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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 Palaeogene, 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 Palaeogene 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, whereas the parent taxon of *Proxapertites operculatus* was probably a member of the coastal vegetation in the manner of *Spinizonocolpites*. This, with sedimentological data, suggests a palaeoenvironmental change from a brackish, tidally influenced environment to a fully freshwater setting through the late Eocene. Additionally, we mapped and compared the geographical distribution of selected Eocene palm taxa and their NLRs, and found that their distributions shrank after the Eocene. Moreover, in the Palaeogene, species diversity of selected PPL taxa seems lower in Myanmar than in the Indian subcontinent and other regions in South-East Asia. We hypothesize that in the Eocene the Indo-Asian collision zone formed a 'hotspot' for palm diversity, which is reflected in species-rich palynofloras. However, the local palm diversity declined after the Eocene, whereas, at the global level, palm distribution was distinctly reduced between the Eocene and the present. We propose that the retreat of the palms may have occurred as early as the Eocene – Oligocene Transition (EOT), but this remains to be confirmed by the study of EOT pollen records in tropical regions.

ADDITIONAL KEYWORDS: Araceae – Arecaceae – biogeography – *Dicolpopollis* – *Longapertites* – palaeoenvironment – Palmae – *Palmaepollenites* – palynology – *Proxapertites* – *Spinizonocolpites*.

INTRODUCTION

The Central Myanmar Basin (CMB) has yielded an extremely rich fossil record including mammals (e.g. Jaeger *et al.*, 1999; Chavasseau *et al.*, 2010;

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De Bonis *et al.*, 2018) and wood (e.g. Gottwald, 1994; Privé-Gill *et al.*, 2004; Licht *et al.*, 2014, 2015). Palynological studies with focus on the CMB are rare (e.g. Potonié, 1960; Reimann & Aye Thuang, 1981; Engelhardt & Wrenn, 1994), but this area is of great interest, particularly for the palaeoecology of palm taxa that have implications for the palaeoenvironmental 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 Mya based on analysis of a tuff layer (Licht *et al.*, 2018). This provides an excellent opportunity to determine how the palynological record in the CMB relates to the Indo–Asian tectonic convergence and the climate change preceding the Eocene–Oligocene Transition (EOT) (as discussed by Coxall & Pearson, 2007; Dupont-Nivet, Hoorn & Konert, 2008; Abels *et al.*, 2011; Hoorn *et al.*, 2012).

In this study we address the following questions. Which PPL pollens occur in the sedimentary record at Kalewa? What are their palaeoecological implications? How do these pollen types compare with morphotaxa from Palaeogene records of adjacent regions? What is the species diversity of these taxa in the region during the Palaeogene? Are there differences in the distribution of NLRs and their fossil counterparts? Are there any environmental shifts detected by the compositional changes of these PPL taxa? What can this new record, placed in a global context, add to our understanding of palm palaeobiogeography?

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

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 the north-western part of the Burma Terrane (BT; Fig. 1A, 23°14' N, 94°15' E). At *c.* 40 Mya, the CMB was located at the margin of Eurasia and was open towards the Indian

Ocean, forming an embayment that was the locus of south-west facing deltas (Fig. 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.*, 2018); 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.*, 2018). 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. 1A; Licht *et al.*, 2013, 2016, 2018). 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 Mya (Licht *et al.*, 2018). The unconformably overlying Letkat Formation consists of coarse fluviatile clastics (Bender, 1983). A dated tuffite layer, from *c.* 38.3 Mya, is positioned at *c.* 500 m above the base of the section, in the upper third of the profile. Sedimentation rates for most of the Yaw Formation are estimated at > 1 m/Kyr (Licht *et al.*, 2018) and, therefore, the studied section is dated as late Bartonian, probably extending into the early Priabonian up-section.

PALMS AND THEIR PALAEOBIOGEOGRAPHICAL CONTEXT

Palms (Arecaceae) comprise 181 genera with *c.* 2600 species (Christenhusz & Byng, 2016), most of which are currently restricted to tropical and subtropical regions (Couvreur, Forest & Baker, 2011). They are an ancient group, with a molecular age of *c.* 114 Myr (Couvreur *et al.*, 2011) and fossils dating back to the Turonian (93.5–89.0 Mya; Crié, 1892; Kvaček & Herman, 2004); the group predominated throughout the equatorial zone during the latest Cretaceous and Paleocene (Morley, 2000). In the Maastrichtian, PPL pollen of the form-genera *Spinizonocolpites* Muller, *Palmaepollenites* Potonié, *Longapertites* van Hoeken-Klinkenberg and *Proxapertites* van der Hammen are found widely across the Palaeotropics (e.g. Hengreen *et al.*, 1996; Vergara & Rodriguez, 1997; Eisawi & Schrank, 2009). The form-taxon *Dicolpopollis* Pflanzl, characteristic of subtribe Calaminae (Harley & Morley, 1995), first appeared 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* Potonié from the Paleocene to early

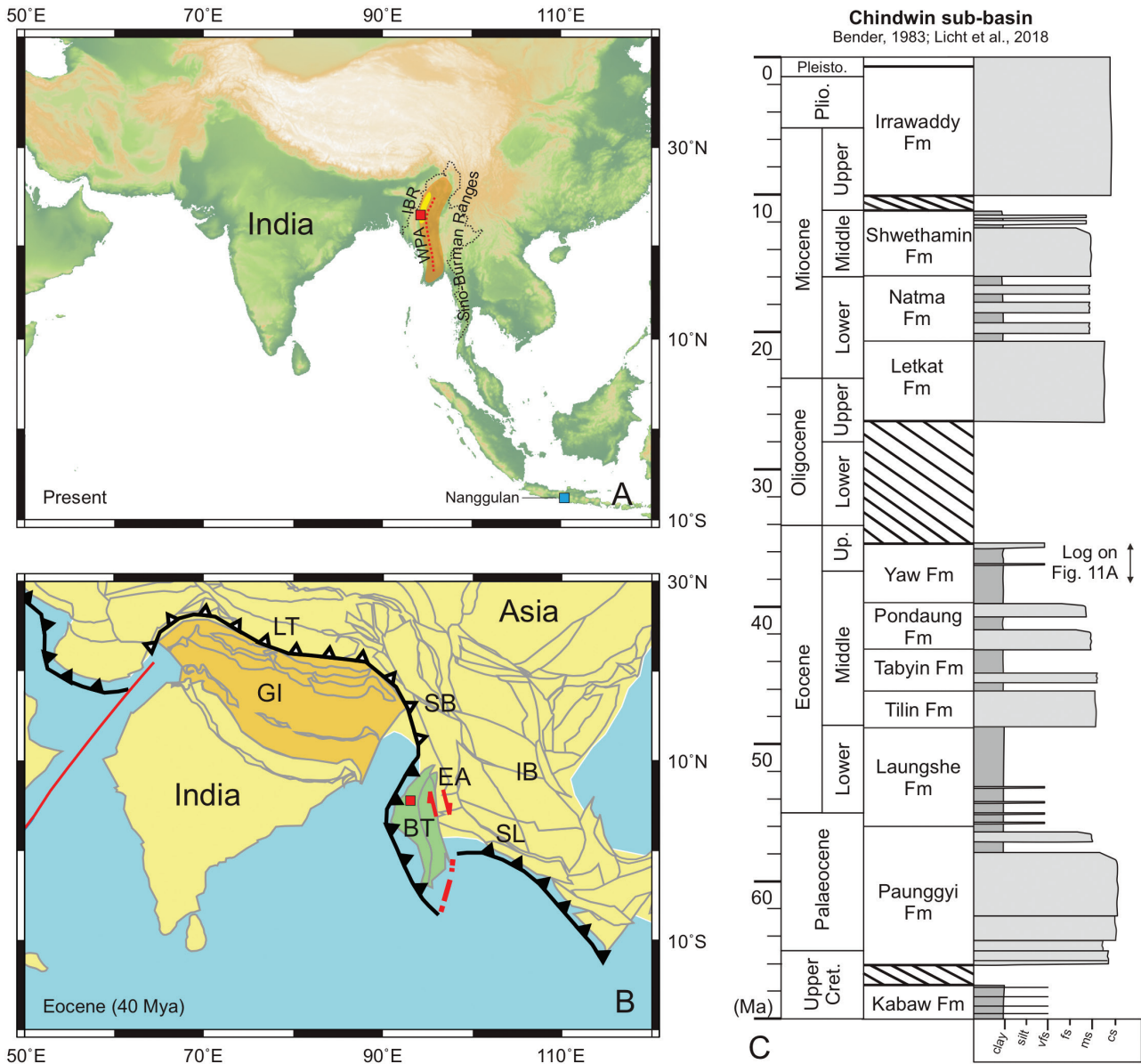


Figure 1. A, Schematic map showing the study area (red square) in the CMB, made with GeoMapApp v.3.6.10. IBR = Indo–Burman Ranges; WPA = Wuntho–Popa volcanic arc, indicated by the red dash line. Light orange shading outlines the CMB; yellow shading outlines the Chindwin sub-basin; black dash line marks the Myanmar borders. Positions of the IBR, Sino-Burman Ranges and the CMB refer to Licht *et al.* (2014), whereas the Chindwin sub-basin follows Licht *et al.* (2018). 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 Mya (modified after Westerweel *et al.*, 2019). BT = Burma Terrane, EA = Eastern Andaman, IB = Indochina Blocks, GI = Greater India, LT = Lhasa Terrane, SB = Sibumasu Block, SL = Sundaland. Red square represents the study area; 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.*, 2018).

Eocene Nindam Formation (Mathur & Jain, 1980). *Dicolpopollis* expanded its range during the Eocene to Australia (MacPhail, Colhoun & Fitzsimons, 1995), New Zealand (Hartwich *et al.*, 2010), central Europe

(Bignot *et al.*, 1985; Riegel, Wilde & Lenz, 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 Palaeogene coastal records (e.g. Oman, Bealy, 1998; India, Tripathi, Kumar & Srivastava, 2009; Prasad *et al.*, 2013; Africa, Jacobs, Pan & Scotese, 2010; Australia, Macphail & 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 (Germeraad, Hopping & Muller, 1968; Schrank, 1987, 1994; Digbehi *et al.*, 1996; Herngreen, 1998), 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).

MATERIAL AND METHODS

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 g 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 and 212- μm meshes were used. The sample material was heated in acetolysis mixture (nine parts of acetic anhydride/one part of concentrated sulphuric 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 a 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 g 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 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.

