Plant turnover in response to climate change in the Cenozoic: Palynological insights from Myanmar, Southeast Asia and beyond

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Eocene palms from central Myanmar in a South-East Asian and global perspective: evidence from the palynological record

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In the Paleogene, pollen assemblages at low and mid latitudes are characterized by abundant palm and palm-like (PPL) taxa. Although these taxa have been widely reported, their occurrence in the Paleogene of Myanmar remains poorly documented. Here we report on the morphology of PPL pollen along a middle to upper Eocene sedimentary sequence in central Myanmar and discuss their nearest living relatives (NLRs). Principal components analysis (PCA) indicates that *Palmaepollenites kutchensis*, *Dicolpopollis* and *Longapertites* were dispersed from freshwater plants, while the parent taxon of *Proxapertites operculatus* was probably a member of the coastal vegetation in the manner of *Spinizonocolpites*. This, together with sedimentological data, suggests a paleoenvironmental change from a brackish tidally-influence environment to a fully freshwater setting through the late Eocene. Additionally, we mapped and compared the geographic distribution of selected Eocene palm taxa and their NLRs, and found that their distributional ranges shrank after the Eocene. Moreover, in the Paleogene species diversity of selected PPL taxa seems lower in Myanmar than in the Indian subcontinent and other regions in SE Asia. We hypothesize that in the Eocene the India-Asia collision zone formed a “hotspot” for palm diversity, which is reflected in species-rich palynofloras. However, the local palm diversity declined after the Eocene, while at global level palm distribution distinctly was reduced between the Eocene and present. We propose that the retreat of the palms may have occurred as early as the Eocene–Oligocene transition (EOT), which remains to be confirmed by the study of EOT pollen records in tropical regions.
4.1 | INTRODUCTION

The Central Myanmar Basin (CMB) has yielded an extremely rich fossil record including mammals (e.g., Chavasseau et al., 2010; De Bonis et al., 2018; Jaeger et al., 1999) and wood (e.g., Gottwald, 1994; Licht et al., 2014a, 2015; Privé-Gill et al., 2004). Palynological studies with focus on the CMB are rare (e.g., Engelhardt and Wrenn, 1994; Potonié, 1960; Reimann and Aye Thaung, 1981). Yet this area is of great interest, particularly for the paleoecology of palm taxa, which have implications for the paleoenvironmental interpretation of the CMB. A >1 km-thick middle to upper Eocene sedimentary sequence in the CMB near the Kalewa Township was recently dated at c. 38.3±0.7-0.9 Ma based on analysis of a tuff layer (Licht et al., 2019). This provides an excellent opportunity to determine how the palynological record in the CMB relates to the India-Asia tectonic convergence and the climate change preceding the EOT (as discussed by Abels et al., 2011; Coxall and Pearson, 2007; Dupont-Nivet et al., 2008; Hoorn et al., 2012).

In this study we address the following questions: Which PPL pollen occur in the sedimentary record at Kalewa? What are their paleoecological implications? How do these pollen types compare with morphotaxa from Paleogene records of adjacent regions? What is the species diversity of these taxa in the region during the Paleogene? Are there differences in the distribution of nearest living relatives (NLRs) and their fossil counterparts? Are there any environmental shifts detected by the compositional changes of these PPL taxa? And finally, what can this new record – placed in a global context – add to our understanding of palm paleobiogeography?

To answer these questions we: (1) described morphological characteristics of PPL pollen along the section near Kalewa; (2) quantified and analyzed pollen types and applied principal components analysis (PCA) in order to determine ecological and environmental changes in the Eocene coastal systems of the CMB; (3) correlated sedimentary changes with sporomorphs composition throughout the studied section, allowing for a better understanding of the paleoecology of the plants producing the PPL pollen for which their NLRs are uncertain (Proxapertites, Longapertites and Palmaepollenites kutchensis); and finally (4) compiled Eocene records of palm pollen taxa and generated maps using GPlates for spatiotemporal comparisons in species distribution and diversity across the globe.

4.2 | REGIONAL SETTING
The studied section is situated near the Kalewa Township in the Sagaing Region, the southern part of the Chindwin sub-basin of the CMB, and northwestern part of the Burma Terrane (BT; Fig. 4.1A; 23°14′ N, 94°15′ E). At c. 40 Ma the CMB was located at the margin of Eurasia and was open towards the Indian Ocean, forming an embayment that was the locus of SW-directed deltas (Fig. 4.1B; Licht et al., 2013; Westerweel et al., 2019). During this time the inner wedge of the Indo-Burman Ranges emerged, providing a barrier that partly closed the embayment (Licht et al., 2019); the BT was located in a more southerly, near-equatorial position (Westerweel et al., 2019).

The c. 650 m-thick sedimentary sequence at Kalewa comprises the Yaw Formation and includes four facies associations deposited in an estuarine system (Licht et al., 2019). Mostly, the sediments consisted of clastic sands and muds primarily provided by the unroofing of the Wuntho-Popa volcanic arc that extended onto the Burmese margin, along the flank of the modern Sino-Burman Ranges (Fig. 4.1A; Licht et al., 2013, 2016, 2019). The studied sedimentary section starts at c. 500 m above the boundary of the Yaw Formation and the underlying Pondaung Formation. This boundary is marked by the first occurrence of lignite seams and black mudstones and dated at c. 39 Ma (Licht et al., 2019). The unconformably overlying Letkat Formation consists of coarse fluviatile clastics (Bender, 1983). A dated tuff layer, of c. 38.3 Ma, is positioned at c. 500 m above the basis of the section, in the upper third of the profile. Sedimentation rates for most of the Yaw Formation are estimated at > 1m/kyr (Licht et al., 2019). Therefore, the studied section is dated as late Bartonian, and likely extends to the early Priabonian up-section.

4.3 | PALMS AND THEIR PALEOBIOGEOGRAPHIC CONTEXT

Palms (Arecaceae or Palmae) comprise 181 genera with c. 2600 species (Christenhusz and Byng, 2016), most of which are currently restricted to tropical and subtropical regions (Couvreur et al., 2011). They are an ancient group, with a molecular age of c. 114 Ma (Couvreur et al., 2011) and fossils dating back to the Turonian (93.5-89.0 Ma; Crié, 1892; Kvaček and Herman, 2004); the group predominated throughout the equatorial zone during the latest Cretaceous and Paleocene (Morley, 2000). In the Maastrichtian, PPL
Fig. 4.1. Location and stratigraphy of the study area (red square). (A) Schematic map showing the study area in the CMB, made with GeoMapApp version 3.6.10. Light orange shading outlines the CMB; yellow shading outlines the Chindwin sub-basin; black dash line marks the Myanmar borders. Positions of the IBR, Sino-Burman Ranges, and the CMB refer to Licht et al. (2014b), while the Chindwin sub-basin follows Licht et al. (2019). It also shows the location (blue square) of Nanggulan (Indonesia) which was used for comparison in the following several texts. (B) Location of Burma Terrane at 40 Ma, modified after Westerweel et al. (2019). (C) Simplified log showing the position of the studied section in the entire stratigraphy of the Chindwin sub-basin, CMB, modified after Licht et al. (2019). Abbreviations: (A) IBR = Indo-Burman Ranges, WPA = Wuntho-Popa volcanic arc, indicated by the red dash line. (B) BT = Burma Terrane, EA = Eastern Andaman, IB = Indochina Blocks, GI = Greater India, LT = Lhasa Terrane, SB = Sibumasu Block, SL = Sundaland. (C) vfs = very fine sand, fs = fine sand, ms = medium sand, cs = coarse sand.
pollen of the form-genera *Spinizonocolpites*, *Palmaepollenites*, *Longapertites* and *Proxapertites* are found widely across the Paleotropics (e.g., Eisawi and Schrank, 2009; Herngreen et al., 1996; Vergara and Rodriguez, 1997). The form-taxon *Dicolpopollis*, characteristic of the subtribe Calaminae (Harley and Morley, 1995), first appears in the Maastrichtian of Somalia (Schrank, 1994) and subsequently in the Paleocene of the Sunda region (Muller, 1968) and China (Sun et al., 1981). There are questionable records from India, such as *D. kalewensis* from the Paleocene Nindam Formation (Mathur and Jain, 1980). *Dicolpopollis* expanded its range during the Eocene to Australia (MacPhail et al., 1995) and New Zealand (Hartwich et al., 2010), as well as central Europe (Bignot et al., 1985; Riegel et al., 2012) and southern North America (Harrington, 2008).

