University. Tillehun Selassie, Misege Birara, Habtewold Habtemichael, Mesfin Mekonnen and Drs Ambachew Kebede and Aklilou Asfaw provided valuable field assistance. We thank: Drs Margaret Collinson and Bruce Tiffney for generously sharing information about Rusinga, Kenya and Fayum, Egypt, respectively; Dr Madeline Harley for advice about the fossil palm pollen record; Dr Terry Sunderland for advice and information about African rattans; Dr Ross Bayton for advice and information about the Borasseae; and Dr Scott Zona and the Fairchild Tropical Botanic Garden for advice and for cuticle specimens, respectively. We gratefully acknowledge help from Chilga field assistants Yohannes Desta, Yeshiwass Sitotaw, Gebremeskel Ayele, Elias Addissu and Teshome Yohannes. Finally, we would like to thank the Linnean Society and the organizers of the Palm symposium for the invitation to present this paper and for funds to attend the symposium. We would also like to thank Drs Scott Zona and Robyn Burnham, as well as an anonymous reviewer, for several helpful comments that significantly improved this paper.

#### REFERENCES

- Aubreville A. 1970.** La flore tropicale Tertiaire du Sahara. *Adansonia Series 2* **10**: 9–14.
- Axelrod DI, Raven PH. 1978.** Late Cretaceous and Tertiary vegetation history of Africa. In: Werger MJA, ed. *Biogeography and ecology of Southern Africa*. The Hague: W. Junk, 77–130.
- Bonnefille R, Riollet G. 1987.** Palynological spectra from the Upper Laetoli Beds. In: Leakey MD, Harris JM, eds. *Laetoli: a Pliocene site in northern Tanzania*. Oxford: Clarendon Press, 52–61.
- Boureau E, Prakash U. 1968.** Sur un pétiole fossile de palmier de Tiemassas (Sénégal) et sur son mode d'accroissement diamétral. *Palaeobotanist* **17**: 247–253.
- Bown TM, Kraus KJ, Wing SL, Fleagle JG, Tiffney BH, Simons EL, Vondra CF. 1982.** The Fayum primate forest revisited. *Journal of Human Evolution* **11**: 603–632.
- Cande SC, Kent DV. 1995.** Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *Journal of Geophysical Research* **100**: 6093–6095.
- Chandler MEJ. 1954.** Some Upper Cretaceous and Eocene fruits from Egypt. *Bulletin of the British Museum (Natural History), Geology* **2**: 147–187.
- Chesters KIM. 1957.** The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica B* **101**: 30–71.
- Chiarugi A. 1933.** Legni fossili della Somalia Italiana. *Palaeontographia Italia* **32**: 97–167.
- Coetsee JA. 1993.** African flora since the terminal Jurassic. In: Goldblatt P, ed. *Biology relationships between Africa and South America*. New Haven: Yale University Press, 37–61.
- Coetsee JA, Rogers J. 1982.** Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* **39**: 71–85.
- Dechamps R. 1987.** Xylotomy of fossil wood from the Sahabi Formation. In: Boaz NT, El-Arnauti A, Gaziry AW, de Heinzelin J, Boaz DD, eds. *Neogene paleontology and geology of Sahabi*. New York: Alan R. Liss Inc., 37–41.
- Dechamps R, Maes F. 1987.** Paleoclimatic interpretation of fossil wood from the Sahabi Formation. In: Boaz NT, El-Arnauti A, Gaziry AW, de Heinzelin J, Boaz DD, eds. *Neogene paleontology and geology of Sahabi*. New York: Alan R. Liss Inc., 43–81.
- Dechamps R, Maes F. 1990.** Woody plant communities and climate in the Pliocene of the Semliki Valley, Zaire. In: Boaz NT, ed. *Evolution of environments and Hominidae in the African Western Rift Valley*. Martinsville: Virginia Museum of Natural History, 71–94.
- Dechamps R, Senut B, Pickford M. 1992.** Fruits fossils pliocènes et pléistocènes du Rift Occidental ougandais. Signification paléoenvironnementale. *Comptes Rendus de l'Académie des Sciences Paris, Série II* **314**: 325–331.