PALYNOLOGICAL ANALYSIS

The Kalewa samples have a poor sporomorph preservation and the organic material is often pyritized or corroded. To construct a reliable pollen diagram, a baseline on pollen sum of 100 grains was maintained. All samples with counts < 100 were excluded resulting in 54 positive samples. Identification of fossil PPL pollen was mainly based on Potonié (1960), Germeraad, Hopping & Muller (1968), Muller (1968), Reimann & Aye Thaug (1981) and Harley & Morley (1995). Palm pollen grains not included in *Longapertites*, *Dicolpopollis*, *Spinizonocolpites*, *Proxapertites* or *Palmaepollenites kutchensis* Venkatachala & Kar were classified as 'other palms' in the pollen diagram. The pollen diagram was constructed using the Tilia v.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 ImageJ (National Institute of Health, USA). PCA was employed in R (R Core Team, 2018) to analyse palaeoecological correlation on PPL taxa. Additionally, an analysis of variance (ANOVA) of pollen abundance among different pollen zones and a non-parametric correlation (Spearman) of taxa were performed with SPSS v.24.0 (SPSS Inc., Chicago, IL, USA).

MICROPHOTOGRAPHY

The micrographs in Fig. 2 were taken at IBED using Fujifilm X-E2 and a Zeiss Universal microscope with 63 \times Plan Neofluar NA1, 25 oil applying Nomarski Differential Interference Contrast (DIC) following Bercovici, Hadley & Villanueva-Amadoz (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



Figure 2. LM micrographs for the PPL pollen under $\times 630$ magnification from the Eocene of Kalewa, CMB. A1, A2. *Proxapertites operculatus*; B, C. *Palmaepollenites kutchensis*; D1, D2, G1, G2. *Dicolpopollis kalewensis*; E. *Longapertites retipilatus*; F. *Spinizonocolpites prominatus* and H, I, J1, J2. *Palmaepollenites* sp. 2. Scale bars = 10 μm .

CC. This stacking technique combines different layers to provide a fully focused image. LM micrographs in Figs 3–10 were taken by a ProgRes Speed XT^{core} 5 camera connected with a Nikon Eclipse 80i LM. SEM micrographs in Figs 3–10 were taken with the JEOL JSM-6400. Figs 2–10 were made with InDesign CC. The background of kerogen in the LM original micrographs was manually edited out.

DISTRIBUTION MAPS

Mapping the global distribution of NLRs

Occurrence data (Supporting Information, Table S1) of the NLRs of the fossil form-genera *Dicolpopollis* (*Calamus* L., *Daemonorops* Blume and *Ceratolobus* Blume ex Schult. & Schult.f. in Calaminae, placed in the single genus *Calamus* by Baker (2015); GBIF.org. 2019d, <https://doi.org/10.15468/dl.wvfy3m>, with 10 438 locality points), *Palmaepollenites kutchensis* (Areceae subtribe Basseliniiae with details for *Basselinia* Vieill. and *Burretiokentia* Pic.Serm.; GBIF.org. 2019b, <https://doi.org/10.15468/dl.bzjazl>,

with 1202 locality points), *Spinizonocolpites* (*Nypa* Steck; GBIF.org. 2019c, <https://doi.org/10.15468/dl.rliz8n>, with 233 locality points) and *Longapertites* (probably *Eugeissona* Griff.; GBIF.org. 2019a, <https://doi.org/10.15468/dl.ag40lq>, 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 v.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) (Supporting Information, Figs S1–S4), as other records fall well within distribution ranges of previous studies.

Mapping the global Eocene distribution of PPL taxa with emphasis on the Palaeogene of India and South-East Asia

We compiled published global Eocene records of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Palmaepollenites kutchensis* (Supporting Information, Table S2) 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 *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* in the Palaeogene of the Indian subcontinent and South-East Asia for the comparison of species diversity (Supporting Information, Tables S3, S4). This compilation is based on the Palynodata database (Palynodata Inc. & 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 v.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 the Eocene (40 Mya), 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 and level 1, records from the inaccessible literature. Distributions were georeferenced when latitudinal and longitudinal data were not provided, and all data points were collated.

RESULTS

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 Mya (Licht *et al.*, 2018) and supported by the presence of age-indicative marker species such as the sporomorphs *Meyeripollis naharkotensis* Baksi & Venkatachala, *Cicatricosisporites dorogensis* Potonié & Gelletich and *Proxapertites operculatus* van der Hammen (Huang *et al.*, 2018). These sporomorphs types define the Sunda palynological Zone E8, which has an age range of c. 37.8–36.5 Myr (Witts *et al.*, 2012; van Gorsel, Lunt & Morley, 2014).

SYSTEMATICS

The morphology of the fossil PPL pollen is described using LM and SEM, and all measurements are available in Table S5. 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 EMEND. SINGH

Type species: Proxapertites operculatus van der Hammen

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 (FIGS 2A1, A2, 3A–R)

Synonym: Monocolpites operculatus van der Hammen, *Proxapertites hammenii* Venkatachala & Rawat (Thanikaimoni *et al.*, 1984).

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 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. 3K); aperture margins rolled inwards, inner side of pollen wall slightly sculptured; thin and folded membrane observed in aperture area (SEM).

Botanical affinity, ecology and distribution: *Proxapertites operculatus* was initially compared to the South American cocosoid palm *Astrocaryum* G.Mey. 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

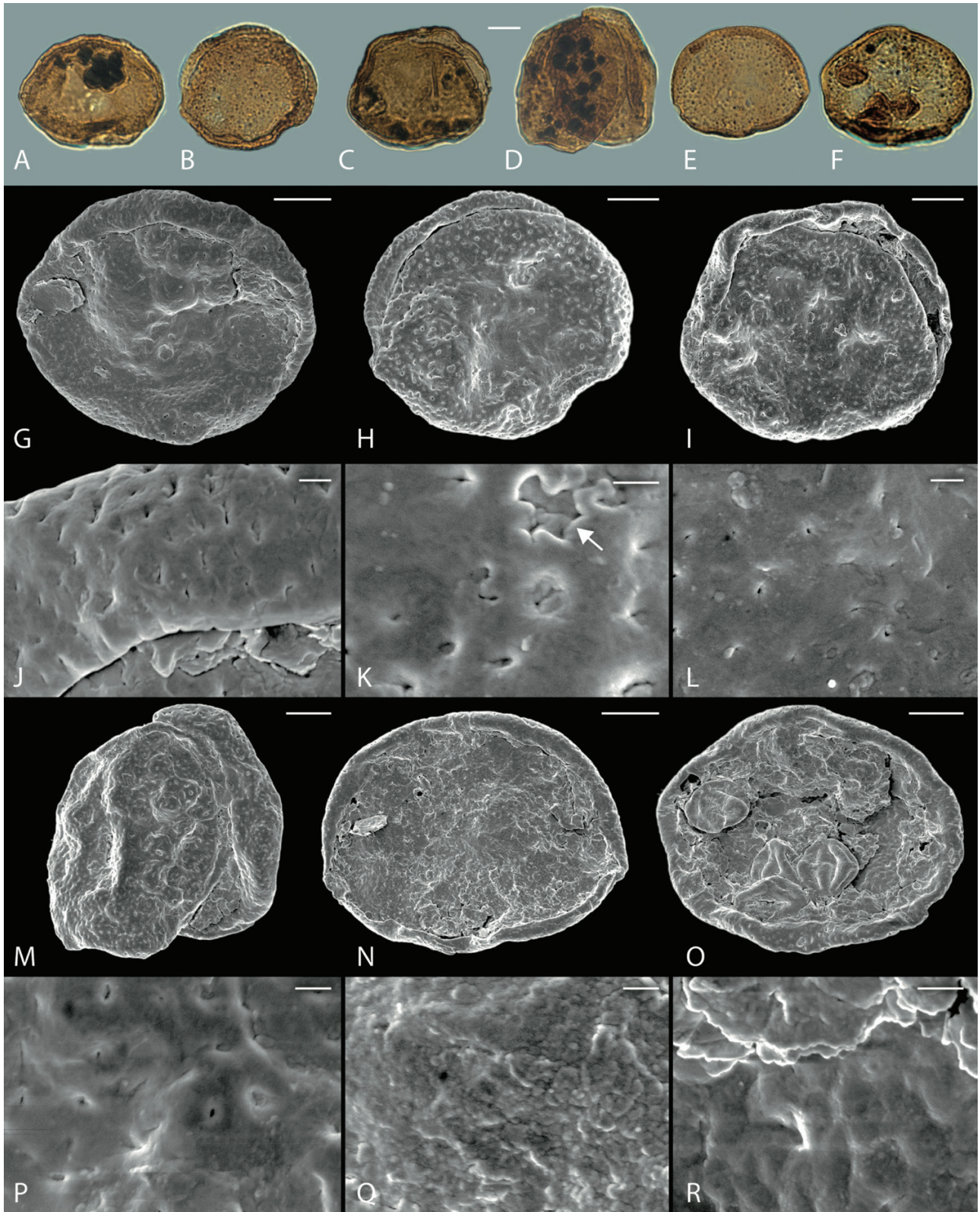


Figure 3. A–F, LM and G–R, SEM micrographs of *Proxapertites operculatus* from the Eocene of Kalewa, CMB. A, G, J, Same grain, close-up (J) of aperture region. B, H, K, Same grain, arrow in (K) pointing to infection of bacteria. C, I, L, Same grain,

been widely followed in subsequent literature (e.g. Morley, 2000). However, several authors note that *Proxapertites* is incompletely zonocolpate, and this prompted Harley & Baker (2001) to compare it with a subgroup of the arecoid palm *Areca* L., especially *A. abdulrahmanii* J.Dransf. and *A. chaiana* J.Dransf. On the other hand, Thanikaimoni *et al.* (1984) and Samant & Phadtare (1997) indicated that similar pollen occurs in Araceae (arum family). This was followed up by Zetter, Hesse & Frosch-Radivo (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* Engl. (Aroideae-Zamioculcaceae in Araceae).

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

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

Type species: Longapertites marginatus van Hoeken-Klinkenberg

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 & Dransfield, 2000) based on its extended colpus (Morley, 2000). Nevertheless, there are some morphological differences between the two taxa, especially in configuration of the two pollen halves, with specimens of *Longapertites* showing a

greater morphological differentiation than observed in *Eugeissona*. *Longapertites* apparently had a pantropical distribution during the Maastrichtian and Palaeogene, with fossil records from South America, West Africa, India and northern Australia (Baker & Dransfield, 2000; McGowran *et al.*, 2000). *Quilonipollenites* Rao & Ramanujam has been considered as a synonym of *Longapertites* (Frederiksen, 1994), and is in fact much closer to extant *Eugeissona* than *Longapertites*. Also, Venkatachala & 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, Kayseri & Akgün, 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 RETIPIILATUS KAR (FIGS 2E, 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 (FIGS 4D–F, M–R, 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

close-up (L) of the tectum. D, M, P, Same grain, close-up (P) of the tectum. E, N, Q, Same half of grain, showing (N, Q) inner side of pollen wall. F, O, R, Same half of grain, showing (O, R) inner side of pollen wall. LM micrographs were taken under ×1000 magnification. Scale bars: A–G, J–L = 10 µm; H–I, M–O = 1 µm.