Zonasulcate taxa, such as *Spinizonocolpites* and *Proxapertites*, are characteristic of the Upper Cretaceous and Paleocene Palmae Province (Herngreen et al., 1996) and are widely reported from Paleogene coastal records (e.g., Oman: Beialy, 1998; India: Prasad et al., 2013; Tripathi et al., 2009; Africa: Jacobs et al., 2010; Australia: Macphail and Hill, 2019; Côte d'Ivoire: Guédé et al., 2019). *Spinizonocolpites* and *Proxapertites* have long been considered to be derived from plants growing in humid tropical mangrove environments (Digbehi et al., 1996; Germeraad et al., 1968; Herngreen, 1998; Schrank, 1987, 1994), with the latter also occurring in freshwater settings (Jaramillo et al., 2007). In contrast, the ecological indication of *Dicolpopollis* always points to a freshwater vegetation (Morley et al., 2019).

### 4.4 MATERIALS AND METHODS

#### 4.4.1 Samples and palynological processing

During fieldwork in 2016 and 2017, 81 samples were collected from clay, silt and fine sandstone units. The palynological processing of samples was performed at the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, The Netherlands. For this purpose, 1.3 grams of sedimentary rock sample was boiled in 10% sodium pyrophosphate to disaggregate the matrix. Then 10% hydrochloric acid (HCl) was used to remove the calcium carbonate. Sieves with 5 μm and 212 μm meshes were used. The sample material was heated in acetolysis mixture (9 parts of acetic anhydride and 1 part of concentrated sulfuric acid) to 100 °C. Bromoform-treatment (gravity = 2.0) was applied to
separate any remaining inorganic fraction. The resulting organic residue was mounted on a slide in glycerin and sealed with paraffin for the observation with light microscope (LM). To ensure maximum recovery, an additional preparation method was conducted on samples 16MAP001, 16MAP003, 16MBP017, 16MWP001 and 17MBPA1 at the Palynological Laboratory Services (PLS) Ltd, Holyhead, United Kingdom. For this method 30 grams of sedimentary rock was treated with 10% HCl to solubilize and remove the carbonate, and then washed and dried, and treated with 40% hydrofluoric acid (HF) to remove the silicates. Fluoride precipitates may be present after the HF stage and these precipitates are soluble in 20% HCl, followed by a heavy liquid separation technique (a solution of Zinc Bromide, density = 2.0) to separate the organic and remaining inorganic fractions. Subsequently, the organic fractions were sieved at 5 μm and the filtrate was collected. This filtrate was first sieved at 10 μm, then at 150 μm to remove large organic particles, while collecting the filtrate. The final residues at 5-10 μm and 10-150 μm were mounted in glycerin jelly. The resulting organic residue was mounted on a slide in glycerin and sealed with paraffin for the observation with LM. Residues were further used for analysis with LM and scanning electron microscopy (SEM) at the Department of Palaeontology, University of Vienna, Austria.

4.4.2 | Palynological analysis

The Kalewa samples have a poor sporomorph preservation and the organic material is often pyritized or corroded. In order to construct a reliable pollen diagram, a baseline on pollen sum of 100 grains was maintained. All samples with counts under 100 were excluded resulting in a total of 54 positive samples. Identification of fossil PPL pollen was mainly based on Germeraad et al. (1968), Harley and Morley (1995), Muller (1968), Potonié (1960), and Reimann and Aye Thaung (1981). Palm pollen grains not included in *Longapertites*, *Dicolpopollis*, *Spinizonocolpites*, *Proxapertites*, or *Palmaepollenites kutchensis*, were classified as “other palms” in the pollen diagram. The pollen diagram was constructed using the Tilia 2.1.1 software (Grimm, 1991), with cluster analysis program CONISS (Grimm, 1987). All of the slides and pollen residues are deposited at IBED.

All pollen grains were counted and described under a LM LEICA DM LB2, and a Zeiss Universal microscope at IBED. In addition, a JEOL JSM-6400 SEM at the Department of Palaeontology, University of Vienna, was used to investigate the pollen
sculpture, applying the single-grain analysis method by Zetter (1989; see also Halbritter et al., 2018). LM and SEM terminologies follow Punt et al. (2007) and Halbritter et al. (2018) respectively. The morphological characters of pollen grains were measured by the software Image J (National Institute of Health, USA). PCA was employed in R (R Core Team, 2018) to analyze paleoecological correlation on PPL taxa. Additionally, an analysis of variance (ANOVA) of pollen abundance among different pollen zones, and a nonparametric correlation (Spearman) of different taxa were performed with SPSS version 24.0 (SPSS Inc., Chicago, IL, USA).

4.4.2 | Microphotography

The micrographs in Fig. 4.2 were taken at IBED using Fujifilm X-E2 and a Zeiss Universal microscope with 63× Plan Neofluar NA1, 25 oil applying Nomarski Differential Interference Contrast (DIC) following Bercovici et al. (2009). While making these micrographs, the varying z-axis was recorded and images were later combined through manual z-stacking in Helicon Focus and Photoshop CC. This stacking technique combines different layers to provide a fully focused image. LM micrographs in Figs. 4.3-4.10 were taken by ProgRes Speed XTcore 5 camera connected with Nikon Eclipse 80i LM. SEM micrographs in Figs. 4.3-4.10 were taken with the JEOL JSM-6400. Figs. 4.2-4.10 were made with InDesign CC. The background of kerogen in the LM original micrographs was manually edited out.

4.4.3 | Distribution maps

4.4.3.1 | Mapping the global distribution of NLRs

Occurrence data (Table S4.1 in Supporting Information (SI)) of the NLRs of the fossil form-genera Dicolpopollis (Calamus, Daemonorops and Ceratolobus in Calaminae, now placed in the single genus Calamus by Baker (2015); https://doi.org/10.15468/dl.wvfy3m, with 10438 locality points), Palmaepollenites kutchensis (Areceae subtribe Basseliniiae with details for Basselinia and Burretiokentia; https://doi.org/10.15468/dl.bzjazl, with 1202 locality points), Spinizonocolpites (Nypa; https://doi.org/10.15468/dl.rliz8n, with 233 locality points) and Longapertites (probably Eugeissona; https://doi.org/10.15468/dl.ag40
145, with 52 locality points) were downloaded from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org) on 5 August 2019. “Observation”, “Human observation” and “Preserved specimen” including coordinates were included to reduce false records. The coordinates of the downloaded occurrences were then imported on the software GeoMapApp version 3.6.10 (http://www.geomapapp.org) to generate modern distribution maps of the NLRs. “Human observation” and “Preserved specimen” data on Calaminae (including Calamus, Daemonorops and Ceratolobus) and Nypa were examined by R package “CoordinateCleaner” (Zizka et al., 2019) to exclude problematic points (e.g., zero coordinates, GBIF headquarters and biodiversity institutions) (Figs. S4.1-S4.4 in SI), as other records fall well with distribution ranges of previous studies.

4.4.3.2 Mapping the global Eocene distribution of PPL taxa with emphasis on the Paleogene of India and SE Asia

We compiled all published global Eocene records of Dicocolpolis, Longapertites, Spinizonocolpites and Palmaepollenites kutchensis (Table S4.2 in SI) without Proxapertites as it has NLRs belonging to different plant families (e.g., Annonaceae, Araceae and Nymphaeaceae). we extended this compilation with data on the distribution of Dicocolpolis, Longapertites, Spinizonocolpites and Proxapertites in the Paleogene of the Indian subcontinent and SE Asia for the comparison of species diversity (Tables S4.3-S4.4 in SI). This compilation is based on the Palynodata database (Palynodata Inc. and White, 2008). However, we cross-checked these records where possible, and augmented the record with additional references. The global Eocene distribution data of the four taxa were plotted in the software GPlates version 2.1 (https://www.gplates.org) to generate maps of global distribution using Mercator projection, which is consistent with the modern maps produced by GeoMapApp. We used the plate model of Westerweel et al. (2019) in Eocene (40 Ma), which was adjusted after Matthews et al. (2016). The confidence of the records was divided into three levels: level 3, records from peer-reviewed literature with pollen micrographs; level 2, records from the peer-reviewed literature without pollen micrographs; level 1, records from the inaccessible literature. Distributions were georeferenced when latitudinal and longitudinal data were not provided and all data points were collated.

