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Journal Pre-proof

At a crossroads: the late Eocene flora of central Myanmar owes its composition to plate collision and tropical climate

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Highlights

- New palynological data from the late Eocene Central Myanmar Basin (CMB).
- Seasonal evergreen forests ruled under seasonal wet climate in the late Eocene CMB.
- Palynological data support a late Eocene north Burma Terrane (BT)-Asia collision.

- Plate collision and tropical climate created the late Eocene flora in the CMB.
- The BT was a crossroads for plant dispersals between Gondwana with Laurasia.

ABSTRACT

Myanmar was shaped by the India-Asia collision, fusion of the Burma Terrane (BT) with Asia, and mountain building. Throughout this process new elevational gradients and habitats were formed, which affected the regional climate, but also forged new dispersal routes into Asia and India. In spite of its importance, the vegetation history of Myanmar is poorly known, and this hinders our understanding on the origins and evolution of SE Asian biodiversity. In this study we reconstruct the late Eocene flora in central Myanmar, based on samples from a sedimentary succession in Kalewa, and extend on the Sapotaceae fossil record with additional early Eocene–early Oligocene samples. We then study the morphology, botanical affinity, source ecology and biogeography of selected sporomorphs, and assess the Gondwanan and Laurasian components. Our results show that the Eocene palynoflora is representative for evergreen forests, typical in a seasonal wet climate, with dryer vegetation away from the area of sedimentation. The abundance of Sapotaceae further suggests that this family became an important component of the SE Asian flora shortly after the India-Asia collision. We conclude that the late Eocene geographic position and Gondwanan origin of Myanmar facilitated floristic exchange between the Indian Plate, BT, mainland and SE Asia, making the BT a crossroads for plant dispersals between Gondwana and Laurasia. The shift from late Eocene seasonal evergreen to present-day moist deciduous forests was likely due to the northward drift of Myanmar, the subsequent two-stage uplift of the Indo-Burman Ranges and posterior Neogene global cooling and drying.

1. Introduction

The vegetation of mainland Southeast (SE) Asia is principally composed of seasonal evergreen, semi-evergreen and moist deciduous forests, while most of Peninsular Malaysia, Borneo and Sumatra are occupied by perhumid rain forests (Fig. 1; Ashton, 2014; Morley, 2018a). Located at the northwestern margin of SE Asia, Myanmar has a flora mainly comprising seasonal evergreen and deciduous taxa. Seasonal evergreen forests occur in the southwest (Rakhine State),

south (Tanintharyi Region), and north (Kachin State and Sagaing Region) (Fig. 1). Characteristic taxa in these forests are Dipterocarpaceae (e.g., genera *Dipterocarpus*, *Hopea* and *Shorea*), Arecaceae (palms, e.g., genera *Calamus*, *Livistoma* and *Salacca*) and Sapotaceae (e.g., genera *Palaquium*, *Pouteria* and *Sarcosperma*) (Kress et al., 2003). Swathes of montane vegetation can be found along the Indo-Burman Ranges (IBR) and Sino-Burman Ranges (SBR) (Fig. 2; Ashton, 2014; Morley, 2018a). Mangrove forests occur in the delta of the Irrawaddy River and the southwestern coastal region (Ashton, 2014) with genera such as *Sonneratia*, *Avicennia*, *Rhizophora*, *Nypa* and *Oncosperma* (Kress et al., 2003). In contrast, moist deciduous forests occur in central Myanmar, in a dry belt (termed in Stamp, 1925) that also includes rarer dry deciduous forests, scrub and savanna (Fig. 1). The IBR separates this dry belt from a narrow western belt of semi-evergreen forests; other semi-evergreen forests are found in the SBR.

To understand the genesis of the modern-day flora in SE Asia, and Myanmar in particular, we need to look back into the past. This region has a complex geology and its configuration likely played an important role in assembling the modern phytogeography. Palynological and palaeobotanical studies in Myanmar are relatively few, but do suggest a substantial contrast between the past and present flora. In the pre-Cenozoic age, Davies (2001) recorded common pollen of *Araucaria*, *Sequoia* and Taxodiaceae from the Albian–early Cenomanian deposits in the Hukawng Valley, northern Myanmar (Fig. 2). This valley has yielded many ambers containing exquisite mid-Cretaceous plant remains (e.g., angiosperm flowers with a present-day Gondwanan distribution; Poinar, 2018). In the Cenozoic, Potonié (1960) was the first to report an Eocene palynoflora from the Thitchaung coalmine near the Kalewa Township, and he compared it with the Cenozoic palynofloras in middle Europe. Also Reimann and Aye Thaung (1981) published a preliminary account of the Eocene and Miocene palynological assemblages from a large sample set in the Chindwin sub-basin, northwestern Myanmar. Subsequently Engelhardt and Wrenn (1994) reported some pollen taxa (e.g., *Lakiapollis ovatus* and *Dicolpopollis kalewensis*) and dinocysts from outcrop samples from the early to late Eocene upper Laungshe, Tilin and Tabyin formations in the Salin sub-basin (also called Minbu sub-basin), which indicate the palaeoenvironments ranging from fluvial/deltaic to inner neritic. More recently, Soe Moe Lwin et al. (2017) discussed the palaeoenvironments based on some sporomorphs from the Miocene Takam Hka Formation in the Hukawng sub-basin, and the early Miocene Letkat Formation in the Chindwin sub-basin. Finally, as part of an ongoing study, Huang et al. (2020) reported the palm

taxa and discussed the palaeoenvironment of the late Eocene Kalewa section. To place all these data in perspective, a comprehensive evaluation and review of the botanical affinities and source taxon ecology of the palynomorph types recovered, along with accurate age constraints for the studied sections, is needed to understand the vegetation history in central Myanmar.

In this study, we focus on the late Eocene record in the Central Myanmar Basin (CMB). The CMB has yielded extremely abundant fossils including mammals (e.g., Marivaux et al., 2005; Takai et al., 2016; de Bonis et al., 2018), plants (including woods, e.g., Prakash and Bande, 1980; Licht et al., 2014a, 2015; pollen, Potonié, 1960; Reimann and Aye Thaung, 1981; Soe Moe Lwin et al., 2017; Huang et al., 2020, see above; leaves and ambers, Licht et al., 2019). In recent years, exposures from the late Eocene Yaw Formation along the Kalewa section in the CMB have been accurately dated (Licht et al., 2019; Westerweel et al., 2020). Here we aim to describe the most important elements of the palynoflora using light- and scanning electron microscopy, assign modern botanical affinities to the sporomorphs, and discuss their source ecology and historical biogeography. We pay particular attention to the Sapotaceae, a family with previously poorly understood pollen types in the Eocene–Oligocene records of the CMB. Based on their botanical affinities, we then determine which vegetation types these sporomorphs reflect, and disentangle the driving factors of the formation of this late Eocene palynoflora. Furthermore, we investigate the composition of Gondwanan *versus* Laurasian and 'out-of-India' *versus* 'out-of-Asia' taxa, and explore possible plant dispersal routes between India, Myanmar, mainland and SE Asia. This assessment then allows us to discuss the origin and role of the Burma Terrane (BT; see section 2.1) from a floristic perspective as well as the timing of BT-Asia collision. Finally, we compare the vegetation of the late Eocene CMB with that of the late middle Eocene and present-day CMB.

Fig. 1. Here.

2. Material and methods

2.1. Geological context

The geological history of Myanmar, is mostly driven by the Burma Terrane (BT, also termed the West Burma Block). The BT is a major tectonic terrane situated at the eastern edge of the

India-Asia collision zone, which played an important role in the process of convergence (Westerweel et al., 2020). In the Eocene, this terrane had a near-equatorial position, with the northern extent colliding with the Asian margin in the late Eocene (Westerweel et al., 2019, 2020). The IBR, that formed part of the BT, was subject to a two-stage uplift in the late Eocene and Mio-Pliocene (Licht et al., 2019). Previous studies (e.g., Licht et al., 2019; Westerweel et al., 2020) suggest that the Wuntho-Popa Arc (WPA) was the dominant provenance of sediments in the late Eocene CMB within the BT (Fig. 2).

The CMB comprises two lateral troughs of Late Cretaceous–Cenozoic sub-basins, located both east in a backarc position (including the northern Shwebo and southern Pegu sub-basins) and west in a forearc position (including the northern Chindwin and southern Minbu sub-basins) of the WPA (Fig. 2; Bender, 1983; Pivnik et al., 1998; Licht et al., 2019). It was located on the margin of Eurasia and was open to the Indian Ocean during the late Eocene (37.8-33.9 Ma) (Licht et al., 2013). The inner wedge of the IBR emerged in the late middle Eocene (Licht et al., 2019).

The Kalewa section is located at southwestern Chindwin sub-basin and is exposed on the west of the Kalewa Township (Sagaing Region, northwestern Myanmar, 23°14′ N, 94°15′ E) (Fig. 2). The section includes the transition from the late middle Eocene Pondaung Formation to the late Eocene Yaw Formation, which is marked by the first occurrence of lignites and dark mudstones. The late Oligocene Tonhe Formation was deposited on top of the Yaw Formation and is characterised by coarse-grained sediments (Licht et al., 2019; Westerweel et al., 2020). The Yaw Formation is mainly composed of massive dark mudstones and siltstones to very fine sandstones, and rarely fine to coarse-grained sandstones, interpreted as reflecting deposition in wide barrier-bound estuaries (Licht et al., 2019), with evidence of marine intervals, freshwater gastropods and lignites with terrestrial vertebrates (Licht et al., 2013, 2014b). It is of late Eocene age (ca. 38-37 Ma), according to dates obtained from a tuff layer (Licht et al., 2019), palynostratigraphy (Huang et al., 2020) and magnetostratigraphy, U-Pb apatite dating, and apatite fission track dating (Westerweel et al., 2020).

In contrast to the exposures in the Chindwin sub-basin, the late Eocene Yaw Formation in the Minbu sub-basin (Fig. 2) is comparatively poorly exposed and solely consists of very uniform lithofacies, dominated by clay to siltstones, forming shallow-marine, fine-sized grain nummulite-yielding deposits (Nagappa, 1959; Adnet et al., 2008; Licht et al., 2013). It precedes the Shwezetaw, Padaung, and Okhmintaung formations which contain shallow-marine Oligocene

invertebrates and foraminifera (Bender, 1983; Gough and Hall, 2017). Descriptions of the early Eocene and early Oligocene sediments in the Minbu sub-basin are provided in Appendix S1.

Fig. 2. Here.

2.2. Palynological samples and processing methods

We collected 83 palynological samples along the 1127.5 m-thick Kalewa section from mudstones and sandstones of the late Eocene Yaw Formation in the Chindwin sub-basin (Table S1). In addition, 16 samples collected from the late Eocene Yaw Formation as well as early Eocene and early Oligocene sediments in the Minbu sub-basin were added into the study of Sapotaceae pollen (Table S2).

Two different processing methods were employed to ensure maximum recovery of palynomorphs. The first method was applied at the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam. It mainly consisted of the following steps: 1.3 grams of rock sample was selected, and 10% HCl was applied to dissolve any $CaCO_2$; the sample was boiled in 10% sodium pyrophosphate; acetolysis mixture and bromoform-treatment were then applied to clean the samples and separate any remaining inorganic fraction from the residue. The second method was applied at PLS Ltd., Holyhead, UK. 30 grams of rock sample was treated with 10% HCl and 40% HF, followed by a heavy liquid separation to separate the organic and remaining inorganic fractions. Subsequently, the organic fractions and filtrate were sieved. All resulting residues were mounted on a slide in glycerin and sealed with paraffin for the observation with light microscopy (LM). Residues were further used to investigate the sporomorph sculpture with scanning electron microscopy (SEM) at the Electron Microscopy Centre Amsterdam (EMCA), The Netherlands and the Department of Palaeontology (DoP), University of Vienna, Austria. For processing details see Huang et al. (2020). All the slides and pollen residues were deposited at the IBED.