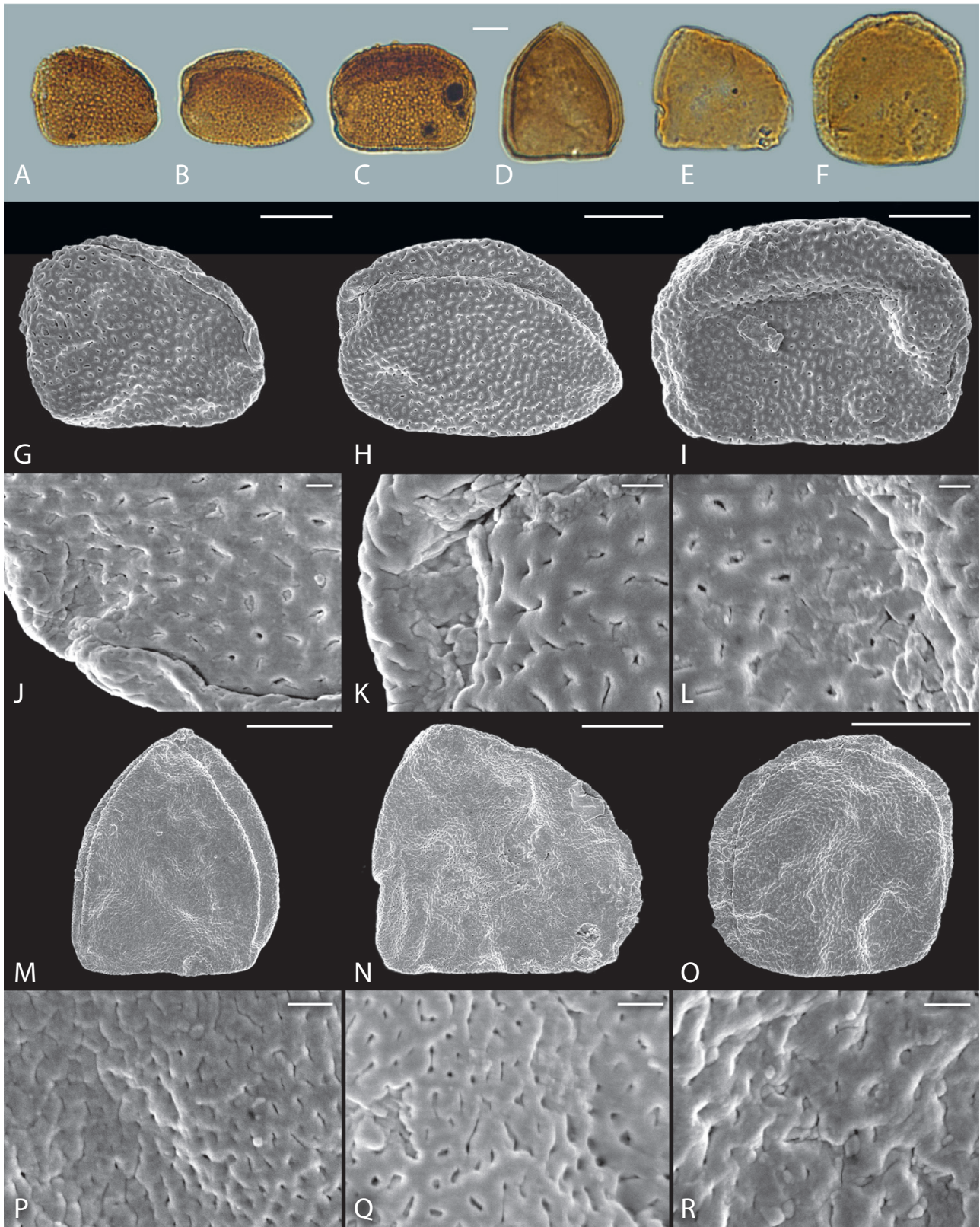


Figure 4. A–F, LM and G–R, SEM micrographs of *Longapertites* from the Eocene of Kalewa, CMB. A–C, G–L, *Longapertites retipilatus*. A, G, J, Same grain, close-up (J) of aperture region. B, H, K, Same grain, close-up (K) showing part of membrane.

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 EMEND. POTONIÉ

Type species: *Dicolpopollis kockelii* Pflanzl

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, Bati & Alişan, 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* and *Ceratolobus*) in Areaceae (Harley & Morley, 1995; Morley, 2000). Calaminae are distributed across central Africa, and from South/southern South-East 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 rain forests, occurring from sea level to mountain tops. Calaminae are sometimes locally abundant in swamps and mangrove forests, and can form thickets along rivers (Dransfield, 1974).

DICOLPOPOLLIS KALEWENSIS POTONIÉ (FIGS 2D1, D2, G1, G2, 6A–R, 7A–D, F–K, M–N)

Synonym: *Disulcites kalewensis* Potonié, *Dicolpopollis kalewensis* (Potonié) Potonié, *Disulcipollenites kalewensis* (Potonié) Nakoman, *Dicolpopollis malesianus* Muller.

Description (based on 12 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 to 26.7–36.9 μm in

polar view, and polar axis 24.3–28.5 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 thick (SEM; Fig. 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).

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 & 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. (FIGS. 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 \times 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

Type species: *Palmaepollenites tranquillus* (Potonié) Potonié (synonym: *Monocolpopollenites tranquillus* (Potonié) Thomson & Pflug)

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 $\times 1000$ magnification. Scale bars: A–I, M–O = 10 μm ; J–L, P–R = 1 μm .

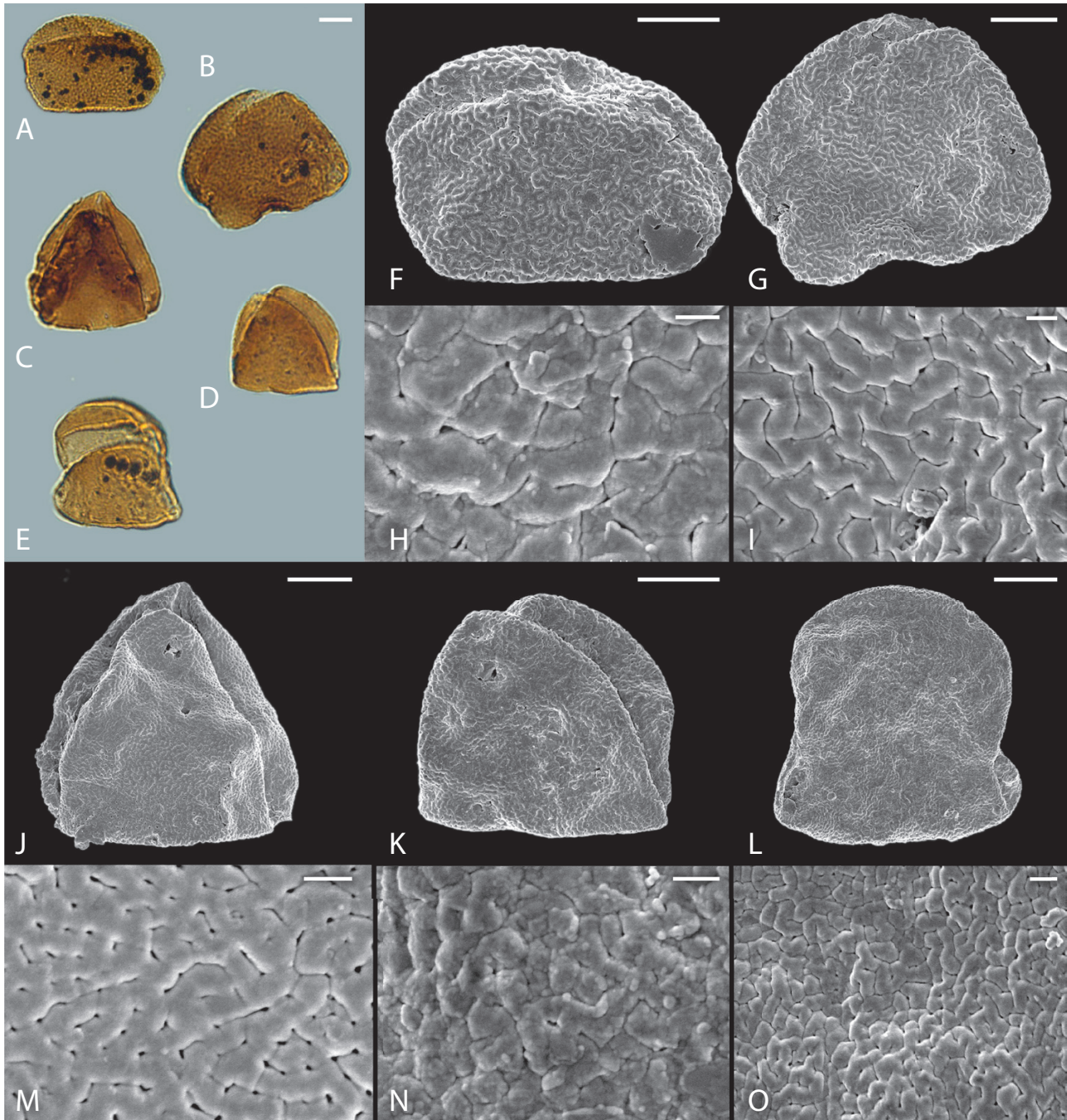


Figure 5. A–E, LM and F–O, SEM micrographs of *Longapertites rugulatus* from the Eocene of Kalewa, CMB. A, F, H, Same grain, close-up (H) of tectum. B, G, I, Same grain, close-up (I) of tectum. C, J, M, Same grain, close-up (M) of tectum. D, K, N, Same grain, close-up (N) of tectum. E, L, O, Same grain, close-up (O) of tectum. LM micrographs were taken under $\times 1000$ magnification. Scale bars: A–G, J–L = 10 μm ; H–I, M–O = 1 μm .

PALMAEPOLLENITES KUTCHENSIS VENKATACHALA & KAR (FIGS 2B, C, 8A–R)

Synonym: *Monocolpites ellipticus* Takahashi; *Palmaepollenites* type 1 of Harley & Morley (1995).