4.5 RESULTS
4.5.1 | Age

The age of the studied sedimentary sequence ranges from latest middle Eocene (late Bartonian) to earliest late Eocene (early Priabonian). This age is based on a dated tuff layer at 38.3±0.7-0.9 Ma (Licht et al., 2019), and supported by the presence of age-indicative marker species such as the sporomorphs Meyeripollis naharkotensis, Cicatriciosporites dorogensis and Proxapertites operculatus (Huang et al., 2018). These sporomorphs types define the Sunda palynological zone E8, which has an age range of c. 37.8-36.5 Ma (van Gorsel et al., 2014; Witts et al., 2012).

4.5.2 | Systematics

The morphology of the fossil PPL pollen is described using LM and SEM, and all measurements are available in Table S4.5 in SI. The pollen grains are assigned to form-genera/species. Each fossil taxon is introduced, including reference to the botanical affinity, ecology and distribution, and discussed based on the existing literature.

Genus Proxapertites van der Hammen 1956 emend. Singh 1975

Type species Proxapertites operculatus (van der Hammen 1954) van der Hammen 1956

General information: Proxapertites was proposed by van der Hammen (1956), who considered it a Maastrichtian–Miocene marker fossil for northern South America.

Proxapertites operculatus van der Hammen 1956 (Fig. 4.2A1-A2; Fig. 4.3A-R)


Description (based on seven specimens): pollen, monad, heteropolar, polar/equatorial (P/E) ratio oblate, hamburger-shaped with two halves in equatorial view, outline irregularly circular to elliptic in polar view, flattened along the equatorial plane; grain size varies from 34.2-38.6 μm to 42.9-48.6 μm in polar view (LM); zona-aperturate, sulcus usually totally open, connecting two adhering, and not quite symmetric halves, with some degrees of collapsing or folding, sometimes isolated halves occur, aperture margin straight to undulating; exine 1.1-1.6 μm thick, nexine thinner than sexine (LM), columellae distinct
and robust; pollen wall tectate; sculpture psilate to scabrate in LM, perforate in SEM, fewer perforation in polar areas, appearing more or less psilate, or similar perforation in polar area as other regions of the grains, number of perforations increase towards the margin of aperture, perforation sometimes connected, diameter up to 1.6 µm (SEM; Fig. 4.3K); aperture margins rolled inwards, inner side of pollen wall slightly sculptured; thin and folded membrane observed in aperture area (SEM).

Fig. 4.2. Light microscopy (LM) micrographs of palm and palm-like pollen under ×630 magnification from the late Eocene Kalewa section, Central Myanmar Basin. (A1-A2) Proxapertites operculatus. (B-C) Palmaepollenites kutchenis. (D1-D2) (G1-G2) Dicolpopollis kaleweensis. (E) Longapertites retipilatus. (F) Spinizonocolpites prominatus. (H) (I) (J1-J2) Palmaepollenites sp. 2. Scale bars = 10 µm.

Botanical affinity, ecology and distribution: Proxapertites operculatus was initially compared to the South American cocosoid palm Astrocaryum by van der Hammen (1957). Muller (1968), however envisaged it as zonocolpate and compared it to a Spinizonocolpites
grain lacking the spines, and thus considered it as an extinct member of Nypoideae. This suggestion was supported by the fact that *Spinizonocolpites* and *Proxapertites* are often associated in the fossil record, and so both were considered to be derived from mangrove palms. This perspective has been widely followed in subsequent literature (e.g., Morley, 2000). However, several authors note that *Proxapertites* is incompletely zonocolpate, and this prompted Harley and Baker (2001) to compare it with a subgroup of the arecoid palm *Areca*, especially *A. abdurrahmanii* and *A. chaiana*. On the other hand, Thanikaimoni et al. (1984) and Samant and Phadtare (1997) indicated that similar pollen occurs in Araceae (arum family). This was followed up by Zetter et al. (2001) who undertook an evaluation of the pollen wall ultrastructure and noted marked differences compared to that observed in palm pollen. They proposed a botanical affinity with the genus *Gonatopus* (Aroideae-Zamioculcadeae in Araceae).

*Proxapertites operculatus* has a pantropical distribution from the Late Cretaceous to early Cenozoic occurring in northern South America, southeastern North America and Europe (Spain, Portugal, Austria and Germany), Africa, Pakistan, India and Borneo (e.g., Chiadikobi et al., 2018; Friis et al., 2004; Hesse and Zetter, 2007; Kingsley and Umeji, 2018; Kwetchi et al., 2018; Mohammed et al., 2017; Morley, 1978; Muller, 1968; Prasad et al., 2018b; Venkatachala et al., 1998; Winantris et al., 2017; Witts et al., 2012; Zetter et al., 2001).

Remarks: Rugulate ornamentation and narrow meandering “grooves” formed by connected perforations presented in Zetter et al. (2001) were not observed in the Kalewa specimens. Stratification, sometimes seen in broken exine was also not observed.

Genus *Longapertites* van Hoeken-Klinkenberg 1964

Type species *Longapertites marginatus* van Hoeken Klinkenberg 1964

General information: *Longapertites* was first described from the Maastrichtian of Nigeria by van Hoeken-Klinkenberg (1964). Individual halves of folded *Proxapertites* are sometimes misidentified as *Longapertites* (Zetter et al., 2001).

Botanical affinity, ecology and distribution: This taxon is thought to be the ancestor of the calamoid *Eugeissona* (confined to Borneo and the Malay Peninsula; Baker and Dransfield, 2000) based on its extended colpus (Morley, 2000). Nevertheless, there are some morphological differences between the two taxa, especially in configuration of the
Fig. 4.3. Light microscopy (LM) (A-F) and scanning electron microscopy (SEM) (G-R) micrographs of *Proxapertites operculatus* from the late Eocene Kalewa section, Central Myanmar Basin. (A) (G) (J) Same grain, close-up (J) of aperture region. (B) (H) (K) Same grain, arrow in (K) pointing to infection of bacteria. (C) (I) (L) Same grain, close-up (L) of the tectum. (D)
two pollen halves, with *Longapertites* specimens showing a greater morphological differentiation than observed in *Eugeissona*. *Longapertites* apparently had a pantropical distribution during the Maastrichtian and Paleogene, with fossil records from South America, West Africa, India and northern Australia (Barker and Dransfield, 2000; McGowran et al., 2000). *Quilonipollenites* has been considered as a synonym of *Longapertites* (Frederiksen, 1994), and is in fact much closer to extant *Eugeissona* than *Longapertites*. Also, Venkatachala and Kar (in Frederiksen, 1994) would prefer it as a separate genus based on the coarse pollen sculpture observed with LM. *Longapertites* has been associated with back-mangrove settings in brackish water (e.g., Akkiraz et al., 2008; Kayseri-Özer, 2013; Mathews et al., 2013; Onuigbo et al., 2015). This should be considered carefully as the pollen may be transported and the accumulation area needs not reflect the habitat/ecology of the parent plant.

*Longapertites retipilatus* Kar 1985 (Fig. 4.2E; Fig. 4.4A-C, G-L)

Description (based on four specimens): pollen, monad, heteropolar, P/E ratio oblate, outline nearly circular in equatorial view (arched to obtuse distal face versus straight to slightly arched proximal face); equatorial diameter 37.5–41.9 µm, polar axis 27.1–37.6 µm (LM); monosulcate, sulcus long, extending to the proximal surface, occupying around two third of the circumference, margins of sulcus infolded; exine 0.8–1.0 µm thick, nexine thinner than sexine (LM); pollen wall tectate, columellae distinct and robust; sculpture perforate to foveolate in LM, perforate in SEM, perforations evenly distribute and become smaller towards the aperture (SEM); margin of the sulcus clearly rolled inwards (SEM).