2.3. Palynological analysis

We identified the palynomorphs following previous palynological studies across the tropics, focusing mainly on those in the Palaeogene (e.g., SE Asia, Muller, 1968; Morley 1998, 2013; India, Sah and Dutta, 1996; Saxena and Trivedi, 2009; the Americas, Jaramillo and Dilcher, 2001; Jardine, 2011). Identification of Sapotaceae, pollen types into its subfamilies, tribes and genera, was based on Harley (1986, 1991), Pennington (1991) and Hofmann (2018).

Single-grain analysis was used to investigate the detailed sculpture of sporomorphs (Zetter, 1989; Halbritter et al., 2018) at the DoP. The description of sporomorphs under the light microscopy (LM) and scanning electron microscopy (SEM) follows Punt et al. (2007) and Halbritter et al. (2018) respectively. Sporomorphs were measured by the software ImageJ (National Institute of Health, USA).

2.4. Microphotography

The palynomorphs were photographed using a FUJIFILM X-M1 digital camera connected to a Zeiss Axiophot Microscope under the 630× magnification (with oil) at the IBED. LM micrographs of Sapotaceae were taken by a Zeiss AX10 optical microscope equipped with an Axiocam 305 color camera under the 1000× magnification (with oil) at the IBED. SEM micrographs were taken by Zeiss Gemini FESEM 300 at the EMCA and JEOL JSM·6400 at the DoP. At the DoP, the LM micrographs were taken with a ProgRes Speed XTcore 5 camera connected with a Nikon Eclipse 80i LM. Palynomorph micrographs were stacked with Helicon Focus 6.0.18 software when palynomorphs were partly in-focus. The plates of sporomorphs were made with CorelDRAW 2019 (Corel Corporation, Ottawa, Canada).

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3. Results

3.1. Systematic palynology

At least 141 sporomorph types were determined in the Kalewa section. 56 sporomorph types are described and discussed in detail below, except most palms, which have been described by Huang et al. (2020). These sporomorph types are important in terms of biogeography, palaeoenvironment and palaeoecology. They are listed in order from pollen to spores, and simple

to complex apertures, and then alphabetically by taxon. The taxa that are referred to modern taxa only, are generally too rare to consider as a form-taxon. Synonyms, description, dimensions, botanical affinity, source ecology and stratigraphic distribution of these sporomorph types are outlined with extra etymology and diagnosis for new species. Information on the numbers of sample/residue/slide and England Finder coordinates of the figures in the plates are listed in Table S3. The arrangement of the figures mostly aligns with the order of descriptions.

Genus: ***Pinuspollenites*** Raatz 1937

Type species: *Pinuspollenites labdacus* (Potonié) Raatz 1937

Pinuspollenites sp.

Plate I, 6

Description: LM: monad pollen, bilateral symmetry, heteropolar; bisaccate, corpus and sacci spheroidal to subspheroidal; amb elliptic; sculpture of corpus psilate, sacci finely reticulate; sacci equal, smaller than the corpus.

Dimensions: equatorial diameter 38.3-47.9 μm (n.n = 2).

Botanical affinity: The presence of a marginal ridge adjacent to the saccus identifies *Pinus* pollen from other conifers. Raatz (1938) made a direct comparison of the type species with pollen of *Pinus sylvestris.*

Source ecology: coniferous trees with generally poorly understood ecology in lowland tropical Asia. Species either occur in the mountains of the Himalayan and Indochinese ranges, such as *P. roxburghii* and *P. wallichii*, or are widespread mainly in the lowlands of Indochina, the Philippines and parts of Sumatra, such as *P. kesiya* and *P. merkusii.* In Indochina, *Pinus* savanna was formerly widespread, occurring as far south as the Sunda Shelf when sea levels were lower during the last glacial maximum (Morley and Morley, 2021), but present populations are relict (Werner, 1997). Examination of pollen assemblages with abundant *Pinus* from the Cuu Long Basin, south of the Mekong Delta, suggested that most *Pinus* pollen originated from lowland habitats (Morley et al., 2019), where in seasonally dry vegetation across Indochina its common occurrence suggests well-drained habitats (Ashton, 2014). In the CMB most *Pinus* pollen is thought to be derived from lowland habitats.

Stratigraphic distribution: The oldest record of the northern Hemisphere genus *Pinus* is of fossil wood from the Lower Cretaceous (Valanginian) of Nova Scotia in Canada (Falcon-Lang et al., 2016), and it was subsequently widespread in the early Cenozoic of China, such as in the

early Eocene Hengyang Basin (Xie et al., 2020) and the late Eocene Xining Basin, China (Hoorn et al., 2012). In the SE Asian region, the oldest record is of *Pinuspollenites* cf. *spherisaccus* from the Paleocene of Borneo (Muller, 1968). *Pinus* pollen was very common in the late Eocene and Oligocene Cuu Long Basin offshore in South Vietnam (Morley et al., 2019), the Oligocene Na Duong Basin in northern Vietnam (Wysocka et al., 2020), the Oligocene Sunda Shelf (Morley et al., 2021) and the late Eocene Yaw Formation in Kalewa (CMB), but it has not been recorded from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000). For India, it has mainly been recorded in the Neogene, but there are a few records from the late Eocene, from Assam, such as from the Disang Group by Mandaokar (1999) and the Kopili Formation (Trivedi and Saxena, 2000).

Remarks: We placed this type into *Pinus* based on its appropriate size, characteristic reticula of sacci and presence of a marginal ridge.

Genus: ***Echimonoporopollis*** Saxena et al. 1991

Type species: *Echimonoporopollis grandiporus* Saxena et al. 1991

Echimonoporopollis grandiporus Saxena et al. 1991

Plate I, 1

Description: LM: monad pollen, radial, anisopolar, spheroidal; monoporate, pore indiscernible; exine up to 0.6 μm thick, without discernible layers, usually folded; sculpture psilate with fine echini, echini conical, evenly distributed, 1.5-5.7 μm long, up to 3.4 μm in basal diameter, with a variety of shapes from almost baculate to pyramid-like, to having a bulbous base with a thin projection

Dimensions: greatest dimension 23.2-39.8 μm (excluding spines, number of measured specimens (nm) = 2).

Botanical affinity: unknown.

Source ecology: unknown.

Stratigraphic distribution: It only has records in India and Myanmar, including the Paleocene Neyveli Formation and late Paleocene–middle Eocene subsurface sediments in Tamil Nadu, India (Saxena and Khare, 2004) and the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: *Echimonoporopollis* has three species described from India, including *E. grandiporus* and *E. neyveliensis* from the Paleocene (Saxena and Kare, 2004), and *E. circularis*, from the early Eocene (Samant and Tapaswi, 2001). *E. grandiporus* differs from *E. neyveliensis*

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in having shorter echini, and with bulbous bases, and from *E. circularis* with more and longer echini. The parent plant of *E. grandiporus* is likely to have been an 'out-of-India' taxon.

Genus: ***Pandaniidites*** Elsik 1968

Type species: *Pandaniidites textis* Elsik 1968

Pandaniidites sp.

Plate I, 2

Description: LM: monad pollen, radial, anisopolar, spheroidal to subspheroidal; amb circular, ovate in equatorial view; monoporate, pore circular, up to 3.0 μm in diameter or indiscernible; exine thin, less than 1.0 μm thick, without discernible layers, usually folded; columellae distinct; sculpture (tectum) psilate to scabrate with fine echini; supratectal echini conical, up to 1.7 μm long, less than 1.0 μm in basal diameter, with acute tips.

Dimensions: greatest dimension 18.3-20.8 μm (excluding spines, nm = 3).

Botanical affinity: In the Palaeotropics, this pollen type is from *Pandanus* (Pandanaceae), whereas in North America, identical pollen is seen in *Limnobiopyllum scutatum* or another member of Lemnoideae in Araceae (Stockey et al., 1997), which misled Muller (1981) when reviewing the time of appearance of pollen of the genus *Pandanus*.

Source ecology: *Pandanus* are trees and shrubs, commonly from swamp or coastal environments throughout the Palaeotropics and tropical Pacific, particularly common in some peat swamps, and also other vegetation (Morley, 1991; Morley and Morley, 2013).

Stratigraphic distribution: The oldest records likely derived from *Pandanus* are from the middle Eocene Nanggulan Formation in central Java, Indonesia (Lelono, 2000), and late Eocene Yaw Formation in Kalewa (CMB).

Remarks: This pollen type has a longer range in Myanmar and SE Asia than in India, being recorded from the early Oligocene sediments in Assam (Kumar and Takahashi, 1991). The pollen type is different from the echinate *Malvacidites* in having a single pore.

Genus: ***Restioniidites*** Elsik 1968

Type species: *Restioniidites hungaricus* (Kedves) Elsik 1968

Restioniidites ?*punctulosus* Takahashi 1982

Plate I, 5

Description: LM: monad pollen, radial, anisopolar, spheroidal to subspheroidal; monoporate, pore distinct, 2.1-3.5 μm in diameter surrounded by large annulus of 1.3-2.0 μm in width; exine 0.8 μm thick; sculpture psilate to punctate.

Dimensions: greatest dimension 17.8-28.1 μm (nm = 4).

Botanical affinity: Restionaceae.

Source ecology: oligotrophic seasonal swamps in areas of dry climate (Morley, 2000).

Stratigraphic distribution: Muller (1981) noted that the earliest record of Restionaceae pollen is from West Africa, recorded as *Graminidites* sp. from the Late Cretaceous of Senegal by Jardiné and Magloire (1965), and was subsequently widely recorded from the Paleocene of Europe and North America. In its present area of distribution in the southern hemisphere, it appears later, with the oldest record from the early Eocene in Australia (Martin, 1994). In SE Asia, the oldest record is of *R. punctulosus* from middle Eocene Ngimbang Formation in subsurface offshore South Sulawesi, where it displays an abundance maximum which is useful for stratigraphic correlation (Morley, 2014; van Gorsel et al., 2014). It was subsequently recorded from the middle Eocene Nanggulan Formation in central Java (Takahashi, 1982; Lelono, 2000). It also occurred in the late Eocene Yaw Formation in Kalewa (GMB).

Genus: ***Racemonocolpites*** González-Guzmán 1967

Type species: *Racemonocolpites bhavnagarensis* (van der Hammen) González-Guzmán 1967

Racemonocolpites hians Legoux 1978

Plate I, 3-4

Synonym: *Clavapalmaedites hammenii* Rao et Ramanujam 1979

Description: LM: monad pollen, radial, anisopolar; in equatorial view oblate; monosulcate, sulcus narrow, as long as the longest axis of the grain; sculpture baculate to clavate, baculae and clavae evenly distribute on the tectum; exine 0.7 μm thick, sexine and nexine indiscernible.

Dimensions: equatorial diameter 22.8-27.1 μm (nm = 3).

Botanical affinity: This taxon resembles pollen of *Oncosperma*, as suggested by Morley (2000). It is widely reported from the Neogene sediments in SE Asia, being illustrated from a Miocene coal in Brunei by Anderson and Muller (1975). With its oldest occurrence in India, *Oncosperma* is thus an ‘out-of-India’ taxon.

Source ecology: mainly trees growing in the back-mangrove belt, namely the brackish settings, such as *Oncosperma tigillarium*. Some pollen may have come from inland settings, in the manner of *O. horridum* which occurs on low undulating hillsides across SE Asia.