General information: This taxon was originally discovered in India, but its Eocene range extended into South-East Asia, west of Wallace's Line (Harley & Morley, 1995; Morley 1998, 2000). The source taxon, *P. kutchensis*, probably originated in India during the Late Cretaceous,

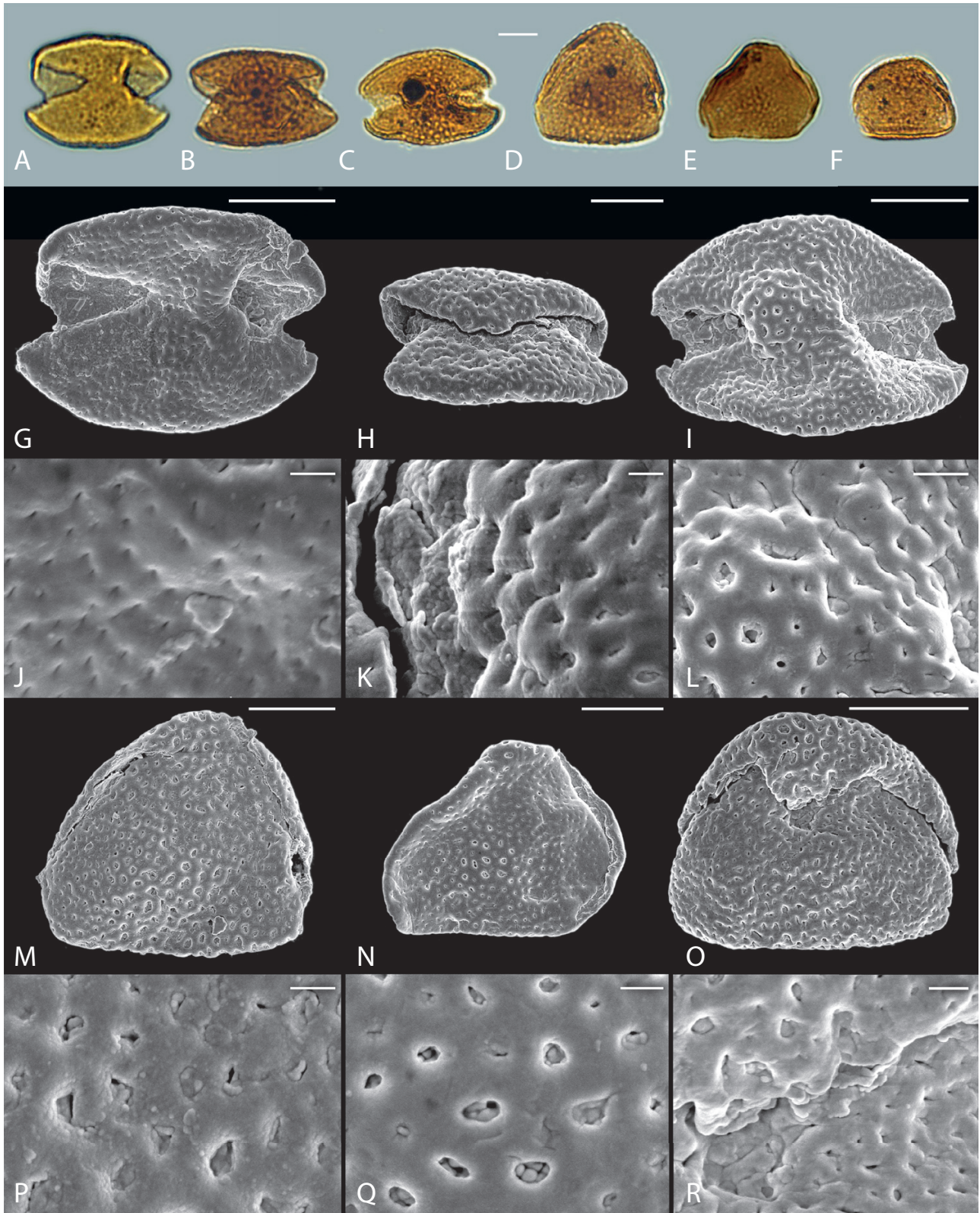


Figure 6. A–F, LM and G–R, SEM micrographs of *Dicolpopollis kalewensis* from the Eocene of Kalewa, CMB. A, G, J, Same grain, close-up (J) of tectum in polar area. B, H, K, Same grain, close-up (K) of aperture with membrane. C, I, L, Same grain,

and subsequently migrated to South-East Asia following the Indo–Asian collision in the middle Eocene (Morley, 2000, 2018). *Palmaepollenites kutchensis* gradually disappeared from the Sundanese record during the Oligocene (Harley & 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 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 *Pritchardia* Seem & H.Wendl. and *Lepidorrhachis* (H.Wendl. & Drude) O.F.Cook (Harley & Morley, 1995), which have a young Neogene molecular age (Baker *et al.*, 2011) and thus the affinity is unlikely. *Palmaepollenites kutchensis* is also similar to pollen of several genera in Areceae, especially *Basselinia* and *Burretiokentia* (both Basseliniae, confined to New Caledonia and formerly in Iguarinae; Harley & Morley, 1995), members of an older 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 southern 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 Guinean flora), 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. 1A) of central Java where it contributes *c.* 40% of the total pollen recovery (figs 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, 2018).

PALMAEPOLLENITES SP. 1 (FIG. 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 22.8–34.9 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 Basselinieae (Areceae, Arecaceae).

Remarks: The sculpture observed with SEM is 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 (FIGS 2H, I, J1, J2, 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 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.

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 *SPINIZONOLPITES* MULLER EMEND. MULLER ET AL.

Type species: *Spinizonolpites echinatus* Muller

General information: *Spinizonolpites* was proposed by Muller (1968). Pollen grains of this type commonly

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 $\times 1000$ magnification. Scale bars: A–I, M–O = 10 μm ; J–K, P–R = 1 μm ; L = 2 μm .

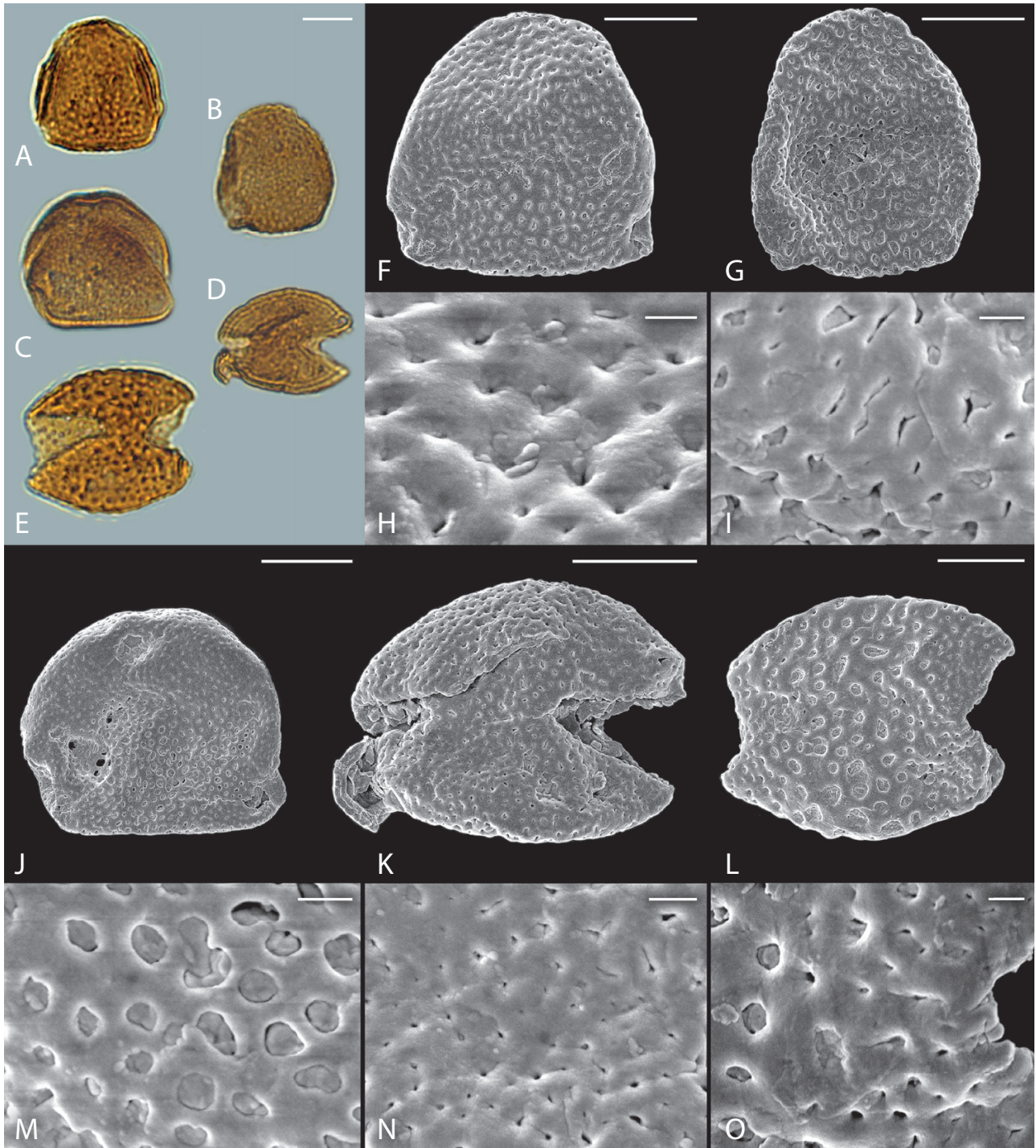


Figure 7. A–E, LM and F–O, SEM micrographs of *Dicolpopollis* from the Eocene of Kalewa, CMB. A–D, F–K, M–N, *Dicolpopollis kalewensis*. A, F, H, Same grain, close-up (H) of tectum. B, G, I, Same grain, close-up (I) of tectum. C, J, M, Same grain, close-up (M) of tectum. D, K, N, Same grain, close-up (N) of tectum. E, L, O, *Dicolpopollis* sp., same grain, close-up (O) of tectum in interapertural area. LM micrographs were taken under $\times 1000$ magnification. Scale bars: A–G, J–L = 10 μm ; H–I, M–O = 1 μm .