Remarks: This pollen type is similar to *Proxapertites operculatus* with respect to the perforate sculpture observed in SEM and the inwards-rolled margin of the sulcus, but the two halves are always clearly joined and the grain does not separate into two parts.

*Longapertites rugulatus* Beilstein 1994 (Fig. 4.4D-F, M-R; Fig. 4.5A-O)

Description (based on eight specimens): pollen, monad, heteropolar, P/E ratio oblate,
outline nearly triangular or circular in equatorial view (arched to angular distal face versus straight to slightly convex proximal face); equatorial diameter 33.0-51.6 µm, polar axis 29.6-43.3 µm (LM); monosulcate, sulcus long, extending to the proximal surface, occupying around two third of the circumference, margins of sulcus thickened (LM), sulcus broader towards poles; exine 1.0-1.5 µm thick (LM); pollen wall tectate, columellae distinct and robust; sculpture psilate to perforate, and rugulate in LM, perforate to rugulate in SEM.

Remarks: This species is distinguished by its perforate to rugulate exine.

Genus *Dicolpopollis* Pflanzl 1956 ex Potonié 1966

Type species *Dicolpopollis kockelii* Pflanzl 1956 ex Potonié 1966

General information: The earliest reliable fossil record of *Dicolpopollis* is from the Upper Cretaceous of northern Somalia (Schrank, 1994). *Dicolpopollis* has been frequently recorded in Cenozoic sediments from low and mid latitudes (Ediger et al., 1990). It is the most frequently recorded form-genus comprising disulcate pollen.

Botanical affinity, ecology and distribution: *Dicolpopollis* is believed to have botanical affinity to Calaminae (*Calamus, Daemonorops, Ceratolobus*) in Arecaceae (Harley and Morley, 1995; Morley, 2000). Calaminae is distributed across central Africa, and from South and southern SE Asia into tropical Australia (Whitmore, 1973; Dransfield et al., 2008). Calaminae are climbing palms (lianas) and generally termed rattans. These palms occur in all habitats, climbing within the canopy of evergreen rainforests, occurring from sea-level to mountain tops. Calaminae palms are sometimes locally abundant in swamps and mangrove forests, and can form thickets along rivers (Dransfield, 1974).

*Dicolpopollis kalewensis* Potonié 1960 (Fig. 4.2D1-D2, G1-G2; Fig. 4.6A-R; Fig. 4.7A-D, F-K, M-N)


Description (based on twelve specimens): pollen, monad, heteropolar, P/E ratio oblate, outline trapezoidal in equatorial view, oval in polar view (proximal side longer than distal side, parallel and both slightly arched); grain size varies from 21.0-30.1 µm to 26.7-36.9 µm in polar view, and polar axis 24.3-28.5 µm to 22.4-31.4 µm in equatorial view, equatorial diameter 21.0-27.7 µm (LM); disulcate, sulci long and gaping; exine 0.7-1.3 µm thick, nexine around 0.5 µm (SEM; Fig. 4.7K), nexine thinner than sexine (LM and SEM);
pollen wall tectate; tectum is supported by robust columellae (SEM); sculpture foveolate to perforate in SEM, foveolate in interapertural areas, becoming perforate towards apertures, lumina/perforations sometimes filled with infratectal granules and rod-like elements (SEM).
Fig. 4.4. Light microscopy (LM) (A-F) and scanning electron microscopy (SEM) (G-R) micrographs of *Longapertites* from the late Eocene Kalewa section, Central Myanmar Basin. (A-C) (G-L) *Longapertites retipilatus*. (A) (G) (J) Same grain, close-up (J) of aperture region. (B) (H) (K) Same grain, close-up (K) showing part of membrane. (C) (I) (L) Same grain, close-up (L) of tectum. (D-F) (M-R) *Longapertites rugulatus*. (D) (M) (P) Same grain, close-up (P) of tectum. (E) (N) (Q) Same grain, close-up (Q) of tectum. (F) (O) (R) Same grain, close-up (R) of tectum. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-L) (P-R) = 1 μm.

Remarks: *Dicolpopollis malesianus* was proposed as a new species because of its pronounced sculpture as compared to *D. kalewensis* by Muller (1968). A comparison of the material from Kalewa with the holotype and specimens of *D. malesianus* from Java by Harley and Morley (1995), suggests that the pollen grains are identical. Muller was probably misled due to the low quality of the LM micrographs of *D. kalewensis* by Potonié (1960), emphasizing the importance of displaying clear LM-SEM micrographs in publications. Therefore, it is concluded that *D. kalewensis* is the senior synonym of *D. malesianus*.

*Dicolpopollis* sp. (Fig. 4.7E, L, O)

Description (based on one specimen): pollen, monad, heteropolar, P/E ratio oblate, outline more or less oval in polar view; grain size 28.5×33.1 μm (LM); disulcate, sulcus long and gaping; exine 0.6-0.8 μm thick, nexine thinner than sexine (LM); pollen wall tectate, columellae distinct and robust; sculpture foveolate to perforate in SEM, foveolate in interapertural areas, becoming perforate towards apertures, lumina variable in size, up to 2.1 μm across, oval to circular in shape (SEM).

Remarks: At Kalewa all *Dicolpopollis* display a sculpture that ranges from foveolate in the interapertural areas towards perforate at the apertures. This pollen has similar ornamentation as *D. kalewensis*, but the lumina are much larger.

Genus *Palmaepollenites* Potonié 1951

Type species *Palmaepollenites tranquillus* (Potonié) Potonié 1951 (synonym: *Monocolpopollenites tranquillus* (Potonié) Thomson et Pflug 1953)
Fig. 4.5. Light microscopy (LM) (A-E) and scanning electron microscopy (SEM) (F-O) micrographs of *Longapertites rugulatus* from the late Eocene Kalewa section, Central Myanmar Basin. (A) (F) (H) Same grain, close-up (H) of tectum. (B) (G) (I) Same grain, close-up (I) of tectum. (C) (J) (M) Same grain, close-up (M) of tectum. (D) (K) (N) Same grain, close-up (N) of tectum. (E)
(L) (O) Same grain, close-up (O) of tectum. LM micrographs were taken under $\times1000$ magnification. Scale bars: (A-I) (M-O) = 10 $\mu$m, (J-L) (P-R) = 1 $\mu$m.

Fig. 4.6. Light microscopy (LM) (A-F) and scanning electron microscopy (SEM) (G-R) micrographs of *Dicolpopollis kalewensis* from the late Eocene Kalewa section, Central Myanmar.
Myanmar Basin. (A) (G) (J) Same grain, close-up (J) of tectum in polar area. (B) (H) (K) Same grain, close-up (K) of aperture with membrane. (C) (I) (L) Same grain, close-up (L) of tectum in polar area. (D) (M) (P) Same grain, close-up (P) of tectum in interapertural area. (E) (N) (Q) Same grain, close-up (Q) of tectum in interapertural area. (F) (O) (R) Same grain, close-up (R) of aperture with membrane. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-K) (P-R) = 1 μm, (L) = 2 μm.
Fig. 4.7. Light microscopy (LM) (A-E) and scanning electron microscopy (SEM) SEM (F-O) micrographs of Dicocolopollis from the late Eocene Kalewa section, Central Myanmar Basin. (A-D) (F-K) (M-N) Dicocolopollis kalewensis. (A) (F) (H) Same grain, close-up (H) of tectum. (B) (G) (I) Same grain, close-up (I) of tectum. (C) (J) (M) Same grain, close-up (M) of tectum. (D) (K) (N) Same grain, close-up (N) of tectum. (E) (L) (O) Dicocolopollis sp., same grain, close-up (O) of tectum in interapertural area. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-L) (P-R) = 1 μm.

*Palmaepollenites kutchensis* Venkatachala et Kar 1969 (Fig. 4.2B-C; Fig. 4.8A-R)


General information: This taxon was originally discovered in India, but its Eocene range extended into SE Asia, west of the Wallace's line (Harley and Morley, 1995; Morley 1998, 2000). The source taxon, *P. kutchensis*, probably originated in India during the Late Cretaceous, and subsequently migrated to SE Asia following the India-Asia collision in the middle Eocene (Morley, 2000, 2018). *P. kutchensis* gradually disappeared from the Sundanese record during the Oligocene (Harley and Morley, 1995), possibly as a result of a change to drier climatic conditions.