Stratigraphic distribution: The oldest records are probably from the early Eocene Cambay Shale Formation in India (Samant, 2000; Samant and Tapaswi, 2001), as *Clavapalmaedites hammeni*, and subsequently from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), the late Eocene Yaw Formation in Kalewa (CMB), Oligocene sediments in Sumatra (Morley, 2013) and middle Eocene–Miocene sediments in Cameroon and Nigeria (Legoux, 1978).

Plate I. Here.

Genus: ***Shorea*** Roxb. ex C.F.Gaertn. 1805

Type species: *Shorea robusta* Gaertn. 1805

cf. *Shorea* type

Plate I, 7

Description: LM: monad pollen, radial, isopolar; amb circular with three lobes; tricolpate with gaping colpi, colpi nearly connecting at the poles, up to 10.6 μm in width; exine 1.2 μm thick with distinct columellae; sculpture psilate or possibly finely reticulate.

Dimensions: equatorial diameter 20.0 μm (nm = 1).

Botanical affinity: *Shorea* (Dipterocarpaceae).

Source ecology: *Shorea* is the most widespread and dominant genus of trees in the lowland forests of SE Asia (Ashton, 2014). The genus includes evergreen trees of perhumid *terra firma* and swamp forests and is also well represented in seasonal forests. It is also a major element of deciduous forests across Indochina, with *S. obtusa*, and in India, with *S. robusta* in the north, and *S. tumbuggaia* in the Western Ghats.

Stratigraphic distribution: *Shorea* fossils have been reported from China, SE Asia, India and Nepal, including wood, leaves, fruits and pollen. The earliest *Shorea* fossil is of wood from the late middle Eocene Pondaung Formation of Myanmar (Licht et al., 2014a). Subsequent records are of fruit and leaves from the late Eocene Maoming Basin in southern China (Feng et al., 2013), and fruit from the middle Miocene Fotan Group in southern China (Shi et al., 2014). There are

many wood and leaf fossils from the Neogene sediments in SE Asia and India, reviewed in Khan et al. (2016). Fossil pollen has been reported from the Oligocene onward in Borneo (Muller, 1981) and the Sunda Shelf (Morley, 2000) and the Cuu Long Basin, offshore southern Vietnam (Morley et al., 2019). *Shorea* pollen has recently been found from the early Eocene of India (Bansal et al., unpubl. data), and from the late Eocene Yaw Formation in the CMB. The pollen record of *Intrareticulites brevis* was considered to be derived from *Shorea* (Prasad et al., 2009) from the late Paleocene–early Eocene of India but cannot be confirmed without a pollen micrograph.

Genus: ***Discoidites*** Muller 1968

Type species: *Discoidites borneensis* Muller 1968

Discoidites angulosus Huang, Morley et Hoorn sp. nov.

Plate I, 8

Etymology: The specific epithet alludes to its angular apices.

Holotype: PLS-17C272 (Plate I, 8).

Paratype: PLS-17C301.

Repository: Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam. The Netherlands.

Type locality: Kalewa Township, Sagaing Region, Myanmar.

Diagnosis: monad, triangular with convex sides and angular apices, tricolpate, angulaperturate, exine thicker at colpate areas, microreticulate.

Description: LM: monad pollen, radial, isopolar, oblate; amb triangular with convex sides; tricolpate, angulaperturate, colpi short and gradually wider to the apices, reaching ca. 2/3 to the pole, 2.2-4.6 μm in length, exine thin, less than 1.0 μm thick, thicker at colpate areas; sculpture finely microreticulate, and psilate in the polar area; columellae indiscernible.

Dimensions: equatorial diameter 22.1-28.1 μm (nm = 3).

Botanical affinity: probably *Brownlowia*.

Source ecology: based on the ecology of *Brownlowia*, possibly trees from riversides in floodplains but may rarely occur in the freshwater intertidal back-mangrove belt.

Stratigraphic distribution: the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: This species is different from other species in having angular apices. The taxonomy and botanical affinity of this genus has been discussed by Morley et al. (2000).

Discoidites cf. *borneensis* Muller 1968

Plate I, 9

Description: LM: monad pollen, radial, isopolar, prolate; tricolpate, angulaperturate, colpi narrow, reaching ca. halfway to the pole, 4.4-7.0 μm in length; exine thin, less than 1.0 μm thick; columellae indiscernible; sculpture psilate to finely reticulate.

Dimensions: equatorial diameter 26.3-27.0 μm (nm = 2).

Botanical affinity: *Brownlowia* or *Pentace* (Malvaceae) (Muller, 1968), and possibly the related rain forest genera *Diplodiscus* and *Berrya* (Morley et al., 2000).

Source ecology: possibly trees from the freshwater intertidal back-mangrove belt or lowland riverbanks in evergreen tropical forests.

Stratigraphic distribution: The oldest specimens of *D. borneensis* are from the Paleocene Kayan Formation in Sarawak, Malaysia (Muller, 1968; Morley, 1998), also from the late Eocene Yaw Formation in Kalewa (CMB). It has been widely reported from the middle Eocene onward in the SE Asian region, but dispersed to India in the Miocene (Morley, 2018a), where it was reported in the Ratnagiri area (Phadtare and Kulkarni, 1984) and Assam (Mandal and Kumar, 2000).

Remarks: The pollen differs from *D. novoguineensis* (Khan, 1976) which is duplibaculate, as in extant *Brownlowia.*

Discoidites cf. *pilosus* (Venkatachala et Rawat 1973) Morley et al. 2000

Plate I, 10; Plate III, 4-6

Synonym: *Lacrimapollis pilosus* Venkatachala et Rawat 1973.

Description: LM: monad pollen, radial, isopolar, oblate; amb near circular; tricolpate, angulaperturate, colpi fairly short and narrow, reaching less than halfway to the pole, 2.0-4.3 μm in length; exine thin, 0.8-1.0 μm thick, thicker at the aperturate areas resulting in the characteristic thickened costae; sculpture psilate; columellae indistinct. SEM: sculpture rugulate.

Dimensions: equatorial diameter 21.1-29.3 μm (nm = 5).

Botanical affinity: Brownlowoideae, the broad morphotype occurs in *Brownlowia*, *Pentace*, *Diplodiscus* and *Berrya* (Morley et al., 2000) but the thickened costae seen in this morphotype cannot be attributed to any extant taxon.

Source ecology: possibly trees from lowland river banks or possibly freshwater intertidal settings.

Stratigraphic distribution: The earliest record is from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000). Subsequent records include the late Eocene Yaw Formation in Kalewa (CMB), and the Oligocene–Miocene Cauvery Basin in Tamil Nadu, India (Venkatachala and Rawat, 1973). It is common in the early and middle Miocene in Indonesia (Morley et al., 2000).

Discoidites sp.

Plate I, 11

Description: LM: monad pollen, radial, isopolar, circular; amb tricolpate, colpi slightly wide, 0.6-1.8 μm, reaching halfway to the pole, 3.1-4.1 μm in length; exine 0.8 μm thick; columellae distinct; sculpture microreticulate.

Dimensions: equatorial diameter 22.0-23.7 μm (nm = 2).

Botanical affinity: probably Brownlowoideae.

Source ecology: possibly trees from lowland river banks or freshwater intertidal settings.

Stratigraphic distribution: the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: This species is similar to *Discoidites* cf. *pilosus*, but differs from the latter in having wider colpi.

Genus: ***Perfotricolpites*** González-Guzmán 1967

Type species: *Perfotricolpites digitatus* González-Guzmán 1967

Perfotricolpites cf. *digitatus* González-Guzmán 1967

Plate I, 13-15

Description: LM: monad pollen, radial, isopolar, circular; tricolpate, colpi long with pointed ends and straight borders; exine 0.9-2.6 μm thick, sexine thicker (up to 1.4 μm) than nexine (up to 0.6 μm); tectum thin, sculpture striate; columellae digitate. SEM: exine microperforate and granulate (unpublished data from the Miocene Letkat Formation).

Dimensions: equatorial diameter 32.2-57.4 μm, polar axis 47.3 μm (nm = 5, one in equatorial view and four in polar view).

Botanical affinity: Germeraad et al. (1968) compared it with two species of *Merremia* in the family Convolvulaceae. Pocknall (1982) pointed out that the *P. digitatus* pollen type also occurs in some species of *Convolvulus*.

Source ecology: climbing and sprawling herbs of floating vegetation mats on rivers and swamps (Morley and Morley, 2013).

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Stratigraphic distribution: The oldest records are from the early to middle Eocene of Colombia (González-Guzmán, 1967), and the middle Eocene of Brazil (Regali et al., 1974), followed by the middle Eocene of Nigeria (Legoux, 1978) and the late Eocene of Cameroon (Salard-Cheboldaeff, 1979). In SE Asia, the oldest record is from the late Eocene Yaw Formation in Kalewa (CMB). It occurs widely in SE Asia, especially in the Oligocene and Miocene in intervals with abundant fern spores such as *Ceratopteris* (Morley and Morley, 2013), but in India it is recorded only from the Neogene (Chandra and Kumar, 1997), although other species of *Perfotricolpites* are recorded back to the early Eocene, such as *P. rajpardiensis* (Samant and Phadtare, 1997). It is also recorded from the late Oligocene Pomahaka estuarine bed sediments in New Zealand (Pocknall, 1982).

Remarks: The Miocene Letkat specimens of *P. digitatus* have perforate exine with supratectal granuli under SEM (unpublished data from the Miocene Letkat Formation), which is similar to the New Zealand specimens (Pocknall, 1982).

Plate II. Here.

Genus: ***Casuarinidites*** Cookson et Pike 1954

Type species: *Casuarinidites cainozoicus* Cookson et Pike 1954

Casuarinidites cainozoicus Cookson et Pike 1954

Plate I, 19-20

Description: LM: monad pollen, radial, isopolar, oblate; amb triangular to subcircular, sides slightly convex; triporate, angulaperturate, pores circular or slightly elliptical, usually aspidate, 1.5-2.9 μm in diameter; exine 0.5-0.7 μm thick, up to 1.4-2.1 μm thick in poral areas; sculpture psilate. The morphology of *Casuarina* has been discussed by Kershaw (1970).

Dimensions: greatest dimension 20.1-27.6 μm (nm = 2).

Botanical affinity: It may be derived either from *Casuarina* (Cookson and Pike, 1954) or *Gymnostoma* (Morley, 2013).

Source ecology: In SE Asia, *Casuarina* trees occur commonly along sandy beaches in the strand flora (van Steenis and Shippers-Lammertse, 1965), whereas *Gymnostoma* are trees of kerangas and inland kerapah peat swamps in Borneo (Brunig, 1974; Morley, 2013).

Stratigraphic distribution: Records are from the early Paleocene of New Zealand, the middle Paleocene of Australia, the early Eocene of Irian (Morley, 2000), the late Eocene Yaw Formation in Kalewa (CMB), and the Oligocene of East Java Sea (Lelono and Morley, 2011). It is a common element in the Neogene of SE Asia and the younger Cenozoic of China (Song et al., 2004). It is also reported from the Paleocene of Argentina (Muller, 1981), where it is also represented by macrofossils (Zamaloa et al., 2006), and the late Miocene of South Africa (Coetzee, 1978) where it is now extinct. Remarkably, it has not been reported from India.

Remarks: This genus originated in southern Gondwana. *Casuarinidites* differs from *Casurinaepollenites* Sun, which was described from the Paleocene Lingfeng Formation in East China Sea, by being aspidate and having psilate or intragranulate ornamentation, rather than granulate or microstriate ornamentation (Song et al., 2004).

Genus: ***Corsinipollenites*** Nakoman 1965

Type species: *Corsinipollenites oculus noctis* (Thiergart) Nakoman 1965

Synonyms: *Trivestibulopollenites* sp. Chmura 1973; *Jussitriporites* sp. Pares Regali 1974

Corsinipollenites sp.