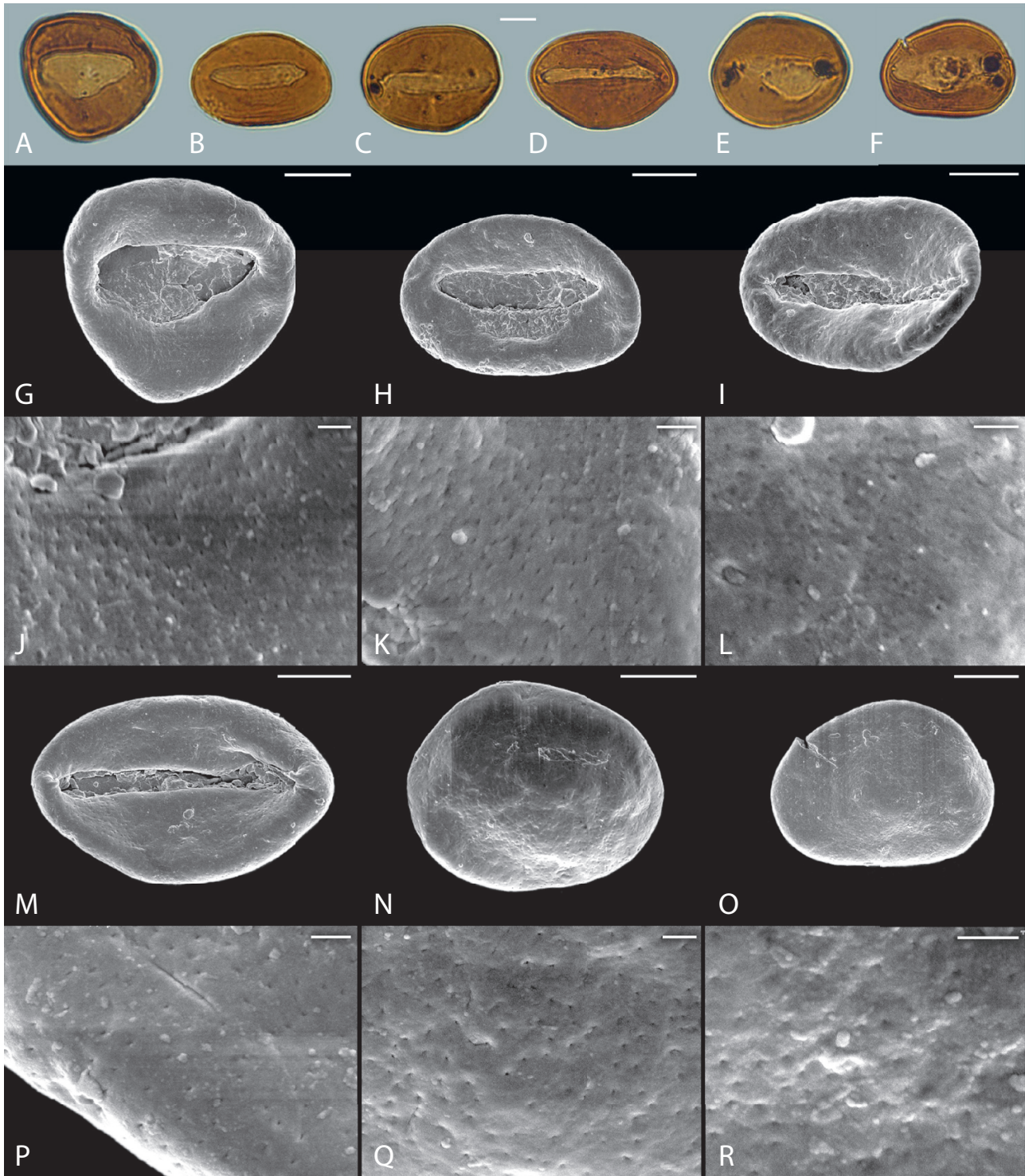


Figure 8. A–F, LM and G–R, SEM micrographs of *Palmaepollenites kutchensis* from the Eocene of Kalewa, CMB. A, G, J, Same grain, close-up (J) of tectum. B, H, K, Same grain, close-up (K) of tectum. C, I, L, Same grain, close-up (L) of tectum. D, M, P, Same grain, close-up (P) of marginal area. E, N, Q, Same grain, close-up (Q) of tectum. F, O, R, Same grain, close-up (R) of tectum. LM micrographs were taken under $\times 1000$ magnification. Scale bars: A–I, M–O = 10 μm ; J–L, P–R = 1 μm .

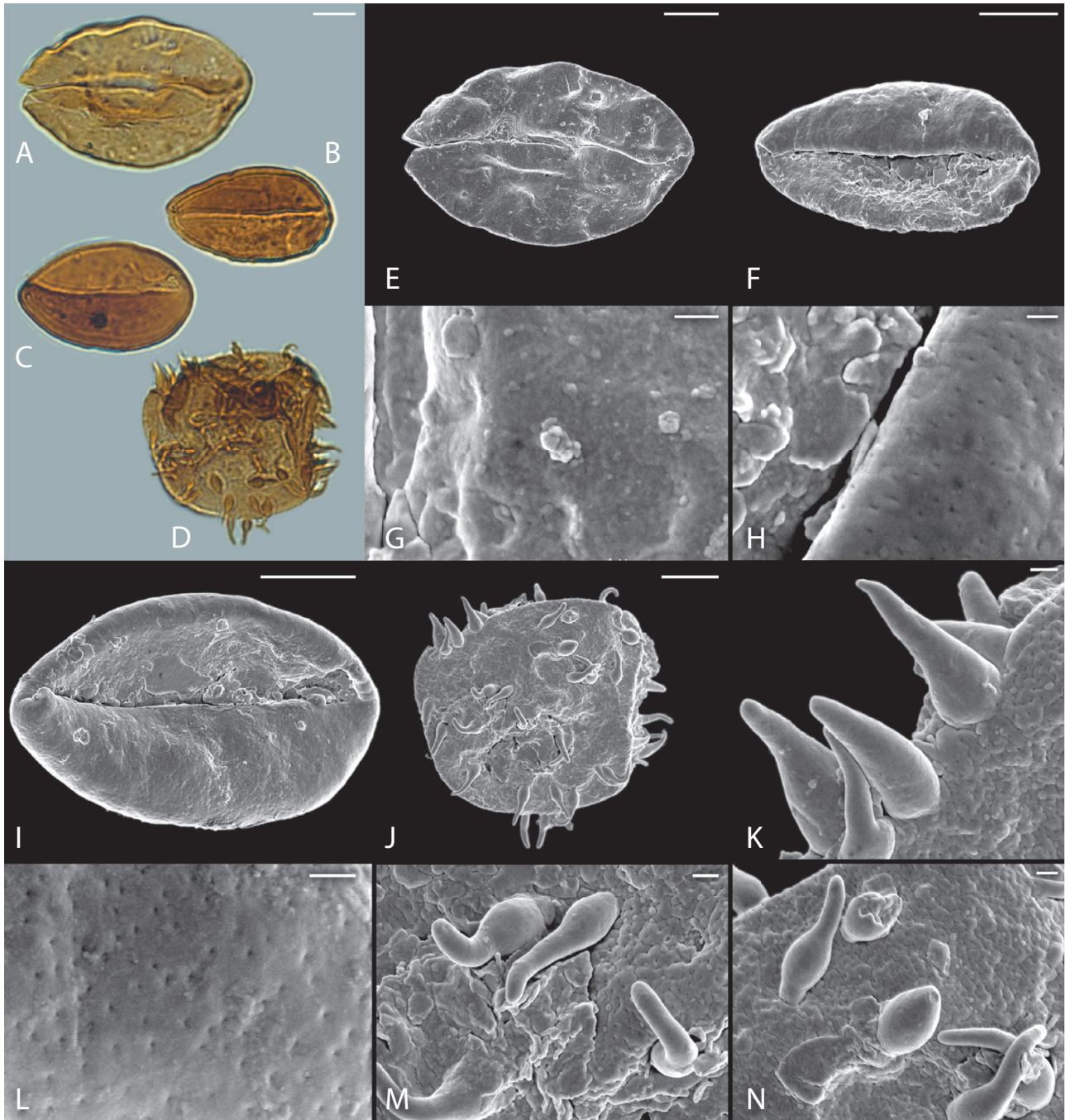


Figure 9. A–D, LM and E–N, SEM micrographs of *Palmaepollenites* sp. 1 and *Spinizonocolpites prominatus* from the Eocene of Kalewa, CMB. A–C, E–I, L, *Palmaepollenites* sp. 1. A, E, G, Same grain, showing (G) inner side of pollen wall. B, F, H, Same grain, close-up (H) of aperture area. C, I, L, Same grain, close-up (L) of tectum. D, J–K, M–N, *Spinizonocolpites prominatus*, same grain, close-up (K, M, N) of tectum and spines. LM micrographs were taken under $\times 1000$ magnification. Scale bars: A–F, I–K = 10 μm ; G–H, L–N = 1 μm .