Description (based on seven specimens): pollen, monad, heteropolar, asymmetrical, P/E ratio oblate to suboblate, outline oval to pyriform with broadly rounded to pointed lateral ends in polar view; grain size varies from 25.8-36.2 μm to 37.9-42.3 μm (LM); monosulcate, sulcus distinct, broader at middle region and tapering at rounded ends, never reaching margins, sulcus length 22.1-33.5 μm, width 4.4-14.1 μm (LM); exine 1.1-2.8 μm thick, nexine thinner than sexine (LM), columellae indistinct; sculpture psilate in LM, perforate in SEM.

Botanical affinity: *P. kutchensis* is similar to two contrasting palm lineages. Its morphology is closest to that observed in the pollen of the Pacific coryphoid palms *Prichardia* and *Lepidorrachis* (Harley and Morley, 1995), which have a young Neogene molecular age (Baker et al., 2011) and thus the affinity is unlikely. *P. kutchensis* is also very similar to pollen of several genera in the tribe Areceae, especially *Basselinia*, *Burretiokentia* of subtribe Basseliniiaceae, both confined to New Caledonia and formerly within Iguarinaceae (Harley and Morley, 1995) which is a much more ancient group and so a better candidate for the Eocene fossils, although no Areceae display a perfect match. The
ancestors to *Basselinia* and *Burretiokentia* most likely had a wide distribution across South Asia and Sunda in the middle Eocene, and dispersed to the Pacific islands eventually finding refuge in New Caledonia prior to the formation of New Guinea (or they would still be expected to be present in the New Guinea flora), and subsequently becoming extinct in India and Sunda.

Remarks: The parent plant of *P. kutchensis* was a member of the middle Eocene peat swamp vegetation in Java, as it dominates the upper part of a 1 m coal from the Nanggulan Formation (Fig. 4.1A) of central Java where it contributes about 40% of the total pollen recovery (Fig. 9.10 in Morley, 2000). It may also have been a constituent of other vegetation, but most likely was better represented in (but not confined to) areas of perhumid climate. The assumption is based on its occurrence, and then increase in abundance, in well sections from offshore South Sulawesi, following amelioration of the climate from seasonally dry to perhumid during the course of the middle Eocene (Morley, 2018a).

*Palmaepollenites* sp. 1 (Fig. 4.9A-C, E-L)

Description (based on three specimens): pollen, monad, heteropolar, P/E ratio oblate to suboblate, outline oval with broadly rounded to pointed lateral ends in equatorial view; grain size varies from 22.77-34.88 µm to 39.1-55.1 µm (LM); monosulcate, sulcus long and narrow, tapering at ends, width 0.7-0.8 µm; exine 1.0-1.3 µm thick, nexine thinner than sexine (LM), columellae indistinct; sculpture psilate in LM, perforate in SEM.

Botanical affinity: subtribe Basseliniieae of Areceae in Arecaceae.

Remarks: The sculpture observed with SEM is very similar to that of *P. kutchensis*. However, the arrangement of the sulcus in this pollen type differs from that normally observed in *P. kutchensis*.

*Palmaepollenites* sp. 2 (Fig. 4.2H-I, J1-J2; Fig. 4.10A-R)

Description (based on eight specimens): pollen, monad, heteropolar, P/E ratio peroblate, oblate to suboblate, outline oval to circular with broadly rounded to pointed lateral ends; grain size varies from 19.7-37.8 µm to 25.5-44.9 µm (LM); monosulcate, sulcus long, tapering at ends, sulcus width 0.8-5.6 µm (LM); exine 0.9-1.5 µm thick, nexine thinner than sexine (LM), columellae distinct and robust; sculpture psilate in LM, rugulate and fossulate in SEM.
Fig. 4.8. Light microscopy (LM) (A-F) and scanning electron microscopy (SEM) (G-R) micrographs of Palmaepollenites kutchensis from the late Eocene Kalewa section, Central Myanmar Basin. (A) (G) (J) Same grain, close-up (J) of tectum. (B) (H) (K) Same grain, close-up (K) of tectum. (C) (I) (L) Same grain, close-up (L) of tectum. (D) (M) (P) Same grain, close-up (P) of marginal area. (E) (N) (Q) Same grain, close-up (Q) of tectum. (F) (O) (R) Same grain, close-up (R) of tectum. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-L) (P-R) = 1 μm.
Fig. 4.9. Light microscopy (LM) (A-D) and scanning electron microscopy (SEM) (E-N) micrographs of *Palmaepollenites* sp. 1 and *Spinizonoocolpites prominatus* from the late Eocene Kalewa section, Central Myanmar Basin. (A-C) (E-I) (L) *Palmaepollenites* sp. 1. (A) (E) (G) Same grain, showing (G) inner side of pollen wall. (B) (F) (H) Same grain, close-up (H) of aperture area. (C) (I) (L) Same grain, close-up (L) of tectum. (D) (J-K) (M-N) *Spinizonoocolpites prominatus*, same grain, close-up (K) (M) (N) of tectum and spines. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-L) (P-R) = 1 μm.
Botanical affinity: Arecaceae.
Remarks: This palm pollen type is quite variable in size. As the pollen is invariably associated with *P. kutchensis*, its parent plant may have had similar ecological preferences.

Genus *Spinizonocolpites* Muller 1968 emend. Muller et al. 1987
Type species *Spinizonocolpites echinatus* Muller 1968
General information: The genus *Spinizonocolpites* was proposed by Muller (1968). Pollen grains of this type commonly occur as whole grains or split into two halves when found dispersed. This pollen is widely distributed from the Maastrichtian onwards (Gee, 1990; Morley, 2000).

Botanical affinity, ecology and distribution: The NLR of *Spinizonocolpites* is *Nypa fruticans* from the monotypic subfamily Nypoideae (Baker and Couvreur, 2013a). *Nypa* is a mangrove palm that often grows in vast natural stands in a variety of estuarine conditions (Baker et al., 1998). It is found in the mangrove habitats in the Indo-Malaysian region (Tomlinson, 1986). Morley et al. (2019) emphasized that *Nypa* is a back-mangrove palm, growing in slightly brackish or freshwater, but mostly within the reach of tidal influence. Today, *Nypa* is restricted to the Indo-Malaysian region, but during the Paleogene it had a pantropical distribution. *Spinizonocolpites* can be used as a marker fossil for the poleward extension of moist tropics during early Eocene which time it was widely distributed in both the northern and southern hemispheres (Morley, 2000; Pole and McPhail, 1996; Vinken, 1988).

*Spinizonocolpites prominatus* (McIntyre 1965) Stover et Evans 1973 (Fig. 4.2F; Fig. 4.10D, J-K, M-N)
Description (based on two specimens): pollen, monad, heteropolar, P/E ratio oblate, outline oval to circular in equatorial and polar view; polar axis (excluding spines) 44.7-51.0 µm (LM and SEM); zonasulcate; exine 1.0-1.7 µm thick (LM and SEM); pollen wall tectate, columellae indistinct; sculpture echinate in LM, perforate and echinate in SEM; echini conical, bulbous above the base, irregularly distributed, echini diameter 1.7-2.8 µm, 5.3-7.3 µm long (LM and SEM).

Botanical affinity: This taxon is comparable to pollen of *Nypa* (Frederiksen, 1980; Muller, 1968). *Nypa* is also represented by fruits, widely recorded from the Eocene of Europe. Statistical analysis of fossil *Nypa* fruits from Belgium (Collinson, 1993) showed
that their variation (in size and shape) is very similar to that observed in modern *Nypa*. Therefore, it is likely that the Eocene species producing the pollen shown herein may have been closely related to modern *Nypa*. However, it is possible that *Nypa* was more diverse during the early Paleogene, as there are other morphotypes, such as *S. baculatus* from Malaysia (Muller, 1968) and several additional taxa from India (such as *S. echinatus*, *S. brevispinosus* and *S. bulbospinosus* in Khanolkar and Sharma, 2019). In the earliest Eocene of Krappfeld, Austria, *Nypa* pollen grains also show variation in the configuration of echini and other morphological details (Zetter and Hofmann, 2001).