Plate I, 21

Description: LM: monad pollen, radial, isopolar; amb nearly circular; triporate, angulaperturate with distinct oculi, up to 3.0 µm in diameter, 1.8-3.0 µm thick, pores voluminous, sharply delimited from the central body; exine up to 2.0 µm thick sexine and nexine indiscernible; columellae indiscernible; sculpture psilate; viscin threads visible on the proximal face, originating from the polar regions of the grain.

Dimensions: equatorial diameter 21.3-33.0 µm (nm = 3).

Botanical affinity: Pollen referable to *Corsinipollenites* is seen in many genera of the Onagraceae, especially *Jussiaea*, which is a common herb or shrub of tropical marshes.

Source ecology: typically herbs in open marshes and swamps.

Stratigraphic distribution: The oldest records of *Corsinipollenites* are from the Maastrichtian of California (Chmura, 1973) and Brazil (Regali et al., 1974). It has subsequently been reported from the Paleocene of the Caribbean and South American regions (e.g., the Paleocene Los Cuervos Formation, Colombia (Jaramillo and Dilcher, 2001), the Paleocene Cuayuca Formation of southern Mexico (Ramírez-Arriage et al., 2006)), and the late Eocene Yaw Formation in Kalewa (CMB). Surprisingly, it has not been reported from India prior to the Oligocene,

occurring in the Barail Group in Upper Assam (Mandal and Kumar, 2000) or from Australia, where it has been reported by Hekel (1972) from the Oligocene and early Miocene of Queensland. Therefore, Onagraceae dispersed into India in the Oligocene.

Genus: ***Proteacidites*** Cookson 1950 ex Couper 1953 emend. Dettmann et Jarzen 1996

Type species: *Proteacidites adenanthoides* Cookson 1950

Proteacidites sp.

Plate I, 23

Description: LM: monad pollen, radial, isopolar, oblate; amb triangular, with sides slightly concave; triporate, angulaperturate, pores circular, 2.2-3.1 μm in diameter; exine thin, 0.6 μm thick, thinner toward the pore margins; sculpture psilate to punctate; columellae indiscernible.

Dimensions: equatorial diameter 23.9 μm (nm = 1).

Botanical affinity: Proteaceae (Cookson, 1950).

Source ecology: trees of various forests.

Stratigraphic distribution: The pollen record suggests the origin of Proteaceae was in northern Gondwana in the late Cenomanian, from where it radiated into southern high latitudes during the Turonian (Dettmann and Jarzen, 1998). Proteaceae pollen was abundant in Late Cretaceous and Palaeogene sediements in Australia (e.g., Dettmann and Jarzen, 1998; Carpenter et al., 2015). In New Zealand proteaceous pollen appeared in the Late Cretaceous and became most diverse in the Eocene (Pole, 1998). In the southern South America-Antarctic Peninsula region, the oldest record of Proteaceae is in the middle-late Santonian of the Antarctic Peninsula. The diversity of Proteaceae pollen increased during the Campanian–Maastrichtian (Askin and Baldon, 1998). *Proteacidites* spp. have been widely reported from the Palaeogene of Nigeria and the Caribbean by Germeraad et al. (1968), and India (e.g., Kar and Bhattacharya, 1992). In SE Asia, the oldest records are from the middle Eocene Nanggulan Formation in central Java (Takahashi, 1982; Lelono, 2000), and the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Triatriopollenites*** Thomson et Pflug 1953

Type species: *Triatriopollenites rurensis* Thomson et Pflug 1953

Triatriopollenites engelhardtioides (Roche 1973) Roche et Schuler 1976

Plate I, 24

Synonyms: *Momipites quietus* group Krutzsch 1966; *Momipites*, *Coryloides*-group of Nichols 1973.

Description: LM: monad pollen, radial, isopolar; in equatorial view triangular-convex; triporate, angulaperturate, pores equatorial in position, round and aspidate, diameter 2.1 μm; exine 1.0 μm thick, psilate, with distinct folds, especially when seen in polar view, thickening around the pores; columellae indiscernible.

Dimensions: equatorial diameter 38.2 μm (nm = 1).

Botanical affinity: The triporate configuration, characteristic apertures, psilate exine and presence of exinal folds when seen in polar view strongly suggest derivation from Engelhardioideae (Juglandaceae) including *Engelhardia*, and the Neotropical *Alfaroa* and *Oreomunnea*. Manchester (1989) indicates that the distinctive pollen of Engelhardioideae appeared just before the appearance of macrofossils, which are first found in the Eocene. Song et al. (2020) date the stem age for Engelhardioideae at 57 Ma, within the late Paleocene.

Source ecology: trees typical of lower montane forest but may occur in lowland forests in Malaysia (Ng, 1972).

Stratigraphic distribution: The oldest records are probably from the Maastrichtian of the Gulf of Mexico and Western Interior of the United States (Muller, 1981). It is subsequently common from the Paleocene onward in North America (Manchester, 1989). There are possible records from the Palaeogene of Argentina (Barreda et al., 2020). *Triatriopollenites engelhardtioides* is widely reported from the Paleocene–Oligocene of Europe (e.g., Gruas-Cavagnetto, 1978; Kedves, 1992) and similar pollen is recorded from the Paleocene onward from China (Song et al., 2004). In SE Asia, it is identified as *Engelhardia* type pollen (Morley, 2018a; Morley et al., 2021). The oldest SE Asian record is from the late Eocene Yaw Formation in Kalewa (CMB). *Engelhardtioidites* spp. have been recorded in India from the Paleocene onward (e.g., the Paleocene–Eocene sediments in the Ganga Basin; Mandaokar, 2003).

Remarks: Engelhardioideae is an amphi-Pacific taxon (van Steenis, 1962, 1963; Morley, 2000). *Triatriopollenites engelhardtioidites* is different from *Momipites* Wodehouse which lacks protruding pores and an annulus (Srivastava, 1972). Peltate trichomes have been found in leaf fragments of Juglandaceae (e.g., Dilcher and Manchester, 1986). The appearance of a peltate trichome (Plate II, 51) could be from the same taxon as *Triatriopollenites engelhardtioides* or *Multiporopollenites maculosus*.

Genus: ***Avicennia*** L. 1753

Type species: *Avicennia officinalis* L. 1753

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Avicennia type

Plate I, 25

Description: LM: monad pollen, radial, isopolar, prolate; tricolporate, colpi long, distinct, 16.9 μm in length, margins straight; exine 0.5 μm thick, layers indiscernible; sculpture reticulate, muri thick, irregular, rounded or polygonal, up to 0.9 μm in diameter, generally largest in polar areas, smaller along colpi and on the mesocolpia.

Dimensions: equatorial diameter 18.2 μm, polar axis 22.7 μm (nm = 1).

Botanical affinity: *Avicennia* (Acanthaceae).

Source ecology: mangrove trees, most characteristic in areas exhibiting regular inundation, mainly growing along rivers on muddy substrate.

Stratigraphic distribution: The oldest records are from the early Eocene of eastern Alps in Krappfeld, Austria (Hofmann et al., 2012), and the middle Eocene of Helmstedt in northern Germany (Riegel et al., 2015). In SE Asia, the oldest records from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000) and the late Eocene Yaw Formation in Kalewa (CMB). Across the Sunda Shelf, where there were many non-marine basins during the mid-Cenozoic, *Avicennia* pollen does not appear until the early Miocene (e.g., Watanasak, 1988; Morley, 2000). Its earliest occurrence in South America and Africa is in the late Miocene (Morley, 2000).

Genus: ***Berlinia*** Sol. ex Hook.f. 1849

Type species: *Berlinia acuminata* Sol. ex Hook.f. et Benth. 1849

Berlinia type

Plate I, 26

Description: LM: monad pollen, radial, isopolar; in equatorial view prolate; tricolporate, colpi long extending to the poles, pores round and up to 1.2 μm in diameter; exine and its layers indiscernible; columellae indiscernible; sculpture striate.

Dimensions: equatorial diameter 24.9-25.9 μm, polar axis 33.7-39.5 μm (nm = 3).

Botanical affinity: *Berlinia* and *Isoberlinia* (Leguminosae: Caesalpinioideae).

Source ecology: trees of lowland forest, including swamp and gallery forest formations (Mackinder and Pennington, 2011) , as well as deciduous forests.

Stratigraphic distribution: the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: *Berlinia* and *Isoberlinia* are trees restricted to tropical Africa within the subfamily Caesalpinioideae (Mackinder and Pennington, 2011). This pollen type could be *Striatopollis catatumbus*.

cf. *Berlinia* type (Plate I, 27-28)

Description: LM: monad pollen, radial, isopolar; amb circular; tricolporate, pores big and round, 3.0-4.0 μm in diameter; exine 1.5 μm thick, nexine (0.9 μm thick) thinner than sexine (0.6 μm thick); columellae distinct and robust; sculpture striate.

Dimensions: equatorial diameter 26.6-36.9 μm (nm = 2).

Botanical affinity: *Berlinia* and *Isoberlinia* (Leguminosae: Caesalpinioideae).

Remarks: This pollen type could also be *Striatopollis catatumbus*

Source ecology: the same as that of *Berlinia* type. See above.

Stratigraphic distribution: the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Campnosperma*** Thwaites 1854

Type species: *Campnosperma zeylanicum* Thwaites 1854

Campnosperma type

Plate I, 29-30

Description: LM: monad pollen, radial, isopolar, prolate; in equatorial view tricolporate, colpi 1.0 μm thick, extending to poles, pores small, less than 1.0 μm in width; exine less than 1.0 μm thick; exine striate.

Dimensions: equatorial diameter 12.5-14.5 μm, polar axis 17.0-19.3 μm (nm = 5).

Botanical affinity: *Campnosperma* (Anarcadiaceae).

Source ecology: pantropical tree genus occurring up to 1600 m, often forming pure stands in swamp forests, becoming dominant in the initial stage of peat swamp formation in Borneo (Anderson, 1964), also common in valleys near streams (Kochummen, 1989).

Stratigraphic distribution: The oldest record is from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000). It has also been recorded from late Eocene coals in the Mangkalihat Peninsula, Kalimantan, Indonesia (Morley, 2000), the late Eocene Yaw Formation in Kalewa (CMB), the Oligocene of the East Java Sea (Lelono, 2007), and throughout the Neogene of the Sunda region (Muller, 1970, 1972, 1981; Anderson and Muller, 1975).

Remarks: It is smaller and more heavily striate than *Rhus* type pollen (Muller, 1981).

Genus: ***Cupanieidites*** Cookson et Pike 1954

Type species: *Cupanieidites major* Cookson et Pike 1954

Cupanieidites flaccidiformis Venkatachala et Rawat 1972

Plate I, 31-32

Description: LM: monad pollen, radial, isopolar; amb triangular to near circular; tricolporate, syncolporate, angulaperturate, colpi long and narrow, reaching to the poles, pores aspidate, lalongate and small; exine in mesocolpi bulged, forming equatorial flange, thin, 0.4 μm and thick at colpate margin, tectate, arcus present; sculpture distinctly to faintly reticulate, lumina 1.0-2.0 μm thick, or microreticulate.

Dimensions: equatorial diameter 32.0-35.3 μm (nm = 5).

Botanical affinity: *Mischocarpus* (Sapindaceae) (Morley, 1998, 2000).

Source ecology: *Mischocarpus* occurs in lowland rain forests from India to Australia. *Mischocarpus sundaicus* is widespread on sandy coasts, estuaries and coastal swamps across the region (Yap, 1989).