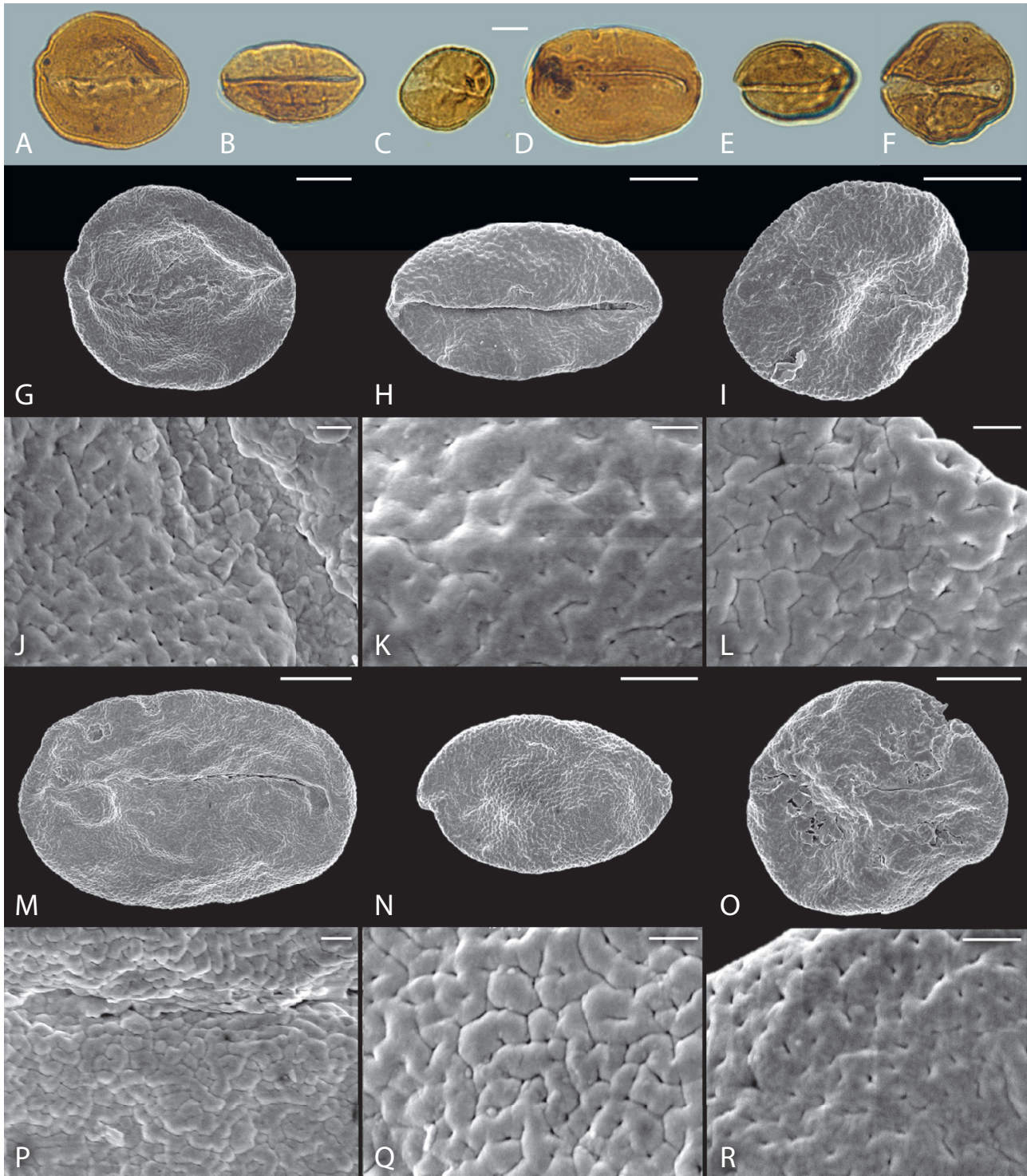


Figure 10. A–F, LM and G–R, SEM micrographs of *Palmaepollenites* sp. 2 from the Eocene of Kalewa, CMB. A, G, J, Same grain, close-up (L) of aperture area. B, H, K, Same grain, close-up (K) of tectum. C, I, L, Same grain, close-up (L) of marginal area. D, M, P, Same grain, close-up (P) of aperture area. 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 $\times 1000$ magnification. Scale bars: A–I, M–O = 10 μm ; J–L, P–R = 1 μm .

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* Wurm from the monotypic subfamily Nypoideae (Baker & Couvreur, 2013), a mangrove palm that often grows in vast natural stands in a range 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 Palaeogene it had a pantropical distribution. *Spinizonocolpites* can be used as a marker fossil for the poleward extension of moist tropics during early Eocene, at which time it was widely distributed in both the northern and southern hemispheres (Vinken, 1988; Pole & MacPhail, 1996; Morley, 2000).

***SPINIZONOCOLPITES PROMINATUS* (MCINTYRE)
STOVER & EVANS (FIGS 2F, 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 & SEM); zonosulcate; exine 1.0–1.7-µm thick (LM & 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 & SEM).

Botanical affinity: This taxon is comparable to pollen of *Nypa* (Muller, 1968; Frederiksen, 1980). *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 Palaeogene, 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 & 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 & 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*.

DISCUSSION

PALYNOLOGICAL ZONES, PALAEOVEGETATION AND PALAEOENVIRONMENT

The Eocene Kalewa pollen assemblage is diverse, reflecting a rich and diverse palaeovegetation, with a predominance of dicotyledons and pteridophytes and a good representation of monocots, particularly palms, but with few gymnosperms. The palynological assemblage represents a seasonally wet flora that mainly includes pollen from tropical plants. There are numerous megathermal tropical forest elements, including *Anacolosidites* Krutzsch (Olacaceae), *Lanagiopollis nanggulanensis* Morley (*Alangium* Lam., Cornaceae), *Cupanieidites flaccidiformis* Venkatachala & Rawat (Sapindaceae) and *Margocolporites* Ramanajuan (*Caesalpinia* L., Fabaceae), some mesothermal and microthermal angiosperms, such as *Alnipollenites* Potonié (*Alnus* Mill., Betulaceae), *Betulapollenites* Potonié (*Betula* L., Betulaceae), *Celtispollenites* (*Celtis* L., Cannabaceae) and *Gothanipollis* Krutzsch (Loranthaceae), Fagaceae and some rare montane gymnosperms [e.g. *Podocarpidites* Cookson (*Podocarpus* L'Hér. ex Pers., Podocarpaceae)] and abundant pteridophytes [e.g. *Acrostichum* L. (Pteridaceae) and *Verrucatosporites* Pflug & Thomson (Polypodiaceae)] (Huang *et al.*, 2018). The pollen diagram (Fig. 11; for raw pollen counts see Table S6) is subdivided into three main zones (Zones A–C) reflecting environmental shifts and ecological changes. The ANOVA result (P value > 0.05; Table S7) 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 palaeofloral elements (Fig. 11B) indicates three main palaeoecological stages in the development of the vegetation in the estuary.

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. *Palmaepollenites kutchensis* and *Dicolpopollis* percentages are relatively low and discontinuous. Other mangrove pollen is rare, but *Acrostichum* (ferns typical of disturbed/open areas in

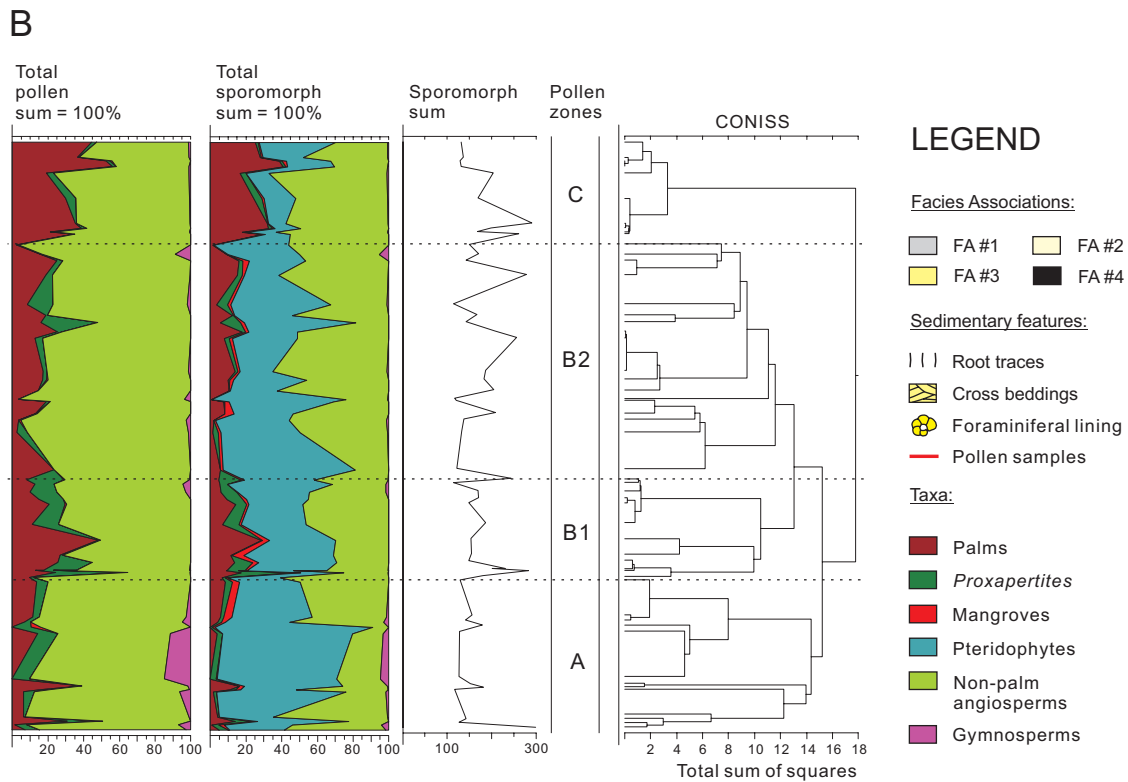
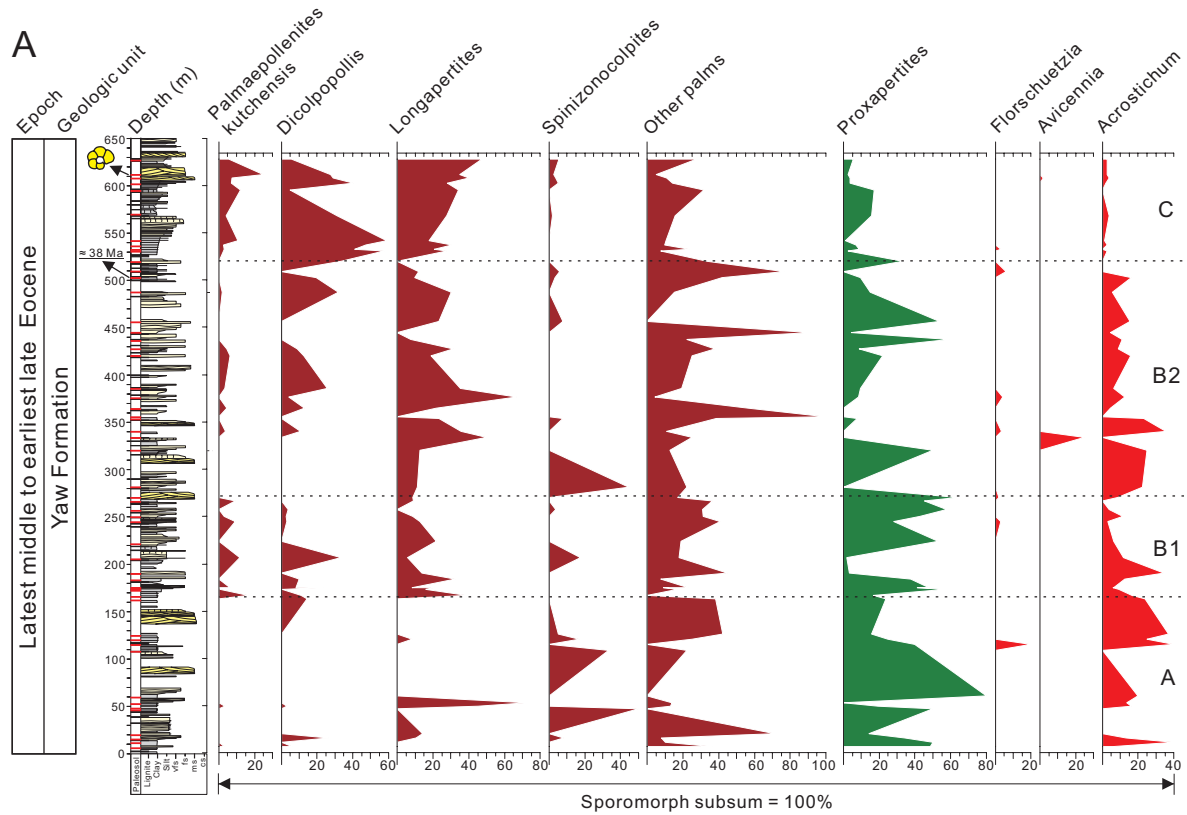


Figure 11. A, B, Pollen diagram, showing the shift of different environmental indicators. In the palaeosol column, black lines indicate histosols. Vfs = very fine sand; fs = fine sand; ms = medium sand; cs = coarse sand; B = Boulder.