- Dransfield J. 1986.** Palmae. In: Polhill RM, ed. *Flora of tropical East Africa*. Rotterdam: A.A. Balkema, 1–55.
- Dransfield J. 1988.** The palms of Africa and their relationships. In: Goldblatt P, Lowry PP, eds. *Systematic studies in African botany*. St. Louis: Missouri Botanical Garden Press, 95–103.
- Dransfield J, Beentje HJ. 1995a.** *Satranala* (Coryphoideae: Borasseae: Hyphaeninae), a new palm genus from Madagascar. *Kew Bulletin* **50**: 85–92.
- Dransfield J, Beentje HJ. 1995b.** *The palms of Madagascar*. Kew: Royal Botanic Gardens Press.
- Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2005.** A new phylogenetic classification of the palm family, Areaceae. *Kew Bulletin* **60**: 559–569.
- El-Saadawi W, Youssef SG, Kamal-El-Din MM. 2004.** Fossil

- palm woods of Egypt: II. seven Tertiary *Palmoxylon* species new to the country. *Review of Palaeobotany and Palynology* **129**: 199–211.
- Ergo AB.** 1997. Nouvelle evidence de l'origine africaine de l'*Elaeis guineensis* Jacq. Par la découverte de graines fossiles en Uganda. *Annales de Gembloux* **102**: 191–201.
- Fritel PH.** 1921. Sur deux fruites fossiles trouvés au Sénégal, dans l'Eocène moyen. *Bulletin du Comité d'Études Historiques et Scientifiques de l'Afrique Occidentale Française* **4**: 549–552.
- Govaerts R, Dransfield J.** 2005. *World checklist of palms*. Kew: Royal Botanic Gardens Press.
- Gregor HJ, Hagn H.** 1982. Fossil fructifications from the Cretaceous–Palaeocene Boundary of SW-Egypt (Danian, Bir Abu Munqar). *Tertiary Research* **4**: 121–147.
- Harley MM, Baker WJ.** 2001. Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of the fossil record of palm-like pollen. *Grana* **40**: 45–77.
- Harley MM, Hall DH.** 1991. Pollen morphology of the African palms. *Palaeoecology of Africa and the Surrounding Islands* **22**: 11–25.
- Henderson A, Galeano G, Bernal B.** 1995. *Field guide to the palms of the Americas*. Princeton: Princeton University Press.
- Herngreen GFW.** 1980. Cretaceous microfloral provinces. (Abstract). *Berliner Geowissenschaft Abhandlungen A* **19**: 79–82.
- Herngreen GFW, Chlonova AF.** 1981. Cretaceous microfloral provinces. *Pollen et Spores* **23**: 441–555.
- Herngreen GFW, Kedves M, Rovinina LV, Smirnova SB.** 1996. Cretaceous palynofloral provinces: a review. In: Jansonius J, Mcgregor DC, eds. *Palynology: principles and applications*. Dallas: American Association of Stratigraphic Palynologists Foundation, 1157–1188.
- van Hoeken-Klinkenberg PMJ.** 1966. Maastrichtian, Paleocene and Eocene pollen and spores from Nigeria. *Leidse Geologische Mededelingen* **38**: 37–48.
- Jacobs BF.** 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society of London B* **359**: 1573–1583.
- Jacobs BF, Tabor N, Feseha M, Pan A, Kappelman J, Rasmussen T, Sanders W, Wiemann Crabaugh J, Garcia Massini JL.** 2005. Oligocene-age (32.7–27.5 MA) terrestrial strata of northwestern Ethiopia: lithology, paleontology, and paleoclimate. *Palaeontologia Electronica* **8**: 25A: 1–19; [http://palaeoelectronica.org/2005\\_1/jacobs25/issue1\\_05.htm](http://palaeoelectronica.org/2005_1/jacobs25/issue1_05.htm).