Stratigraphic distribution: The oldest record is from the Paleocene Lower Indus coal region in Pakistan (Frederiksen, 1994). It is also recorded from the Paleocene–Eocene Cauvery Basin in Tamil Nadu (Venkatachala and Rawat, 1972), the middle Eocene Mallawa Formation in south Sulawesi, Indonesia (Morley, 1998), the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene *Yaw* Formation in Kalewa (CMB). This is thus an 'out-of-India' taxon (Morley, 2000, 2018a).

Cupanieidites sp.

Plate I, 33-34

Description: LM: monad pollen, radial, isopolar; amb triangular-convex to near circular; 3-syncolporate, angulaperturate, colpi long till the poles and narrow; exine up to 0.6 μm thick; sculpture microreticulate, heterobrochate, muri thin, lumina diameter up to 0.4 μm.

Dimensions: equatorial diameter 21.1-28.1 μm (nm = 2).

Botanical affinity: Cupanieae (Sapindaceae).

Source ecology: trees in rain forests (Yap, 1989).

Stratigraphic distribution: *Cupanieidites* has been recorded from the Coniacian onward (Muller, 1981). The oldest record is *C. reticularis* from Gabon (Belsky et al., 1965). It is subsequently recorded from the Senonian of India (Venkatachala and Sharma, 1974), the Maastrichtian of Brazil (Herngreen, 1975), USA (Leffingwell, 1971; Chmura, 1973) and the

Eocene of Australia (Stover and Evans, 1973; Stover and Partridge, 1973). In tropical Asia, it has been reported from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), the late Eocene Yaw Formation in Kalewa (CMB), and the Miocene Alleppy area in India (Ramanujam, 1987). Thus *Cupanieidites* originated in the Late Cretaceous of Africa, and migrated to India, the Americas, and Australia. The Eocene taxa in SE Asia might have been dispersed from India.

Genus: ***Cupuliferoipollenites*** Potonié 1951 ex Potonié 1960

Type species: *Cupuliferoipollenites pusillus* (Potonié 1934) Potonié 1960

Cupuliferoipollenites spp.

Plate I, 35-38

Description: LM: monad pollen, radial, isopolar, prolate to oblate spheroidal; in equatorial view near circular or oval; tricolporate, colpi long, extending 4/5 of the polar axis, pores small and circular; exine thin, 0.5 μm thick, without indiscernible layers; sculpture psilate to faintly scabrate; columellae indiscernible.

Dimensions: equatorial diameter 10.3-13.2 μm, polar axis 13.5-16.0 μm (nm = 4).

Botanical affinity: Fagaceae.

Source ecology: lower montane and possibly lowland trees.

Stratigraphic distribution: Pollen referable to *Cupuliferoipollenites* is widely reported in the northern hemisphere (Muller, 1981). From China, it has been reported from the Paleocene (Li, 1989), Eocene (Tong et al., 2001; Yuan et al., 2020) and Oligocene (Tang et al., 2020). From Myanmar, it is reported from the late Eocene Yaw Formation in Kalewa (CMB), Surprisingly, it has also been reported from the early Eocene of Argentina (Barreda et al., 2020). Records from the Nanggulan Formation in central Java by Takahashi (1982), were not confirmed by Lelono (2000).

In India, there are many records from the Neogene (Saxena and Trivedi, 2006), but also some from the early Eocene, such as from the Cambay Basin by Kar and Bhattacharya (1992). Bearing in mind that Fagaceae are conspicuously absent from the flora of Peninsula India (Ashton, 2014), such pre-collision records must be viewed with caution.

Remarks: *Cupuliferoipollenites* differs from *Cupuliferoidaepollenites* in being tricolporate rather than tricolpate.

Genus: ***Florschuetzia*** Germeraad et al. 1968

Type species: *Florschuetzia trilobata* Germeraad et al. 1968

Florschuetzia cf. *trilobata* Germeraad et al. 1968

Plate I, 40

Description: LM: monad pollen, radial, isopolar, trilobate; in equatorial view prolate/subprolate; tricolporate, colpi long, pores distinct, circular, 1.7 μm in diameter and equatorial; exine tectate; columellae indiscernible; sculpture scabrate.

Dimensions: equatorial diameter 19.1 μm, polar axis 27.7 μm (nm = 1).

Botanical affinity: *Florschuetzia trilobata* is ancestral to *Sonneratia* (Lythraceae) (Germeraad et al., 1968).

Source ecology: fresh or brackish swamps.

Stratigraphic distribution: The distribution of *Florschuetzia* has been discussed in detail by Morley (2000) and subsequently by Mao and Foong (2013) with a range from the middle Eocene to middle Miocene. Its oldest records are from the Ngimbang Formation in offshore South Sulawesi (Morley, 2014) and subsequently from the Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene Yaw Formation in Kalewa (CMB). Although the oldest confirmed occurrence is from South Sulawesi, an origin on the Indian Plate is suspected since Lythraceae evolved in West Gondwana (Berger et al., 2016) and *Florschuetzia* morphotypes have been reported from the early Eocene Cambay Basin (Samant and Phadare, 1997).

Genus: ***Gothanipollis*** Krutzsch 1959

Type species: *Gothanipollis gothani* Krutzsch 1959

Gothanipollis sp.

Plate I, 41

Description: LM: monad pollen, radial, isopolar, trilobate; amb triangular-concave; tri-syncolporate with polar cushions, colpi with costae, costae 2.3 μm thick, pores narrow; exine thin and indiscernible; sculpture sparsely baculate with small baculae.

Dimensions: equatorial diameter 21.4 μm (nm = 1).

Botanical affinity: Loranthaceae (Morley, 2000).

Source ecology: widespread parasitic shrubs of perhumid and seasonal forests.

Stratigraphic distribution: *Gothanipollis* was first described from the middle Eocene of Germany (Krutzsch, 1959). It ranges from early Eocene–late Oligocene in Europe (Tschudy, 1973). Other records include the early to middle Eocene Changchang Basin, Hainan, China (Yao

et al., 2009), the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene Yaw Formation in Kalewa (CMB). In Myanmar, it was also found in the early Miocene Letkat Formation in the CMB (Soe Moe Lwin et al., 2017)

Genus: ***Ilexpollenites*** Thiergart 1937 ex Potonié 1960

Type species: *Ilexipollenites iliacus* (Potonié 1931) Potonié 1960

Ilexpollenites sp.

Plate I, 42

Description: LM: monad pollen, radial, isopolar; amb lobate and near circular, in equatorial view prolate or round; tricolporate, colpi deeply incised and gaping, long, endoapertures circular; exine 1.2 μm thick and layers indiscernible; columellae indiscernible; sculpture densely clavate with clavae 0.9-1.5 μm high, 0.9-2.3 μm wide, slightly bigger toward polar area.

Dimensions: equatorial diameter 20.8-25.3 μm, polar axis 18.5-23.2 μm (excluding clavae, nm = 3).

Botanical affinity: This type is comparable to *Ilex cymosa* comp. (Aquifoliaceae) from central Sumatra (Indonesia; Morley, 1976).

Source ecology: common in alluvial and peat swamps in the tropics, also occurs in mountains. In CBM, it could be a component of alluvial swamps.

Stratigraphic distribution: the fossil and evolutionary history of *Ilex* has been reviewed by Loizeau et al. (2005). *Ilexpollenites* has been reported from the Turonian of Australia (Martin, 1977) and the Coniacian of equatorial Africa (Boltenhagen, 1976) suggesting a Gondwanan origin. There is subsequently a gap in its distribution, until the Maastrichtian, where it has been reported from California (Chmura, 1973). From the Paleocene and Eocene, it is widely reported from the Americas, Eurasia and Australia but not from Africa or India (Loizeau et al., 2005).

In SE Asia, the oldest record is *Gemmatricolpites pergemmatus* from the Paleocene of Sarawak (Muller, 1968; Morley, 2000), with subsequent records from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene Yaw Formation in Kalewa (CMB), and subsequently from the Oligocene onward (Muller, 1972). The oldest records from India are all from Assam, and restricted to the Neogene (e.g., Mandaokar, 2004) suggesting that *Ilex* dispersed into India during the Neogene.

Remarks: This pollen type differs from *Gemmatricolpites pergemmatus* in the presence of clavae.

Genus: ***Iugopollis*** Venkatachala et Rawat 1972

Type species: *Iugopollis tetraporites* Venkatachala et Rawat 1972

Iugopollis sp.

Plate I, 46

Description: LM: monad pollen, radial, isopolar, prolate; in equatorial view oval; tricolporate, lalongate, pores small and costate, colpi reach ca. 1/2 to the poles; exine thin, 0.9 μm thick, sexine and nexine indiscernible; sculpture psilate; columellae indiscernible.

Dimensions: equatorial diameter 15.0-26.3 μm, polar axis 21.6-28.6 μm (nm = 2).

Botanical affinity: *Aglaia* (Meliaceae).

Source ecology: trees of rain forests, possibly presenting in seasonal forests.

Stratigraphic distribution: *Iugopollis* is regularly present in low numbers through the Oligo–Miocene in Malaysia (Jais, 1997). Other records include the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: This type differs from other *Iugopollis* types that have affinities with Sapotaceae, in having shorter colpi and narrow pores.

Genus: ***Malvacipollis*** Harris 1965 emend. Krutzsh 1966

Type species: *Malvacipollis diversus* Harris 1965

Malvacipollis ?*diversus* Harris 1965

Plate I, 47

Description: LM: monad pollen, radial, isopolar, prolate; in equatorial view near oval; tricolporate, pores invisible; exine 0.5 μm thick, sexine and nexine indiscernible; sculpture psilate with short, sparse, evenly-distributed spines; columellae indiscernible.

Dimensions: equatorial diameter 13.6 μm, polar axis 21.8 μm (nm = 1).

Botanical affinity: *Dissiliaria*, a genus occurring in Australia and New Caledonia, and *Austrobuxus* (Picrodendraceae) (Morley, 2018a).

Source ecology: trees of seasonal evergreen rain forests in Australia and New Caledonia (Harris, 1965).

Stratigraphic distribution: Records are from the Palaeogene of New Zealand (Harris, 1965), the Eocene Murray Basin (Macphail, 1999), the early Eocene of Irian as *Austrobuxus* type (Morley, 2000), the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the

late Eocene Yaw Formation in Kalewa (CMB). In Myanmar, it was also reported in the early Miocene Letkat Formation in the CMB (Soe Moe Lwin et al., 2017).

Remarks: Without the SEM analysis, identification of the pollen grains of *Malvacipollis* are best compared only to the family level.

Genus: ***Margocolporites*** Ramanujam 1966 ex Srivastava 1969

Type species: *Margocolporites tsukadae* Ramanujam 1966 ex Srivastava 1969

Margocolporites spp.

Plate I, 48-51; Plate III, 19-21

Description: LM: monad pollen, radial, isopolar, prolate; amb circular and trilobate, lobes smoothly arched, in equatorial view oval; 3-zonimargocolporate, colpi 35.6 µm long with thickened costae (margines), nearly reaching halfway to the poles, margines 1.3-1.7 µm thick, psilate to finely baculate with straight edges and pointed ends, pores round, 1.6-1.7 µm in diameter, slightly protruding; mesocolpial area tectate-reticulate, muri multicolumellate, 0.8-1.1 µm thick and high, lumina 0.9-1.9 µm wide at the equator, 0.8 µm wide in maximum at the poles; exine 0.7-0.8 µm thick, sexine and nexine indiscernible; columellae indistinct. SEM: colpate margins baculate.

Dimensions: equatorial diameter 41.6 µm, polar axis 32.4-43.6 µm (nm = 5, one in polar view, two in oblique polar view, one in equatorial view and one in oblique equatorial view).