Remarks: *Spinizonocolpites* is not well preserved in the studied samples. This may be due to up-river transport by tides from the coastal regions. The *Spinizonocolpites* specimens from Kalewa have sparse echini, on the basis of which it was assigned to *S. prominatus* and not *S. echinatus*.

### 4.5.3 Palynological zones, paleovegetation and paleoenvironment

The Eocene Kalewa pollen assemblage is very diverse, reflecting a rich and diverse paleovegetation, with a predominance of dicotyledons and pteridophytes, but also a good representation of monocots, particularly palms, but with only few gymnosperms. The palynological assemblage represents a seasonally wet flora that mainly includes pollen from tropical plants. There are numerous megathermal tropical forest elements, such as *Anacolosidites* (Olacaceae), *Lanagiopollis nanggulanensis* (*Alangium*, Cornaceae), *Cupanieidites flaccidiformis* (Sapindaceae) and *Margocolporites* (*Caesalpinia*, Fabaceae), some mesothermal and microthermal angiosperms, such as *Alnipollenites* (*Alnus*, Betulaceae), *Betulapollenites* (*Betula*, Betulaceae), *Celtispollenites* (*Celtis*, Cannabaceae) and *Gothanipollis* (Loranthaceae), as well as Fagaceae and some rare montane gymnosperms (e.g., *Podocarpidites* (*Podocarpus*, Podocarpaceae)), and abundant Pteridophytes (e.g., *Acrostichum* (Pteridaceae) and *Verrucatosporites* (Polypodiaceae)) (Huang et al., 2018). The pollen diagram (Fig. 4.11; for raw pollen counts see Table S4.6 in SI) is subdivided into three main zones (Zones A-C) reflecting environmental shifts and ecological changes. The ANOVA result (*P*-value>0.05; Table S4.7 in SI) indicates that there are no significant differences in pollen abundances among the three pollen zones, which means that the establishment of the pollen zones is feasible. The summary diagram showing palm taxa versus other paleofloristic elements (Fig. 4.11B) indicates three main
paleoecological stages in the development of the vegetation in the estuary.

Fig. 4.10. Light microscopy (LM) (A-F) and scanning electron microscopy (SEM) (G-R) micrographs of *Palmaepollenites* sp. 2 from the late Eocene Kalewa section, Central Myanmar Basin. (A) (G) (J) Same grain, close-up (L) of aperture area. (B) (H) (K) Same grain, close-up (K) of tectum. (C) (I) (L) Same grain, close-up (L) of marginal area. (D) (M) (P) Same grain, close-up (P) of aperture area. (E) (N) (Q) Same grain, close-up (Q) of tectum. (F) (O) (R) Same grain, close-
up (R) of marginal area. LM micrographs were taken under ×1000 magnification. Scale bars: (A-I) (M-O) = 10 μm, (J-L) (P-R) = 1 μm.

In Zone A, the percentage of palms in relation to the total sporomorph sum is low (up to 16.4%). However, there are peaks of Longapertites, Proxapertites, Spinizonocolpites and “other palms”, at c. 50 m, of which the former three achieved the highest abundance in the entire section. P. kutchensis and Dicolpopollis percentages are relatively low and discontinuous. Other mangrove pollen is rare, but Acrostichum (ferns typical of disturbed/open areas in mangrove/back-mangrove swamps) reaches its highest peak. This implies an association with a coastal environment subjected to regular disturbance.

In Zone B, there is a gradual increase of palm percentages (up to 28.6%). Longapertites, Proxapertites and other palms have several peaks, while Spinizonocolpites has a solitary peak at c. 280 m. P. kutchensis and Dicolpopollis increase gradually and their general trends are very similar, not only in this zone, but throughout the entire succession (Fig. 4.11A). This is consistent with the indication from the middle Eocene Nanggulan coal (Fig. 4.1A) that P. kutchensis is a swamp taxon (Morley, 2000), and its association with the commonly occurring D. kalewensis suggests extensive freshwater swamps. This zone is divided into two subzones, subzone B1 and subzone B2. In the subzone B1, Longapertites has low percentages, whereas the percentages of Spinizonocolpites and Proxapertites are relatively high. This indicates closer proximity to the paleoshoreline. At the transition into subzone B2, Spinizonocolpites is absent, Proxapertites is reduced, and Longapertites increases in abundance. Other mangrove pollen is rare in this subzone, whereas Acrostichum spores are still very common. This could be explained by that Acrostichum may also occur in disturbed floodplain settings, as emphasized by Moreno-Dominguez et al. (2016). The compositional changes in the palynoflora suggest an environmental shift from the coastal plain to more freshwater conditions, upstream the estuary.

In Zone C, Dicolpopollis is the dominant palm pollen type, but P. kutchensis and Longapertites are also very common. The increase in palm pollen (up to 40.9%) coincides with a decrease in pteridophyte spores, suggesting that ferns no longer were a major part of the regional vegetation. Also, Proxapertites and Acrostichum spores decrease, and Spinizonocolpites and other mangrove pollen become rare. This suggests deposition in a fluvial setting.
Fig. 4.11. Pollen diagram, showing the shift of different environmental indicators. In the paleosol column, black lines indicate histosols. Abbreviations: vfs = very fine sand, fs = fine sand, ms = medium sand, cs = coarse sand, B = Boulder.
4.5.4 | Paleoecological correlation of selected PPL taxa

The PCA (Fig. 4.12) of PPL pollen (Spinizonocolpites, Proxapertites, Longapertites, Dicolpopollis and Palmaepollenites kutchensis) and Acrostichum from Kalewa shows that P. kutchensis correlates very well with Dicolpopollis, both of which display an inverse correlation with Spinizonocolpites and Acrostichum that are mangrove/back-mangrove taxa. The closeness of P. kutchensis and Dicolpopollis in the PCA indicates they are likely to originate from a similar swamp environment, a theory also supported by analysis of the Nanggulan coal (Fig. 9.10 in Morley, 2000). Longapertites has a positive correlation with both P. kutchensis and Dicolpopollis, and possibly also belongs to a freshwater taxon. Longapertites is very well represented at Kalewa, but rare at Nanggulan (Morley, 2000), which may relate to the higher Eocene latitude and increased seasonality in Kalewa compared to Nanggulan (Huang et al., unpubl. data). Proxapertites shows an inverse correlation with P. kutchensis, Dicolpopollis, Longapertites and Spinizonocolpites, and a positive correlation with Acrostichum. A nonparametric correlation (Spearman, Table S4.7 in SI) between Proxapertites versus Acrostichum, and Proxapertites versus Spinizonocolpites shows that the levels of significance 96.5% and 84.8% respectively, which illustrates that the result of the correlation with Acrostichum is reliable. Thus its parent plant is more likely to have been a member of coastal vegetation. Accordingly, axis 1 of the PCA (Fig. 4.12) reflects proximity to the coast/salinity. Arrows towards positive values indicate freshwater settings, while arrows towards negative values suggest brackish environment.

4.5.5 | Eocene and modern geographic distribution of selected palms

At present, Calaminae (including Calamus, Daemonorops and Ceratolobus) occur in SE Asia, central Africa, South China, India, Sri Lanka, the Pacific islands and Australia (Fig. 4.13B), while Basselinia and Burretiokentia have a relict New Caledonian distribution (Fig. 4.13D). The tribe Areceae occurs in SE Asia, South China, southern India, northern Australia, North Island of New Zealand, and Madagascar (Fig. 4.13D). Nypa occurs naturally in SE Asia, the Ganges Delta, the western Pacific, Sri Lanka and northern Australia (Fig. 4.13F), and Eugeissona is distributed in the Malay Peninsula and Borneo.
LATE EOCENE PALMS FROM MYANMAR

Fig. 4.12. PCA biplot, showing the correlation between the palm and palm-like pollen and *Acrostichum* from the Eocene of Kalewa, Central Myanmar Basin. Palm and palm-like pollen include *Spinizonocolpites*, *Proxapertites*, *Longapertites*, *Dicolpopollis* and *Palmaepollenites kutchensis*. Axis 1: explained variance 35.1%; axis 2: 19.4%. Blue, yellow, and green circles indicate samples from Zone A, B and C respectively. Abbreviations: Dicol = *Dicolpopollis*, Palku = *Palmaepollenites kutchensis*, Longa = *Longapertites*, Spini = *Spinizonocolpites*, Proxa = *Proxapertites* and Acros = *Acrostichum*.