- Jan du Chêne RE, Onyike MS, Sowunmi MA.** 1978. Some new Eocene pollen of the Ogwasbi-Asaba Formation, south-eastern Nigeria. *Revista Española de Micropaleontología* **10**: 285–322.
- Jardiné S, Magloire L.** 1965. Palynologie et stratigraphie du Cretace des bassins du Sénégal et de Côte D'Ivoire. *Mémoires du Bureau de Recherches Géologiques Ministère* **32**: 187–245.
- Kappelman J, Rasmussen DT, Sanders WJ, Feseha M, Bown T, Copeland P, Crabaugh J, Fleagle J, Glantz M, Gordon A, Jacobs B, Maga M, Muldoon K, Pan A, Pyne L, Richmond B, Ryan T, Seiffert ER, Sen S, Todd L, Wiemann MC, Winkler A.** 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature* **426**: 549–552.
- Kräusel R.** 1939. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. *Abhandlungen der Bayerischen Akademie der Wissenschaften Neue Folge* **47**: 1–140.
- Lakhanpal RN.** 1966. Some middle Tertiary plant remains from South Kivu, Congo. *Annales du Musée Royal de l'Afrique Centrale Serie 8* **52**: 21–30.
- Legoux O.** 1978. Quelques espèces de pollen caractéristiques du Neogene du Nigeria. *Bulletin Centre Recherche Exploration-Production Elf-Aquitaine* **2**: 265–317.
- Lemoigne Y.** 1978. Flores Tertiaires de la Haute Vallée de L'Omo (Ethiopie). *Palaeontographica B* **165**: 89–157.
- Mahmoud MS.** 2003. Palynology and palaeoenvironment of the Quseir Formation (Campanian) from central Egypt. *Journal of African Earth Sciences* **36**: 135–148.
- Maley J, Brenac P.** 1998. Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Review of Palaeobotany and Palynology* **99**: 157–187.
- Medus J.** 1975. Palynologie de sédiments Tertiaires du Sénégal méridional. *Pollen et Spores* **17**: 545–601.
- Mendis NM, Ferguson IK, Dransfield J.** 1987. The pollen morphology of the subtribe Oncospermatinae (Palmae: Arecoideae: Areceae). *Kew Bulletin* **42**: 47–63.
- Menzel P.** 1920. Über Pflanzenreste aus Basalttuffen des Kamerungebietes. *Beiträge zur Geologischen Erforschung der Deutschen Schutzgebiete* **18**: 17–32.
- Meon H.** 1990. Palynologic studies of the Cretaceous–Tertiary boundary interval at El Kef outcrop, northwestern Tunisia: paleogeographic implications. *Review of Palaeobotany and Palynology* **65**: 85–94.
- Monteillet J, Lappartient J.** 1981. Fruits et graines du Cretace-Superieur des Carrieres de Paki (Senegal). *Review of Palaeobotany and Palynology* **34**: 331–344.
- Moore HE, Jr.** 1973. Palms in the tropical forest ecosystems of Africa and South America. In: Meggers BJ, Ayensu ES, Duckworth WD, eds. *Tropical forest ecosystems in Africa and South America: a comparative review*. Washington, D.C.: Smithsonian Institution Press, 63–88.
- Morley RJ.** 1978. Palynology of Tertiary and Quaternary sediments in southeast Asia. In: *Proceedings of Indonesian Petroleum Association 6th Annual Convention*, 255–276.
- Morley RJ.** 2000. *Origin and evolution of tropical rain forests*. Chichester: John Wiley and Sons, Ltd.
- Nichols DJ, Ames HT, Traverse A.** 1973. On *Arecipites* Wodehouse, *Monocolpopollenites* Thomson & Pflug, and the species '*Monocolpopollenites tranquillus*'. *Taxon* **22**: 241–256.
- Richards PW.** 1996. *The tropical rain forest*, 2nd edn. Cambridge: Cambridge University Press.
- Salard-Cheboldaeff M.** 1979. Palynologie Maestrichtienne et Tertiaire du Cameroun. Étude qualitative et repartition verticale des principales especes. *Review of Palaeobotany and Palynology* **28**: 365–388.