Botanical affinity: Fabaceae, mostly similar to *Caesalpinia* and related genera such as *Adipera, Brasilletia, Haematoxylon, Mezoneuron* and *Poincianella* (Muller, 1981).

Source ecology: trees of perhumid to seasonally dry forests.

Stratigraphic distribution: The oldest record of *Margocolporites* that show affinity to the *Caesalpinia* type is of *Margocolporites complexum* (Sah, 1974) and the related *Paleocaesalpiniaceaepites eocenica* described by Baksi (1974) from the early Eocene of Assam, which then becomes abundant in the Indian Eocene (Baksi, 1962). It is subsequently recorded from the middle Eocene of South America and the late Eocene of Nigeria (Germeraad et al., 1968) where it shows additional morphological variation (Jan du Chêne et al., 1978). It is also reported from the early to middle Eocene Changchang Basin (Yao et al., 2009), the late Eocene Yaw Formation in Kalewa (CMB), the Miocene Takem Hka Formation in the Hukawng Basin, northern Myanmar (Soe Moe Lwin et al., 2017), the Miocene Hmawgyi Chaung (Myanmar; Reimann and Aye Thaung, 1981), the early Miocene Letkat Formation in the CMB (Soe Moe

Lwin et al., 2017), the late Miocene–Pliocene CMB (Reimann and Aye Thaung, 1981), and the Pliocene of New Guinea (Playford, 1982). Tricolporate pollen with margi from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000) are different from the *Caesalpinia* type. Muller (1981) suggests that India may have formed the 'cradle' for caesalpinoid taxa, and thus may be considered an 'out-of-India' taxon.

Remarks: It is different from *Retitricolporites* van der Hammen et Wymstra in having margines and usually wider lumina. There is some degree of diversity in the *Margocolporites* spp. from the Yaw Formation. Plate I, 49 compares to *Margocolporites tricuneatus* (Playford, 1982). Plate I, 48, 50-51 are a more strongly reticulate type such as *M. foveolatus* (Jan du Chêne et al., 1978).

Genus: ***Meyeripollis*** Baksi et Venkatachala 1970

Type species: *Meyeripollis naharkotensis* Baksi et Venkatachala 1970

Meyeripollis naharkotensis Baksi et Venkatachala 1970

Plate I, 52-54

Synonym: *Nonaperturites evansi* Biswas 1962

Description: LM: monad pollen, radial isopolar; amb trilobate, triangular with rounded angles and slightly convex sides, angles distinguished by the appearance of two large gemmae on each side, gemmae 2.4-3.9 long and 2.2-3.6 wide, in equatorial view rhombic; trisyncolporate, pores lalongate, colpi long, almost reaching the poles, with costae, costae 1.2-2.5 μm thick, long and meet at the distal pole, obscured by ornamentation; exine thin, 0.8 μm thick; the distal pole also characterised by a large gemmae; sculpture gemmate and scabrate. Its pollen grains usually gather as a tetrad (Plate I, 54).

Dimensions: equatorial diameter 28.0-33.0 μm, polar axis 35.1 μm (nm = 5, one in equatorial view, others in polar view).

Botanical affinity: probably Myrtaceae.

Source ecology: trees of swamp forests.

Stratigraphic distribution: This pollen type has been reported from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), the late Eocene–early Miocene of Assam (Baksi and Venkatachala, 1970), the late Eocene Tanjung Formation in East Kalimantan (Witts et al., 2012; Morley, 2014), the late Eocene Yaw Formation in Kalewa (CMB), and the Miocene Hmawgyi Chaung in Myanmar (Reimann and Aye Thaung, 1981). In Myanmar, it was also

commonly found in the early Miocene Letkat Formation in the CMB (Soe Moe Lwin et al., 2017). It is also characteristic of the Oligocene sediments in the East Java Sea (Lelono, 2007) and the early Miocene of the west Java Sea (Morley, 2000). Its oldest stratigraphic appearance is dependent on climate and marine influence, and so first appears across northern Sunda only in the late Oligocene (Morley, 1991).

Remarks: This genus was first described as a gemmate-syncolpate pollen by Baksi (1962). It is a fossil marker of ages from late Eocene–basal Miocene and helps define the age of the Yaw Formation.

Genus: ***Ranunculacidites*** Sah 1967

Type species: *Ranunculacidites communis* Sah 1967

Ranunculacidites operculatus (van der Hammen et Wymstra 1964) Jaramillo et Dilcher 2001

Plate III, 13-15

Description: LM: monad pollen, radial, isopolar, oblate; amb triangular-convex to circular; tricolporate, colpi marginate, with distinct opercula covering pores, opercula 2.8-4.9 μm long, 1.0-2.0 μm wide at the equator; exine quite thin, 0.3-0.5 μm thick, slightly thicker at margins of the colpi; sculpture psilate to scabrate. SEM: sculpture granulate.

Dimensions: equatorial diameter 18.0–26.1 μm (nm = 5).

Botanical affinity: *Alchornea* (Euphorbiaceae) (Germeraad et al., 1968).

Source ecology: widespread trees of swamp forests in tropical and subtropical regions.

Stratigraphic distribution: The oldest record is 56.1 Ma in Venezuela and Colombia (Jaramillo et al., 2010, 2011). It is subsequently recorded from the middle Eocene of Caribbean area and Nigeria (Germeraad et al., 1968), and the late Eocene Yaw Formation in Kalewa (CMB), but not until the Oligocene in Australia (Martin, 1994) and the early Miocene in India (Ramanujam et al., 1991).

Genus: ***Retibrevitricolpites*** van Hoeken-Klinkenberg 1966

Type species: *Retibrevitricolpites triangulatus* van Hoeken-Klinkenberg 1966

Retibrevitricolpites cf. *triangulatus* van Hoeken-Klinkenberg 1966

Plate II, 4-5

Description: LM: monad pollen, radial, isopolar, oblate; amb subtriangular, tricolporate, colpi thin and short, 1.9-2.9 μm in length, marginate with thickenings and finely reticulate

tectum, pores vestibulate; exine 0.5-0.8 μm thick, thicker at the poles; sculpture microreticulate, lumina up to 0.4 μm wide, rather angular in shape, muri up to 0.4 μm thick and wide.

Dimensions: equatorial diameter 26.4-29.2 μm (nm = 5).

Botanical affinity: unknown, apparently extinct (Germeraad et al., 1968).

Source ecology: This pollen type is associated with *Proxapertites* (Muller et al., 1987), which occurred in the brackish environment in the manner of *Nypa* (Huang et al., 2020). The parent plant may therefore also have been a coastal taxon.

Stratigraphic distribution: The oldest records are from the middle Eocene of Nigeria and the Neotropics (Germeraad et al., 1968) and the late Eocene Yaw Formation in Kalewa (CMB). Its only record from India is from the Oligocene of Assam (Kumar, 1994). It has not been reported from Australasia.

Remarks: This pollen type is different from *R. triangulatus*, which has a reticulate lumina that decreases from equator to poles.

Genus: ***Scollardia*** Srivastava 1966

Type species: *Scollardia trapaformis* Srivastava 1966

cf. *Scollardia* sp.

Plate II, 6-7

Description: LM: monad pollen, radial, isopolar; in equatorial view triangular; tricolporate, angulaperturate, brevicolpate, pores small, 0.5-1.3 μm in diameter, slightly protruding, apertures without any margin; exine 0.6-1.2 μm thick, thicker around the polar areas, up to 2.2 μm, columellae distinct; sculpture striate in meridional direction and coarser at the equator, diverging from poles.

Dimensions: equatorial diameter 19.9-22.0 μm (nm = 4).

Botanical affinity: *Scollardia* is often referred to as Loranthaceae (e.g., Song et al., 2004) but it lacks the polar cushions characteristic of that family and may be from Sapindaceae.

Source ecology: unknown.

Stratigraphic distribution: *Scollardia* is widely distributed in the Late Cretaceous, and especially the Maastrichtian of North America, such as in the Turtle Mountain areas of western Canada (Braman and Sweet, 1999), and the Edmonton Group from Alberta (Srivastava and Braman, 2013). However, it is also present in the late Maastrichtian of Venezuela (Muller et al., 1987). In India, it is well represented in the Maastrichtian, where it is used to characterise a

palynological zone (Venkatachala, 1974) and is reported from the Deccan intertrappean beds by Prasad et al. (2018) and Samant and Mohabey (2009). The record from the late Eocene Yaw Formation in Kalewa (CMB) is one of the youngest.

Genus: ***Striasyncolpites*** Germeraad et al. 1968

Type species: *Striasyncolpites zwaardi* Germeraad et al. 1968

Striasyncolpites sp.

Plate II, 8

Description: LM: monad pollen, radial, isopolar, oblate; amb triangular; tricolporate, angulaperturate, syncolporate, colpi long, and connected at the poles, pores small and slightly protruding; exine thin, 0.5 μm thick, thicker around the poral areas, columellae distinct; sculpture finely striate and coarser at the equator.

Dimensions: equatorial diameter 20.1-22.9 μm (nm = 2).

Botanical affinity: probably Lythraceae.

Source ecology: forest trees in various environments.

Stratigraphic distribution: The record from the late Eocene Yaw Formation in Kalewa (CMB) is the oldest in the genus *Striasyncolpites*. Other records include *Striasyncolpites laxus* (with affinity to *Villarsia* in family Menyanthaceae) from the early Oligocene Marillana Formation of northwestern Australia (Macphail and Stone, 2004), the late Oligocene to early Miocene in Tasmania (Macphail et al., 1991), and the late Oligocene to middle Miocene Cullen Formation in Argentina (Zamaloa, 2000); and *Striasyncolpites zwaardi*, with affinity to *Cuphea* in the family Lythraceae, from the middle Miocene Caribbean area (Germeraad et al., 1968).

Remarks: *Striasyncolpites* includes two form-species, *Striasyncolpites laxus* and *S. zwaardi*. Our pollen type is more comparable to *S. zwaardi* (Germeraad et al., 1968), as *S. laxus* is parasyncolporate (e.g., Macphail et al., 1991; Palamarczuk and Barreda, 2000; Macphail and Stone, 2004). But the pores of our *Striasyncolpites* species are less protruding than *S. zwaardi*. This pollen type could be a new species in this genus.

Plate III. Here.

Genus: ***Lanagiopollis*** Morley 1982

Type species: *Lanagiopollis regularis* Morley 1982

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Lanagiopollis nanggulanensis Morley 1982

Plate I, 43; Plate II, 17

Description: LM: monad pollen, radial, isopolar; amb triangular-obtuse or quadrangular; tricolporate or tetracolporate, tetralobate (Plate II, 17), angulaperturate, colpi reach 1/4-2/3 to pole, pores large and circular, up to 4.5 μm in diameter; exine up to 2.3 μm thick, nexine thicker than sexine; sculpture rugulate to reticulate, heterobrochate; columellae indistinct. This tetracolporate specimen (Plate II, 17) is closely comparable to the tetracolporate *L. nanggulanensis* illustrated by Morley (1982) in Plate 2, Fig. 2.

Dimensions: equatorial diameter 41.6-60.0 μm (nm = 2).

Botanical affinity: *Alangium* sect. *Conostigma* (Alangiaceae), probably *Alangium ebenaceum* type and *A. havilandii* type (Morley, 1982).

Source ecology: *Alangium* sect. *Conostigma* are mostly megathermal trees and are characteristic of swamp and riverine habitats in evergreen tropical forests (Morley, 1982).