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, whereas *Spinizonocolpites* has a solitary peak at c. 280 m. *Palmaepollenites kutchensis* and *Dicolpopollis* increase gradually and their general trends are similar, not only in this zone, but throughout the entire succession (Fig. 11A). This is consistent with the indication from the middle Eocene Nanggulan coal (Fig. 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 subzone B1, *Longapertites* has low percentages, whereas the percentages of *Spinizonocolpites* and *Proxapertites* are relatively high. This indicates closer proximity to the palaeo-shoreline. 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 common. This could be explained by that *Acrostichum* may also occur in disturbed floodplain settings, as emphasized by Moreno-Domínguez 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 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.

PALAEOECOLOGICAL CORRELATION OF SELECTED PPL TAXA

The PCA (Fig. 12) of PPL pollen (*Spinizonocolpites*, *Proxapertites*, *Longapertites*, *Dicolpopollis* and *Palmaepollenites kutchensis*) and *Acrostichum* from Kalewa shows that *P. kutchensis* correlates 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 (Figs 9.10, in Morley, 2000).

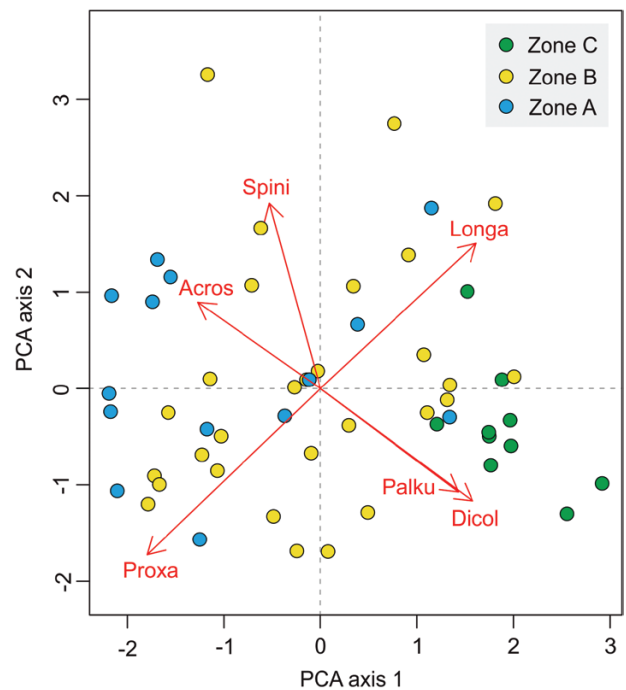


Figure 12. PCA biplot showing correlation between the PPL pollen (*Spinizonocolpites*, *Proxapertites*, *Longapertites*, *Dicolpopollis* and *Palmaepollenites kutchensis*) and *Acrostichum* from the Eocene of Kalewa, CMB. Variance explained: axis 1: 35.1%; axis 2: 19.4%. Dicol = *Dicolpopollis*, Palku = *Palmaepollenites kutchensis*, Longa = *Longapertites*, Spini = *Spinizonocolpites*, Proxa = *Proxapertites* and Acros = *Acrostichum*.

Longapertites has a positive correlation with both *P. kutchensis* and *Dicolpopollis*, and possibly also belongs to a freshwater taxon. *Longapertites* is well represented at Kalewa, but rare at Nanggulan (Morley, 2000), which might 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 non-parametric correlation (Spearman, Table S7) between *Proxapertites* vs. *Acrostichum* and *Proxapertites* vs. *Spinizonocolpites* shows that the levels of significance 96.5 and 84.8%, respectively, illustrating 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. 12) reflects proximity to the coast/salinity. Arrows towards positive values indicate freshwater settings, while arrows towards negative values suggest brackish environment.

EOCENE AND MODERN GEOGRAPHICAL DISTRIBUTION
OF SELECTED PALMS

At present, Calaminae (including *Calamus*, *Daemonorops* and *Ceratolobus*) occur in South-East Asia, central Africa, southern China, India, Sri Lanka, the Pacific islands and Australia (Fig. 13B), whereas *Basselinia* and *Burretiokentia* have a relict New Caledonian distribution (Fig. 13D). Areceae occur in South-East Asia, southern China, southern India, northern Australia, North Island of New Zealand and Madagascar (Fig. 13D). *Nypa* occurs naturally in South-East Asia, the Ganges Delta, the western Pacific, Sri Lanka and northern Australia (Fig. 13F), and *Eugeissona* is distributed in the Malay Peninsula and Borneo (Fig. 13H). GBIF data on Basseliniae (including *Basselinia* and *Burretiokentia*; one unlikely record in Italy was excluded; see Fig. 13B), *Eugeissona* (see Fig. 13H), Calaminae (including *Daemonorops* and *Ceratolobus*) and 'Observation' data on *Calamus* and *Nypa* falls well within the ranges from previous studies (Ruddle, 1979; Baker *et al.*, 1998; Mehrotra, Tiwari & Mazumder, 2003; Dransfield *et al.*, 2008). The Eocene maps show that *Dicolpopollis*, *Spinizonocolpites* and *Longapertites* had a pantropical distribution, whereas *P. kutchensis* was restricted to the Indian subcontinent and South-East Asia. Also, *Dicolpopollis* was absent from Africa and South America and present in southern North America and Europe, whereas *Longapertites* was absent from Europe. The presence of *Calamus deeratus* G.Mann & H.Wendl. in equatorial Africa may therefore reflect a Neogene dispersal (Fig. 13A, B). Basseliniae, producing *P. kutchensis* Pollen type, were widespread across the Indian Plate and South-East Asia. This pollen type is now restricted to the relict *Basselinia* and *Burretiokentia* that occur in New Caledonia (Fig. 13C, D). *Nypa* became extinct across the Americas, Africa and Europe after the Eocene (Fig. 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 climatic change and competition from other plants (Fig. 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.

A COMPARISON OF PPL POLLEN DIVERSITY IN THE
PALAEOGENE OF THE INDIAN SUBCONTINENT,
MYANMAR AND SOUTH-EAST ASIA

The composition at genus level of PPL pollen at Kalewa is similar to that of adjacent areas during the Palaeogene, whereas the species diversity of

these palm taxa is quite different. This becomes clear when the fossil records and diversity of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* from the Indian subcontinent, Myanmar and other areas in South-East Asia are compared (Supporting Information, Tables S3, S4; Fig. 14).

The oldest reliable Asian records of *Dicolpopollis* (*D. malesianus* = *D. kalewensis* and *D. elegans* Muller) are from the Paleocene of Sarawak, tropical Asia (Muller 1968; Morley, 1998). *Dicolpopollis* is also recorded from the Paleocene of India (e.g. Mathur & 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 (Takahashi, 1982; Harley & Morley, 1995; Lelono, 2000; Morley, 2000), and from southern Sulawesi (Morley, 1998). Lelono (2000) noted various morphotypes from the middle and late Eocene Nanggulan Formation (Fig. 1A), supported by data from the late Eocene of west Java (Morley & 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, Morley & Restrepo-Pace, 2003; Morley *et al.*, 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* Salujha, Kindra & Rehman, *D. kalewensis*, *D. fragilis* Salujha, Kindra & Rehman, *D. cuddalorensis* Krutzsch and *D. psilatus* A.Kumar & K.Takah. to the types extending from the Eocene. Several studies (e.g. Kumar & Takahashi, 1991; Saxena & 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 might 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 Palaeogene of the Indian subcontinent than in contemporaneous Myanmar and other areas in South-East Asia. Two *Longapertites* spp. (*L. retipilatus* and *L. rugulatus*) occur in Myanmar, and one (*L. vaneendenburgi* Geermerad *et al.*) in the late Eocene of South-East 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 & Phadtare (1997) reported 12 different *Longapertites* pollen types from an Eocene assemblage in India, and Frederiksen (1994) identified seven *Longapertites* spp. in a Paleocene assemblage from