(Fig. 4.13H). GBIF data on Basseliniae (including *Basselinia* and *Burretiokentia*; one unlikely record in Italy was excluded; see Fig. 4.13B), *Eugeissona* (see Fig. 4.13H), Calaminae (including *Daemonorops* and *Ceratolobus*), and “Observation” data on *Calamus* and *Nypa* falls very well with the ranges from previous studies (Baker et al., 1998; Dransfield et al., 2008; Mehrotra et al., 2003; Ruddle, 1979). The Eocene maps show that *Dicolpopollis*, *Spinizonocolpites* and *Longapertites* had a pantropical distribution, while *Palmaepollenites kutchensis* was restricted to the Indian subcontinent and SE Asia. Also, *Dicolpopollis* was absent from Africa and South America, and present in southern North America and Europe, while *Longapertites* was absent from Europe. The presence of *Calamus deeratus* in equatorial Africa may therefore reflect a Neogene dispersal (Fig. 4.13A-B). Basseliniae, producing *P. kutchensis* type pollen, were widespread across the
Indian Plate and SE Asia. This pollen type is now restricted to the relict *Basselinia* and *Burretiokentia* which occur in New Caledonia (Fig. 4.13C-D). *Nypa* became extinct across the Americas, Africa and Europe after the Eocene (Fig. 4.13E-F), possibly as a result of changing climate and/or sea level (Morley, 2000). *Eugeissona* became restricted to the Malay Peninsula and Borneo from a possible global distribution due to climate change and competition from other plants (Fig. 4.13G-H). Based on the comparison between the Eocene and modern distribution maps, we suggest that their distributional ranges shrank due to changing climatic and tectonically forced factors, as well as sea level change and competition from other plants.

### 4.5.6 A comparison of PPL pollen diversity in the Paleogene of the Indian subcontinent, Myanmar and SE Asia

The composition at genus level of PPL pollen at Kalewa is very similar to that of adjacent areas during the Paleogene, whereas the species diversity of these palm taxa is quite different. This becomes very clear when the fossil records and diversity of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* from the Indian subcontinent, Myanmar and other areas in SE Asia are compared (Tables S4.3-S4.4 in SI, Fig. 4.14). The oldest reliable Asian records of *Dicolpopollis* (*D. malesianus* = *D. kalewensis* and *D. elegans*) are from the Paleocene of Sarawak, tropical Asia (Morley, 1998; Muller 1968). *Dicolpopollis* is also recorded from the Paleocene of India (e.g., Mathur and Jain, 1980), but the age of this deposit is still under debate. *Dicolpopollis* is also a frequent component in middle Eocene samples from the southern Sunda margin, from central Java (Harley and Morley, 1995; Lelono, 2000; Morley, 2000; Takahashi, 1982), and from South Sulawesi (Morley, 1998). Lelono (2000) noted various morphotypes from the middle and late Eocene Nanggulan Formation (Fig. 4.1A), supported by data from the late Eocene of west Java (Morley and Morley, unpubl. data). *Dicolpopollis* is common in the Oligocene of Sunda, but is of reduced diversity compared to the middle and late Eocene (Jais, 1997; Morley et al., 2003, 2019).

In the Eocene and Oligocene of the Indian subcontinent, *Dicolpopollis* shows a different pattern, with just a couple of morphotypes, such as *D. kalewensis* and *D. elegans*, known from the Eocene. The diversity increased during the Oligocene, adding *D. proprius*,...
Fig. 4.13. Global distribution maps of selected palm pollen records (Table S4.2 in SI) in the Eocene and their nearest living relatives. The red circle indicates the Kalewa site. In (A) (C) (E) (G) dark, intermediate, and light colors indicate level 3, 2, 1 on the confidence of the records. Noting that there are three Eocene level-2 records (square) with the name of Nypa (E). Range between dash line in B is from Baker et al. (1998), indicating the distribution of Calamus in SE Asia. Range of dash line in F is from Mehrotra et al. (2003), showing the global distribution of Nypa. Range of dash line in H is from Ruddle (1979) and Baker et al. (1998), illustrating the global distribution of Eugeissona. Ranges of light orange areas in (B) (D) (F) (H) are from Dransfield et al. (2008), demonstrating the
global distribution of Calaminae (including Calamus, Daemonorops and Ceratolobus), Basseliniiae (including Basselinia and Burretiokentia), Nypa and Eugeissona respectively.

*D. kalewensis, D. fragilis, D. cuddalorense and D. psilatus* to the types extending from the Eocene. Several studies (e.g., Kumar and Takahashi, 1991; Saxena and Trivedi, 2009) suggest that different species occur at different localities in India, but with no more than two species at one locality. It is possible that some of these may be synonyms. In Myanmar *Dicolpopollis* is not diverse and only represented by two species (*D. kalewensis* and *D. sp.*). Thus, the diversity of Eocene *Dicolpopollis* is high in Java, intermediate in India, and low in Myanmar.

*Longapertites, Spinizonocolpites* and *Proxapertites* are more diverse in the Paleogene of the Indian subcontinent than in contemporaneous Myanmar and other areas in SE Asia. Two *Longapertites* species (*L. retipilatus* and *L. rugulatus*) occur in Myanmar, and one (*L. vaneendenburgi*) in the late Eocene of SE Asia (Lelono, 2000; Morley et al., 2003; Winantris et al., 2017). In the Indian subcontinent, *Longapertites* seems to be diverse, especially in the Paleocene and early Eocene. Samant and Phadtare (1997) reported twelve different *Longapertites* pollen types from an Eocene assemblage in India, and Frederiksen (1994) identified seven *Longapertites* species in a Paleocene assemblage from Pakistan. *Spinizonocolpites prominatus* is the only representative of that genus in Myanmar, but seven different *Spinizonocolpites* were described from a single palynoflora from the Paleocene of India (Singh, 1990), and four distinct species were found in a Paleocene palynoflora from Pakistan (Frederiksen, 1994). Three *Spinizonocolpites* pollen types occur in the early Eocene of Irian Jaya (Indonesia), which would have formed part of the northern Australian margin at the time (Morley, 1998, 2000). Two species were reported by Muller (1968) from the Paleocene and Eocene of Malaysia. All these records suggest that the diversity of *Spinizonocolpites* was high in the Paleocene of northern India, intermediate in the Paleocene and early Eocene of SE Asia and the northern Australian margin (but reduced to a single species during the middle Eocene to Oligocene), and low in Myanmar. *Proxapertites operculatus* is the only representative of that genus from Myanmar. Interestingly, *Proxapertites* is exceptionally diverse in the Paleocene of the Indian subcontinent, represented by 19 species in the Paleocene and 22 species in the Eocene (e.g., Frederiksen, 1994; Samant and Phadtare, 1997; Table S4.4 in SI). However, only three *Proxapertites* species were recorded in Indonesia (e.g., Lelono, 2000, 2007b; Morley, 1998;
Muller, 1968), showing greatest diversity in the late Eocene. This suggests that *Proxapertites* was more diverse in the Indian subcontinent and other areas of SE Asia than in Myanmar during the Paleogene.

**Fig. 4.14. Comparison of species diversity.** It shows the species diversity of selected palm and palm-like pollen from the Paleogene of the Indian subcontinent, Myanmar and other areas in SE Asia.

### 4.6 DISCUSSION

**4.6.1 Paleoenvironmental, paleoclimatic and tectonic implications**

The palynological record at Kalewa is divided into two general stages, with the boundary lying at c. 520 m and dividing pollen zones B and C. The first stage is characterized by a low proportion of palms. *Dicolpopollis* is rare but pteridophytes, *Spinizonocolpites*, *Proxapertites* and *Acrostichum* spores are more frequent. Few additional mangrove pollen also occur. This suggests a freshwater setting that is just within reach of tidal influence. During the second stage, *Dicolpopollis* increases but both *Spinizonocolpites*, *Proxapertites* and *Acrostichum* spores are reduced. This composition suggests a lower energy environment than during the previous stage. Therefore, based on the shift in pollen
composition (palms and mangrove elements), an environmental change from a tidally influenced setting to a setting without tidal influence is suggested.