Stratigraphic distribution of L. nanggulanensis and L. emarginatus (Plate I, 44): Fossils of *Alangium* sect. *Conostigma* are abundant in India and SE Asia since the early Eocene (Morley, 2018a). 1) *L. nanggulanensis* has been reported from the Indian early Eocene by Tripathi et al. (2000), the middle Eocene of Java and late Eocene of Kalimantan (Morley, 1982), the late Eocene Yaw Formation in Kalewa (CMB), and the early to middle Miocene of Thailand (Watanasak, 1990). It is widely distributed throughout the younger Cenozoic of SE Asia. With the oldest record from India, this is an 'out-of-India' taxon; 2) *L. emarginatus* was recorded from the early to middle Eocene Tarkeswar Formation in the Rajpardi lignite in Gujarat, India (Phadtare and Thakur, 1990), and the late Eocene Yaw Formation in Kalewa (CMB), and is common in the late Miocene and Pliocene of Java Sea, East Kalimantan, Brunei/Sarawak and the South China Sea (Morley, 1982). It is also an 'out-of-India' taxon.

Remarks: *L. nanggulanensis* differs from *L. emarginatus* in the presence of thickened margines bordering the ectoapertures and longer colpi (Morley, 1982).

Genus: ***Sapotaceoidaepollenites*** (Potonié) Thomson et Thiergart 1950

Type species: *Sapotaceoidaepollenites manifestus* (Potonié) Thomson et Thiergart 1950

(The dichotomous identification key to the five Sapotaceae pollen types is provided in Appendix S2.)

Sapotaceoidaepollenites type 1

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Plate IV, 2-4, 13; Plate V, 1-5; Plate VI, 1-2, 5-6, 9-10, 13-14

Description: LM: monad pollen, radial, isopolar occasionally heteropolar, prolate to subspheroidal; tricolporate, tetracolporate to pentacolporate, in equatorial view elliptical to spheroidal; endoapertures thin, lalongate to spheroidal or elliptical, colpi 15.0-27.0 μm long, covering less than or equal to 0.7, rarely 0.9 of polar axis; exine less than 1.5 μm thick; without costae; sculpture scabrate. SEM: sculpture areolate to rugulate.

Dimensions: equatorial diameter 15.0-32.0 μm, polar axis 20.0-40.0 μm (nm = 13).

Botanical affinity: Chrysophylleae (Sapotaceae: Chrysophylloideae).

Source ecology: The family Sapotaceae is a good indicator of lowland and coastal rain forests in SE Asia (Morley, 2018a; Cheng et al., 2020). It is also one of the most prominent components in both the understory and canopy of SE Asian lowland forests (Morley, 2018a). Thus the parents plants of this type are likely to have been trees of lowland evergreen forests.

Stratigraphic distribution: This pollen type has been found in early Eocene to early Oligocene deposits in the CMB. However, molecular studies propose the ancestral area of the earliest diversification of Chrysophylloideae during the Campanian in Africa at ca. 83-73 Ma. Colonization events took place between Africa and Madagascar at ca. 68-54 Ma and several others occurred after Madagascar detached and drifted from Africa (Bartish et al., 2011; McLoughlin, 2001). The most probable area of origin of the subfamily is within Africa and it could either have reached the CMB directly from Africa or via the Indian Plate.

Remarks: This pollen type has three subtypes: 1) subtype 1a (Sapotaceae: Chrysophylloideae: Chrysophylleae: *Elaeoluma*): apocolpium and mesocolpium not differentiated but only coarsely perforate towards apocolpial regions; ornamentation entirely areolate/nanoverrucate, tectum not protruding (Plate VI, 1-2); 2) subtype 1b (Sapotaceae: Chrysophylloideae: Chrysophylleae: *Sarcaulus*): apocolpium and mesocolpium not differentiated although sometimes increasingly coarsely perforate towards apocolpia; ornamentation rugulate with sparse coarse granules, tectum not protruding (Plate VI, 5-6, 9-10); 3) subtype 1c (Sapotaceae: Chrysophylloideae: Chrysophylleae: *Pichonia*): apocolpium and mesocolpium not differentiated and both coarsely perforate; ornamentation entirely low-relief finely striate-rugulate, tectum not protruding (Plate VI, 13-14). This type differs from type 2 in having an average polar axis of more than 25.0 μm and colpi more than 15.0 μm, occasionally up to ca. 27.0 μm covering up to 0.75 of polar axis. It differs from types 3 and 4 in having a prolate to commonly subspheroidal polar axis/equatorial

diameter ratio. It differs from the other types in occasionally showing areolate/nano-verrucate ornamentation.

Plate IV. Here.

Sapotaceoidaepollenites type 2

Plate IV, 1, 5-6; Plate VI, 11-12

Description: LM: monad pollen, radial, isopolar occasionally heteropolar; tricolporate to tetracolporate, prolate to spheroidal; in equatorial view elliptical to spheroidal; endoapertures lalongate thin elliptical, occasionally spheroidal, colpi 11.0-20.0 µm long, covering ca. 0.65-0.8 of polar axis; exine 1.0-1.5 µm thick; without costae; sculpture scabrate. SEM: rugulate.

Dimensions: equatorial diameter 11.0-19.0 µm, polar axis 15.0-23.0 µm (nm = 8).

Botanical affinity: Sideroxyleae (Sapotaceae: Sapotoideae).

Source ecology: trees of lowland evergreen forests. See that of type 2.

Stratigraphic distribution: This pollen type has only been found in early Eocene to early Oligocene deposits in the CMB.The origins of Sideroxyleae have been suggested to lie within Africa (Anderberg and Swenson, 2003; Swenson and Anderberg, 2005; Smedmark and Anderberg, 2007). After the divergence of Sideroxyleae, the age of the Isonandreae-Mimusopeae stem node was estimated to be middle Eocene (Hofmann, 2018; Richardson et al., 2014). Similarly, Armstrong et al. (2014) estimated 58–48 Ma for the Isonandreae/Mimusopeae clade. Smedmark and Anderberg (2007) estimated that extant Sideroxyleae diverged from Isonandreae-Mimusopeae node at between 65 and 34 Ma into different lineages.

Remarks: This pollen type has one subtype (Sapotaceae: Sapotoideae: Sideroxyleae: *Sideroxylon*): apocolpium and mesocolpium not differentiated and both coarsely perforate; ornamentation entirely low-relief rugulate and tectum not protruding (Plate VI, 11-12). This type differs from other types in having an average polar axis of less than 25.0 µm and in having colpi of commonly less than 15.0 µm long. It differs from type 3 in its low-relief rugulate ornamentation.

Plate V. Here.

Sapotaceoidaepollenites type 3

Plate IV, 7-10, 12, 14; Plate V, 6-10; Plate VII, 9-14

Description: LM: monad pollen, radial, isopolar occasionally heteropolar; tricolporate to pentacolporate, prolate to subprolate, rarely subspheroidal; in equatorial view elliptical, commonly rhomboidal, rarely spheroidal; endoapertures circular or lalongate elliptical, colpi commonly more than 2.0 μm thick, 17.0-27.0 μm long, covering 0.5-0.8 of polar axis; exine 1.0-2.0 μm thick, rarely 1.0 μm; with or without costae; sculpture scabrate. SEM: sculpture granulate.

Dimensions: equatorial diameter 13.0-37.0 μm, polar axis 16.0-37.0 μm (nm = 26).

Botanical affinity: *Mimusops* (Sapotaceae: Sapotoideae: Mimusopeae).

Source ecology: In present-day Myanmar, Sapotaceae is diverse and one of the most characteristic families in evergreen forests, with *Mimusops* (five species) and *Palaquium* (four species) as two of the predominant genera (Kress et al., 2003). Thus we propose the parents of this pollen type were trees of lowland evergreen forests.

Stratigraphic distribution: This pollen type occurs in early Eocene to early Oligocene sediments in the CMB. Armstrong et al. (2014) concluded Mimusopeae evolved at 52 Ma and diversified at 43 Ma, during the Eocene, when global climate presented higher temperatures and humidity. With an origin in Africa based on molecular data, this taxon may have reached Myanmar either directly from Africa or via the Indian Plate.

Remarks: This pollen type has three subtypes: 1) subtype 3a: apocolpia coarsely perforate. Apocolpium and mesocolpium not differentiated; tectum finely granular and protruding, occasionally bulging around apertures (Plate VII, 9-10); 2) subtype 3b: apocolpia not coarsely perforate. Apocolpium and mesocolpium not differentiated; tectum finely granular and not protruding (Plate VII, 13-14); 3) subtype 3c: apocolpia not perforate. Apocolpium and mesocolpium not differentiated; tectum coarsely granular and protruding or not protruding (Plate VII, 11-12). This type differs from type 2 in having an average polar axis of more than 25 μm and colpi more than 15.0 μm. It differs from type 4 in having colpi occasionally covering less than 0.65 of polar axis. It differs from other types in having granular ornamentation exclusively.

Plate VI. Here.

Sapotaceoidaepollenites type 4

Plate IV, 11, 15-18; Plate V, 11-13; Plate VI, 7-8, 15-16; Plate VII, 1-8, 15-16

Description: LM: monad pollen, radial, isopolar occasionally heteropolar; tricolporate to tetracolporate, subprolate, sometimes prolate; in equatorial view elliptical to rarely spheroidal; endoapertures thin, spheroidal or lalongate to elliptical sometimes protruding, colpi 15.0-25.0 μm long, rarely less than 15.0 μm, covering 0.65-0.8, occasionally 0.9 of polar axis; exine 1.0-2.0 μm thick; with or without costae; sculpture psilate to scabrate. SEM: sculpture reticulate to rugulate.

Dimensions: equatorial diameter 13.0-27.0 μm, polar axis 20.0-35.0 μm (nm = 21).

Botanical affinity: *Palaquium* (Sapotaceae: Sapotoideae: Isonandreae).

Source ecology: trees of lowland evergreen forests. See that of type 3.

Stratigraphic distribution: In this study, it occurs in early Eocene to early Oligocene deposits in the CMB. The tribe Isonandreae currently extends across the tropics of the Old World, from India across Asia and SE Asia and the Pacific Islands. The stem and crown ages of Isonandreae were estimated to be 40.5 and 36.5 Ma (corroborated by the presence of all of the three subtribes in the subfamily Sapotoideae in the mid-Eocene of Europe) respectively by Richardson et al. (2014), who also postulated Africa as the most plausible source area for stem Isonandreae (Hofmann et al., 2018). Migration patterns of Isonandreae are suggested from Africa to Asia via Laurasia at 40.5 Ma. It is hypothesised that Isonandreae first diversified in Laurasia or Sundania (Richardson et al., 2014).

Remarks: This pollen type has two subtypes: 1) subtype 4a: apocolpium and mesocolpium not differentiated and both coarsely perforate; ornamentation entirely low-relief reticulate or microrugulate and tectum not protruding (Plate VI, 15-16; Plate VII, 1-8, 15-16); 2) subtype 4b: apocolpia psilate and coarsely perforate; apocolpium and mesocolpium differentiated; ornamentation finely rugulate, tectum occasionally protruding slightly bulging around endoapertures (Plate VI, 7-8). This type differs from type 2 in having an average polar axis of more than 25.0 μm and colpi more than 15.0 μm. It differs from type 3 in having rugulate/reticulate ornamentation, and from other types in occasionally presenting differentiated apocolpium and mesocolpium.

Plate VII. Here.

Sapotaceoidaepollenites type 5

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Plate V, 14-16

Description: LM: monad pollen, radial, isopolar; in equatorial view tricolporate to tetracolporate, prolate to subprolate; endoapertures indistinct, slightly rounded and occasionally lalongate; thick colpi 2.0 µm, or medium thickness 1.5 µm, length 22.0-27.0 µm covering from less than 0.65 (rarely more than 0.75) of polar axis; without costae; exine very thin, less than 1.0 µm to 1.0-1.2 µm equally thick at mesocolpia; sculpture psilate to scabrate.

Dimensions: equatorial diameter 24.0-29.0 µm, polar axis 33.0-35.0 µm (nm = 3).