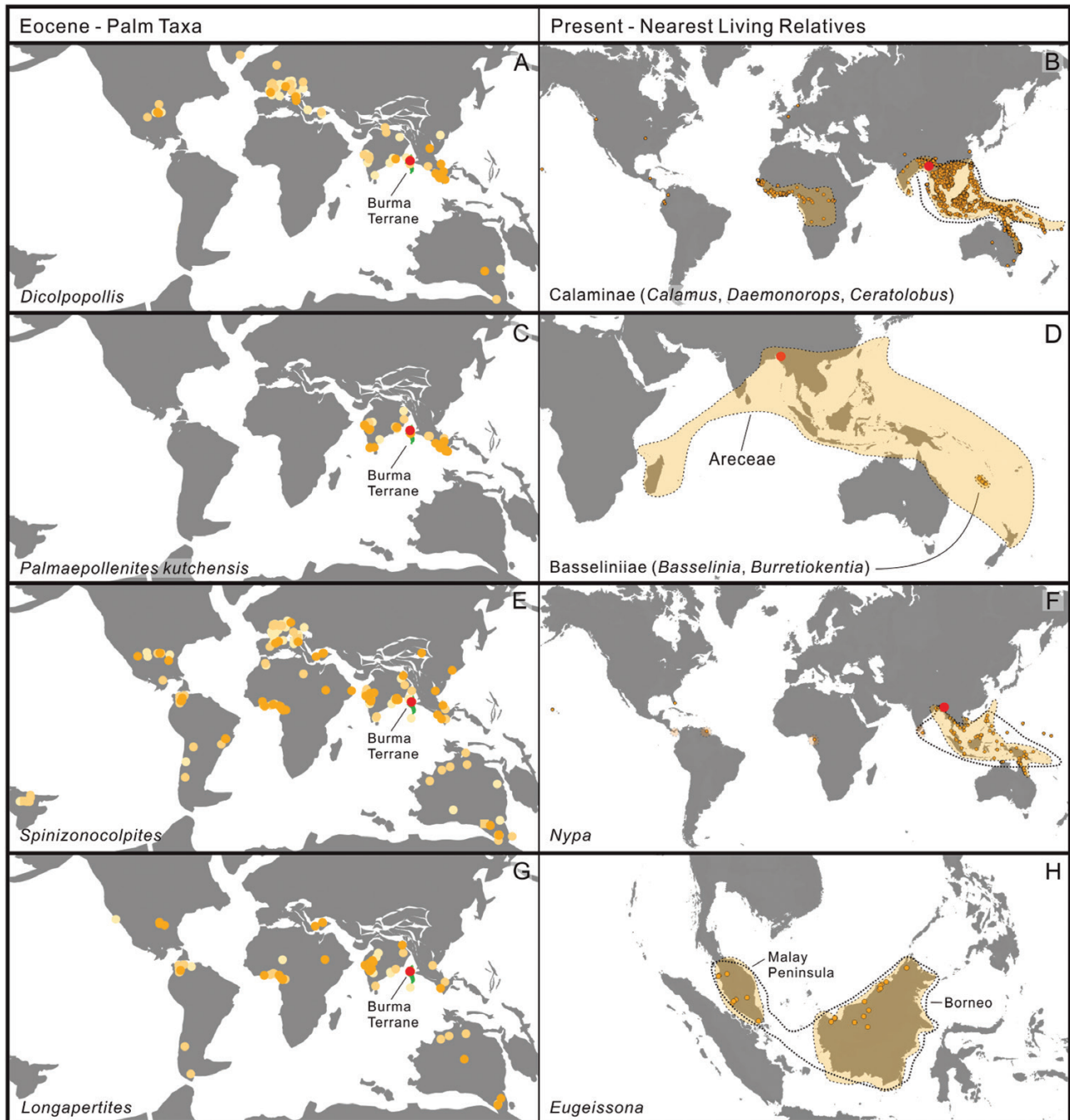


Figure 13. Global distribution maps of selected palm pollen records (Supporting Information, Table S2) in the Eocene and their NLRs. The red circle indicates the Kalewa site. In A, C, E and G, dark, intermediate and light colours indicate level 3, 2, 1 on the confidence of the records. Noting that there are three Eocene level-2 records (square) with the name of *Nypa* (E). Range between the dashed 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 and 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.

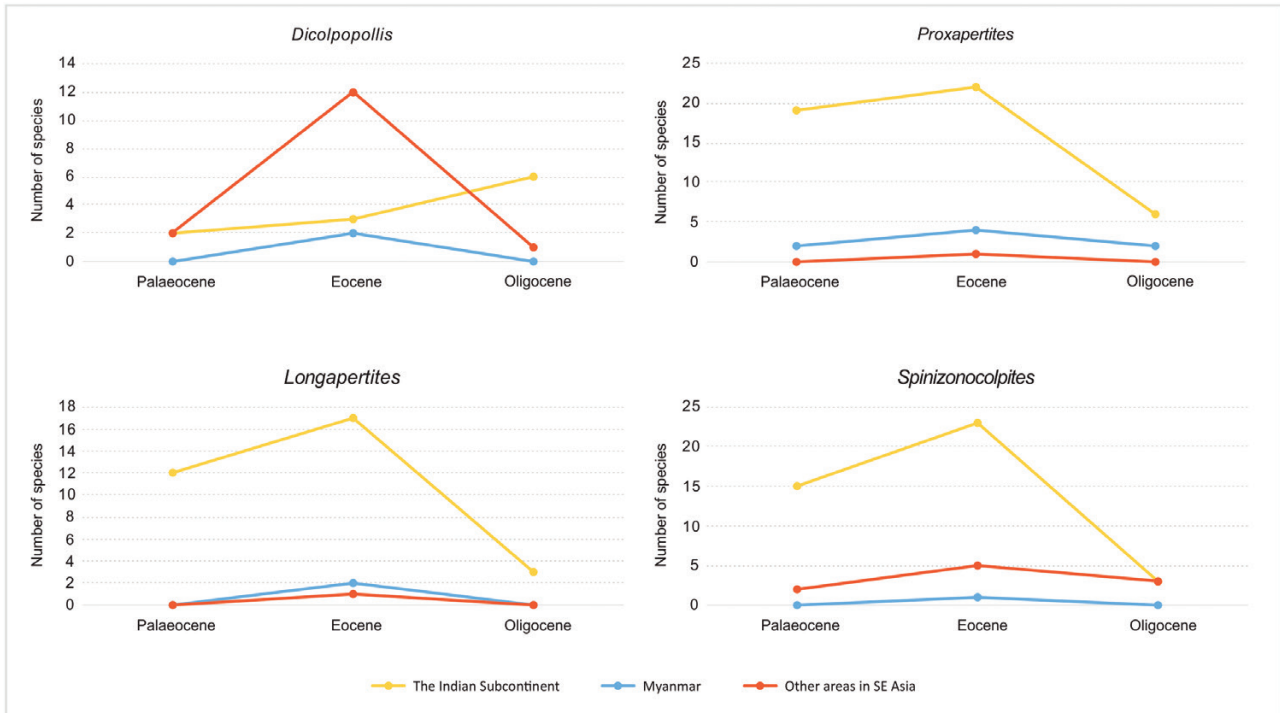


Figure 14. Species diversity of selected PPL pollen from the Palaeogene of the Indian subcontinent, Myanmar and other areas in South-East Asia.

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 and early Eocene of South-East 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. *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 & Phadtare, 1997; Table S4). However, only three *Proxapertites* spp. were recorded in Indonesia (e.g. Muller, 1968; Morley, 1998; Lelono, 2000, 2007), showing greatest diversity in the late Eocene. This suggests that *Proxapertites* was more diverse in the Indian subcontinent and other

areas of South-East Asia than in Myanmar during the Palaeogene.

PALAEOENVIRONMENTAL, PALAEOCLIMATIC 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 pteridophyte *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 *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 Mya (Fig. 1B, Licht *et al.*, 2013, 2014, 2018; 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.*, 2018). 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.*, 2018; 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.

SPATIOTEMPORAL CHANGES IN PALM POLLEN DIVERSITY DURING THE PALAEOGENE OF THE INDIAN SUBCONTINENT AND SOUTH-EAST ASIA

The Paleocene and Eocene represent a time of high palm (pollen) diversity across the region (Fig. 14). This is noticeable in *Longapertites*, *Spinizonocolpites* and *Proxapertites* from the Indian subcontinent, which were particularly diverse in the early Eocene, and in *Dicolpopollis*, which was diverse in the middle and late Eocene of South-East Asia. There is a decline in the diversity of *Longapertites*, *Spinizonocolpites* and *Proxapertites* across the whole region, and in *Dicolpopollis* of South-East Asia in the late Palaeogene. 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 South-East Asia, but declines during the Oligocene, which is probably due to the change from a perhumid to a more monsoonal climate following the EOT (Morley, 2018). 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 Indo–Asian 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 & Scotese, 1999), and their subsequent collision with Asia, would have resulted in an archipelagic area comparable with 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.*, 2014). The rainforest taxa may subsequently have dispersed to the Sunda region following the Indo–Asian collision (Morley, 2018).

Sunda was a diversity hotspot for *Dicolpopollis* during the Eocene, possibly, but not exclusively, due to the warm climate. Although there are some putative Paleocene *Dicolpopollis* records from India (e.g. Mathur & Jain, 1980), the ages of these deposits are still under debate. There are firm records of *Dicolpopollis* from the Eocene of India, whereas South-East Asia has Paleocene records (such as in Sarawak, Muller, 1968), indicating a dispersal from South-East Asia to India. This is consistent with the point stated in Morley (2018) and supported by molecular data that Indian Calamoideae are deeply nested in 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 might be due to problems of synonymy in the Paleocene, and insufficient localities in Eocene, or other reasons. These problems could also exist in other taxa, but they have been well resolved in the Sunda Shelf.

Since only few sites with Palaeogene fossil pollen have been discovered in Myanmar, it is not reasonable to take them as conclusive evidence for the palaeogeographic 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 South-East Asia (Fig. 14). As portrayed in Figure 1B, during the Eocene Kalewa was farther north than most of the Indian subcontinent and South-East Asia, while the latter two were closer to the equator. This might 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.

CONCLUSIONS

In this study we investigate fossil PPL pollen of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites*, *Palmaepollenites* and *Proxapertites* from the Eocene of Kalewa, CMB. We revise all *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* taxa using both light and SEM, 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 palaeo-shoreline and (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 Palaeogene of the Indian subcontinent and South-East 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, palaeoecology and

palaeoenvironment extends the general understanding on the species evolution of Arecaceae and its relation with palaeoclimate. Moreover, we anticipate that these data may prove useful for palaeobiogeographic modelling of the history of Arecaceae, particularly in India and South-East Asia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Flagged result of global GBIF data on basis of record 'Human observation' of *Calamus* using the R package 'CoordinateCleaner'.

Figure S2. Flagged result of global GBIF data on basis of record 'Preserved specimen' of *Calamus* using the R package 'CoordinateCleaner'. Some records in northern America and Europe are problematic likely because of misidentification, cultivation or planting.

Figure S3. Flagged result of global GBIF data on basis of record 'human observation' of *Nypa* using the R package 'CoordinateCleaner'.

Figure S4. Flagged result of global GBIF data on basis of record 'preserved specimen' of *Nypa* using the R package 'CoordinateCleaner'.

Table S1. Coordinates of global occurrences of Calaminae (including *Calamus*, *Daemonorops* and *Ceratolobus*), Basseliniae (including *Basselinia* and *Burretiokentia*), *Nypa* and *Eugeissona* accessed from GBIF.

Table S2. Global Eocene pollen records of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Palmaepollenites kutchensis*.

Table S3. Palaeogene pollen records of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* in the Indian subcontinent, Myanmar and other areas in South-East Asia.

Table S4. Species diversity of *Dicolpopollis*, *Longapertites*, *Spinizonocolpites* and *Proxapertites* in the Indian subcontinent, Myanmar and other areas in South-East Asia.

Table S5. Measurements on some palm pollen grains from the Eocene of Kalewa, CMB.

Table S6. Pollen raw counts on the sporomorphs from the Eocene of Kalewa, CMB that generated the pollen diagrams (Fig. 11).

Table S7. The results of analysis of variance (ANOVA) among three pollen zones, and a non-parametric correlation (Spearman) between *Proxapertites* vs. *Acrostichum* and *Proxapertites* vs. *Spinizonocolpites*.