The above scenario fits well within the geological context. The CMB was placed on the southern margin of Eurasia and open towards the Indian Ocean at c. 40 Ma (Fig. 4.1B; Licht et al., 2013, 2014b, 2019; Westerweel et al., 2019). The sedimentological study of the Yaw Formation has shown that through the studied interval, the depositional environment of the Chindwin sub-basin shifted from barrier-bound estuary to fluvial setting (Licht et al., 2019). This was the result of basin overfilling due to the incipient uplift of the Indo-Burman Ranges, blocking the direct connection between central Myanmar and the Indian Ocean (Licht et al., 2019; Westerweel et al., 2019). This tectonically-controlled shift in depositional environment is now corroborated by the palynological data presented herein, supporting the concept that late Eocene was a period of environmental change in the broader geographic setting of the Burma Terrane.

4.6.2 Spatiotemporal changes in palm pollen diversity during the Paleogene of the Indian subcontinent and SE Asia

The Paleocene and Eocene represent a time of high palm (pollen) diversity across the region (Fig. 4.14). This is noticeable in the genera *Longapertites*, *Spinizonocolpites* and *Proxapertites* from the Indian subcontinent, which were particularly diverse in the early Eocene, and in *Dicolpopollis* which was very diverse in the middle and late Eocene of the SE Asia. Interestingly, there is a decline in the diversity of *Longapertites*, *Spinizonocolpites* and *Proxapertites* across the whole region, and in *Dicolpopollis* of SE Asia in the late Paleogene. This poses the question if climatic events such as the Early Eocene Climatic Optimum and the global cooling at the EOT influenced the species diversity of these lineages. For example, the diversity of *Dicolpopollis* is high in the middle and late Eocene of SE Asia, but declines during the Oligocene, which is likely due to the change from a perhumid to a more monsoonal climate following the EOT (Morley, 2018a). Still, climate change does not explain the patterns observed in *Longapertites*, *Spinizonocolpites* and *Proxapertites*.

Here we propose that tectonic activity played a critical role, with the India-Asia collision situated in a tropical location generating a northern Indian “hotspot”. During the late Paleocene and early Eocene, the collision of the Indian Plate with the Kohistan-Ladakh
Arc (Chatterjee and Scotese, 1999), and their subsequent collision with Asia, would have resulted in an archipelagic area comparable with the Western Tethys during the Eocene, the Arabian Sea during the early Miocene, and the present-day Indonesian Archipelago. Such a high-relief archipelago in a wet tropical region would have provided an ideal setting for species differentiation in the sense of “hopping hotspots” of Renema et al. (2008). Diversification of coastal taxa in such a setting would be expected, and could explain the greatly increased numbers of taxa in *Spinizonocolpites*, *Longapertites* and *Proxapertites* compared to other tropical regions of the Paleocene and Eocene. Such a “hotspot” would have been in place with respect to coastal taxa until the late Eocene establishment of a land connection between the Indian Plate and Asia (Klaus et al., 2016). A diversity hotspot, in an archipelagic area with a perhumid climate could have facilitated the early diversification of rainforest taxa, such as Dipterocarpaceae preserved as wood fossils in the underlying Pondaung Formation (Licht et al., 2014a). The rainforest taxa may subsequently have dispersed to the Sunda region following India-Asia collision (Morley, 2018a).

It is noteworthy that Sunda was a diversity hotspot for *Dicolpopollis* during the Eocene. This was possibly, but not exclusively due to the warm climate. Although there are some putative Paleocene *Dicolpopollis* records from India (e.g., Mathur and Jain, 1980), the ages of these deposits are still under debate. There are firm records of *Dicolpopollis* from the Eocene of India, whereas SE Asia has Paleocene records (such as in Sarawak, Muller, 1968), indicating a dispersal from SE Asia to India. This is consistent with the point stated in Morley (2018a), and supported by molecular data that Indian Calamoidae are deeply nested within Sunda clades (Baker et al., 2009; Barrett et al., 2016). Additionally, caution should be taken concerning the increase of *Dicolpopollis* species during EOT in the Indian subcontinent, as this may be due to problems of synonymy in the Paleocene, and insufficient localities in Eocene, or other reasons. These problems could exist in other taxa as well, but have been well resolved in the Sunda Shelf.

Since only few sites with Paleogene fossil pollen have been discovered in Myanmar, it is not reasonable to take them as conclusive evidence for the paleogeographic distribution and diversity of palms in this area. However, first indications are that in terms of the diversity of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites*, Myanmar is less diverse than the Indian subcontinent and other areas in SE Asia (Fig. 4.14). As portrayed in Fig. 4.1B, during the Eocene Kalewa was farther north than most of the Indian subcontinent and SE Asia, while the latter two were closer to the equator. This may explain
a northwards decline due to the latitudinal gradient, which affects the distribution of modern palms including Calamoideae (Eiserhardt et al., 2011), showing that species diversity increased closer to the equator. Nevertheless, it will take further work in Myanmar and elsewhere to fully explain the perceived changes noted in the species richness of the fossil palm pollen.

4.7 | CONCLUSIONS

In this study we investigate fossil PPL pollen of *Dicolpopollis, Longapertites, Spinizonocolpites, Palmaepollenites* and *Proxapertites* from the Eocene of Kalewa, Central Myanmar Basin. We revise all *Dicolpopollis, Longapertites, Spinizonocolpites* and *Proxapertites* taxa using both light and scanning electron microscopy, and classify them at species level where possible. Based on the pollen morphology we conclude that *D. kalewensis* is the senior synonym of *D. malesianus*. Following a quantitative analysis of the PPL pollen, and additional mangrove elements throughout the Kalewa section, we conclude that: (1) the lower part of the Kalewa section is characterized by abundant *Acrostichum* spores but low mangrove elements, indicating a fluvial environment within the uppermost reaches of tidal influence; (2) in the middle part of the section, mangrove elements increase, suggesting a closer proximity to a paleoshoreline; (3) towards the top, the increase in *Dicolpopollis* coupled with the reduction of *Acrostichum* spores indicates a fluvial setting without tidal influence. Our PCA further confirms that the parent plants of *Proxapertites* and *Spinizonocolpites* co-occurred in tidal-influenced settings. Whereas parent plants of *Palmaepollenites kutchensis, Dicolpopollis* and *Longapertites* probably derived from freshwater settings without tidal influence, as they are closely associated and the former two show inverse correlation with *Spinizonocolpites* and *Acrostichum*. Together, the change in pollen composition and the PCA suggest an environmental change, from a tidally influenced estuary to a fluvial setting without tidal influence.

When comparing the global distribution of the Eocene palm taxa with the distribution of their NLRs, a compelling reduction in the distribution ranges is visible. We propose that this shrinking is related to the changing global climate and geography at the EOT, but this will need to be tested further. A comparison of the species diversity of *Dicolpopollis, Longapertites, Spinizonocolpites* and *Proxapertites* in the Paleogene of the Indian subcontinent and SE Asia, further suggests that their increased diversity reflects a diversity
hotspot prior to, and during the time of collision of the Indian Plate with the Kohistan-Ladakh Arc and their subsequent collision with Asia. We hypothesize that these collisions in tropical locations with island settings and significant topographic gradients influenced the species diversity of coastal palms, and resulted in a northern Indian diversity “hotspot” with respect to palms that may have extended to other rainforest taxa.

Our study forms a basis for further palynological work in Myanmar, particularly in other CMB sub-basins. Most importantly, the study of selected PPL pollen taxa on morphology, paleoecology, and paleoenvironment extends the general understanding on the species evolution of Arecaceae and its relationship with paleoclimate. Moreover, we anticipate that these data may prove useful for paleobiogeographic modeling of the history of Arecaceae, particularly in India and SE Asia.

4.8 | ACKNOWLEDGEMENTS

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4.9 | SUPPORTING INFORMATION

Supporting Information can be found online in figshare doi: 10.21942/uva.14312474.