- Salard-Cheboldaeff M.** 1981. Palynologie Maestrichtienne et

- Tertiaire du Cameroun. Resultats botaniques. *Review of Palaeobotany and Palynology* **32**: 401–439.
- Salard-Cheboldaeff M. 1990.** Intertropical African palynostratigraphy from Cretaceous to Late Quaternary times. *Journal of African Earth Sciences* **11**: 1–24.
- Salard-Cheboldaeff M, Dejax J. 1991.** Evidence of Cretaceous to Recent West African intertropical vegetation from continental sediment spore-pollen analysis. *Journal of African Earth Science* **12**: 353–361.
- Sanders WJ, Kappelman J, Rasmussen DT. 2004.** New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica* **49**: 365–392.
- Schrank E. 1992.** Nonmarine Cretaceous correlations in Egypt and northern Sudan: palynological and palaeobotanical evidence. *Cretaceous Research* **13**: 351–368.
- Schrank E. 1994.** Palynology of the Yesomma Formation in northern Somalia: a study of pollen, spores and associated phytoplankton from the Late Cretaceous Palmae Province. *Palaeontographica Abteilung B* **231**: 63–112.
- Schrank E, Awad MZ. 1990.** Palynological evidence for the age and depositional environment of the Cretaceous Omdurman Formation in the Khartoum area, Sudan. *Berliner Geowissenschaft Abhandlungen A* **120**: 169–182.
- Scotese CR, Gahagan LM, Larson RL. 1988.** Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins. *Tectonophysics* **155**: 27–48.
- Sowunmi MA. 1999.** The significance of the oil palm (*Elaeis guineensis* Jacq.) in the late Holocene environments of West and west central Africa; a further consideration. *Vegetation History and Archaeobotany* **8**: 199–210.
- Sunderland TCH. 2001.** The taxonomy, ecology and utilization of African rattans (Palmae: Calamoideae). D. Phil Thesis, University College London.
- Sunderland TCH. 2003.** Two new species of rattan (Palmae: Calamoideae) from the forests of West and Central Africa. *Kew Bulletin* **58**: 987–990.
- Tiffney BH. 1991.** Paleoenvironment of the Oligocene Jebel Qatrani Formation, Fayum Depression, northern Egypt, based on floral remains. *Geological Society of America Abstracts* **23**: 456.
- Tiffney BH. 2004.** Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution and Systematics* **35**: 1–29.
- Tomlinson PB. 1990.** *The structural biology of palms*. Oxford: Oxford Science Publications.
- Tralau H. 1964.** The genus *Nypa* van Wurmb. *Kungl Svenska Vetenskapsakademiens Handlingar* **10**: 5–29.
- Tuley P. 1995.** *The palms of Africa*. St. Ives: Trendrline Press.
- Uhl NW, Dransfield J. 1987.** *Genera Palmarum: a classification of palms based on the work of Harold E. Moore, Jr.* Lawrence: Allen Press.
- Vaudois-Miéja N, Lejal-Nicol A. 1987.** Paléocarpologie africaine: apparition des l'Aptien en Égypte d'un palmier (*Hyphaeneocarpon aegyptiacum* n. sp.). *Comptes Rendus de l'Académie des Sciences Paris Série II* **304**: 233–238.
- Vincens A. 1993.** Nouvelle sequence pollinique du lac Tanganyika: 30,000 ans d'histoire botanique et climatique du bassin Nord. *Review of Palaeobotany and Palynology* **78**: 381–394.
- Vincens A, Tiercelin J-J, Buchet G. In press.** New Oligocene-early Miocene microflora from the southwestern Turkana Basin. Palaeoenvironmental implications in the northern Kenya Rift. *Palaeogeography, Palaeoclimatology, Palaeoecology* in press.
- Zetter R, Hesse M, Frosch-Radivo A. 2001.** Early Eocene zona-aperturate pollen grains of the *Proxapertites* type with affinity to Araceae. *Review of Palaeobotany and Palynology* **117**: 267–279.