Botanical affinity: *Pouteria* or *Pichonia* (Sapotaceae: Chrysophylloideae: Chrysophylleae).

Source ecology: trees of lowland evergreen forests. See discussion in type 1.

Stratigraphic distribution: In this study, it occurs in the late Eocene Yaw Formation from the Chindwin sub-basin (CMB).

Remarks: This type differs from other types in having colpi of average 25.0 µm length, and an average polar length of more than 30.0 µm.

Genus: ***Alnipollenites*** Potonié 1931

Type species: *Alnipollenites verus* (Potonié 1931) ex. Potonié 1934

Alnipollenites verus (Potonié 1931) ex. Potonié 1934

Plate II, 18

Synonym: *Pollenites verus* Potonié 1931; *Alnipollenites verus* Potonié 1934; *Polyvestibulopollenites verus* (Potonié) Thomson et Pflug 1953.

Description: LM: monad pollen, radially symmetrical, isopolar, oblate; amb near circular; pentaporate, angulaperturate, five pores connected by distinct arcus, 1.0 µm wide, pores vestibulate; exine 1.5 µm in thick, thicker (2.5 µm) at the near the pores; exine layers and columellae indiscernible; sculpture psilate.

Dimensions: equatorial diameter 23.0 µm (nm = 1).

Botanical affinity: *Alnus* (Betulaceae).

Source ecology: lower montane generally deciduous trees, growing in northern seasonal wet evergreen montane forests from Vietnam to the Himalayan foothills (Ashton, 2014).

Stratigraphic distribution: The oldest records are from the Santonian of Japan (Miki, 1977) and similar age deposits from China (Song et al., 2004). It is widely reported from the Maastrichtian of North America, but not until the Paleocene of Europe (Muller, 1981). This

Laurasian taxon dispersed to South America following the closure of the Panama Isthmus (Hooghiemstra, 1984).

In SE Asia, the oldest record is from the late Eocene Yaw Formation in Kalewa (CMB), and it is subsequently recorded from the Oligocene and Miocene of the Sunda Shelf (Muller, 1966; Morley, 2018b), Tibet (Wei et al., 2011), Thailand (Watanasak, 1990; Songtham et al., 2003). Its common occurrence in the Oligocene to middle Miocene sediments of the Sunda Shelf reflects former uplands along the Natuna Arch and Con Son Swell (Morley, 2018b). In Myanmar, it is abundant in the early Miocene Letkat Formation from the CMB (Soe Moe Lwin et al., 2017).

Remarks: This species differs from *A. scoticus* in the absence of a characteristic thickening at the poles (Zetter et al., 2011).

Genus: ***Anacolosidites*** Cookson et Pike 1954

Type species: *Anacolosidites luteoides* Cookson et Pike 1954

Anacolosidites luteoides Cookson et Pike 1954

Plate II, 20

Description: LM: monad pollen, radial isopolar; amb triangular, with straight or slightly concave sides, apices obtuse; hexaporate, three pores towards the angles of each hemisphere, forming six nonequatorial pores, pores circular and 2.1-3.7 μm in diameter, located ca. 1/3 of the equatorial diameter from the equator; exine 0.5 μm thick; exine layers indiscernible; sculpture psilate.

Dimensions: equatorial diameter 20.1 μm (nm = 1).

Botanical affinity: Pollen attributed to *Anacolosidites lutoides* is derived from the genera *Cathedra*, *Anacolosa* and *Phanerodiscus* (Olacaceae: Anacoloseae) (Malécot and Lobreau-Callen, 2005), a tropical angiosperm subfamily with a pantropical distribution.

Source ecology: trees of perhumid forests and swamps. This genus is used as a stratigraphic and environmental marker for tropical and megathermal climate conditions (Malécot and Lobreau-Callen, 2005).

Stratigraphic distribution: Reference is made only to morphotypes that can be referred to Olacaceae, as some striate *Anacolosidites* are probably from Loranthaceae (Malécot and Loubreau-Callen, 2005). The oldest occurrence is *Anacolosidites sectus* from the Campanian of Antarctica, followed by *A. cretacicus* from the Maastrichtian of Germany (Krutzsch and Lenk, 1969). There are a number of species recorded from the Paleocene including *A. efflatus* from

Europe and *A. lutoides* and *A.* cf. *luteoides* from the Paleocene of China, Africa, Borneo and Australia and may thus be viewed as a 'cosmopolitan' taxon. The genus reached its maximum distribution and diversity in the Eocene, occurring in all continents (Malécot and Loubreau-Callen, 2005). The morphotype then reduced its range dramatically in the Oligocene, with only a few records from Africa, South America, India and Australia in the Oligo–Miocene. *A. luteoides* is recorded from the late Eocene Yaw Formation in Kalewa (CMB).

Remarks: The pollen morphology of the genus is peculiar, being hexaporate with three apertures on each hemisphere.

Anacolosidites reticulatus Morley, Huang et Hoorn sp. nov.

Plate II, 21; Plate III, 22-24

Synonym: reticulate *Anacolosidites* sp. in Morley et al. (2000)

Etymology: The specific epithet alludes to its microreticulate surface ornamentation.

Holotype: IBED-T41.221 (Plate II, 21).

Paratypes: IBED-T40.968 (Plate III, 22-24), PLS-17C267.

Repository: Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam. The Netherlands.

Type locality: Kalewa Township, Sagaing Region, Myanmar.

Diagnosis: monad, near circular, hexaporate, columellae robust, reticulate to microreticulate.

Description: LM: monad pollen, radial, isopolar; amb near circular, with slightly or strongly concave sides, apices obtuse; hexaporate, three pores towards the angles of each hemisphere, forming six non-equatorial pores, pores circular with 2.5-4.8 μm in diameter, located at ca. 1/4 of the equatorial diameter from the equator; exine with 0.6-1.3 μm thickness, sexine thicker than nexine; columellae robust; sculpture reticulate to microreticulate. SEM: sculpture microreticulate to perforate.

Dimensions: equatorial diameter 26.3-35.1 μm (nm = 4).

Botanical affinity: This pollen type is probably derived from *Ptychopetalum* (Olacaceae: Olacaeae), a tropical angiosperm genus which today occurs in Africa and South America. The South American species are, however, triporate. Only the African *Ptychopetalum anceps* is reticulate with a circular amb (Malécot and Lobreau-Callen, 2005) as in *A. reticulatus.*

Source ecology: trees of perhumid forests. This genus is used as a marker for megathermal climate conditions (Morley, 2000).

Stratigraphic distribution: This pollen type was first alluded by Handique (1992) and Morley (2000) from the middle and late Eocene of Assam as 'reticulate *Anacolosa*' pollen, and subsequently from the middle and late Eocene of Java as reticulate *Anacolosidites* sp. (Morley et al., 2000). Its other locality is the late Eocene Yaw Formation in Kalewa (CMB). The species is a valuable marker for the middle to late Eocene for the tropical Asian region (Morley et al., 2000; van Gorsel et al., 2014).

Remarks: This species is different from other species in the genus with its near circular shape, and finely reticulate sculpture.

Anacolosidites trilobatus Venkatachala et Rawat 1971

Plate II, 22

Description: LM: monad pollen, radial, isopolar; amb triangular, with slightly or strongly concave sides, apices obtuse; hexaporate, three pores towards the angles of each hemisphere, forming six nonequatorial pores, pores circular with 2.4-3.1 μm in diameter, locate ca. 1/3 of the equatorial diameter in from the equator; exine 0.3 μm thick; exine layers indiscernible; columellae robust; sculpture psilate to microperforate.

Dimensions: equatorial diameter 20.7 μm (nm = 1).

Botanical affinity: As with *Anacolosidites luteoides*, this species belongs to the tribe Anacoloseae (*Cathedra*, *Anacolosa* and *Phanerodiscus*) of Olacaceae, having a pantropical distribution.

Source ecology: trees of perhumid forests and swamps.

Stratigraphic distribution: the Paleocene?–Eocene of India (Malécot and Lobreau-Callen, 2005) and the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Ephedripites*** Bolchovitina 1953 ex Potonié 1958 emend. Krutzsch 1961

Type species: *Ephedripites eocenipites* Wodehouse 1933

Ephedripites sp.

Plate II, 26

Description: LM: monad pollen, symmetry bilateral, isopolar, peroblate; polyplicate, elongate shape, 10-12 straight or slightly sinuous plicae fusing at the tips; plicae 1.0-2.1 μm wide; exine indiscernible; sculpture psilate at non-plicae area.

Dimensions: equatorial diameter 15.0 μm, polar axis 45.2 μm (nm = 1).

Botanical affinity: *Ephedra* (Ephedraceae).

Source ecology: herbs/shrubs of dry and warm scrub (e.g., Warny et al., 2018), possibly growing in dry areas and along braided rivers beyond the upper deltaic plain in the CMB.

Stratigraphic distribution: *Ephedripites* pollen has been widely reported from Cretaceous deposits across the tropics, where it dominates in areas of semi-arid climate, such as across large parts of tropical Africa and South America (e.g., Herngreen and Chlonova, 1981; Crane and Lidgard, 1989) and in Borneo (Muller, 1968). In the early Cenozoic, the diversity of *Ephedripites* decreases (Krutzsch, 1961, 1970) and the group shifts in distribution to arid regions of the mid latitude high pressure zones and is abundant in the Palaeogene of Tibetan Plateau and China (e.g., Han et al., 2016; Tang et al., 2020; Xie et al., 2020; Yuan et al., 2020). In SE Asia, it tends to be present in very low numbers. It has been recorded form the early and late Eocene CMB (Reimann and Aye Thaung, 1981), the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and the late Eocene Yaw Formation in Kalewa (CMB) and from the Oligocene to early Miocene Sunda Shelf (Muller, 1966).

Genus: ***Heterocolpites*** van der Hammen 1956 ex van der Hammen et Garcia de Mutis 1965

Type species: *Heterocolpites palaeocenicus* van der Hammen et Garcia de Mutis 1965

Heterocolpites combretoides Rao et Ramanujam 1982

Plate II, 25

Description: LM: monad pollen, radial, isopolar, prolate to subpheroidal; polycolporate, probably stephanocolporate, brevicolpate, ora lalongate, costate, pores large and distinct with diameter up to 2.7 μm; exine indiscernible; sculpture rugulate to reticulate.

Dimensions: equatorial diameter 18.3-25.4 μm, polar axis 19.1-31.4 μm (nm = 2).

Botanical affinity: *Lumnitzera* and other Combretaceae genera (Ramanujam, 1987).

Source ecology: This pollen may be derived from the mangrove taxon *Lumnitzera*, but also from deciduous forest trees, of which Combretaceae are an important component (Ashton, 2014).

Stratigraphic distribution: Records include those from the late Eocene Yaw Formation in Kalewa (CMB), the early Oligocene South Cambay Basin (Govindan and Mallikarjuna, 2019), and the early to middle Miocene Warkalli Beds of Kerala State in India (Rao and Ramanujam, 1982; Ramanujam, 1987).

Genus: ***Retistephanocolpites*** Leidelmeyer 1966

Type species: *Retistephanocolpites williamsi* Germeraad et al. 1968

Retistephanocolpites williamsi var. Germeraad et al. 1968

Journal Pre-proof

Plate II, 24

Description: LM: monad pollen, radial, isopolar, oblate; amb spheroidal and eight-lobed; polycolpate with eight short colpi, 5.7-6.2 μm deep, reaching 1/3 to the poles; exine up to 2.1 μm thick; sculpture scabrate to microreticulate.

Dimensions: equatorial diameter 32.6 μm (nm = 1).

Botanical affinity: *Ctenolophon parvifolius* (Ctenolophonaceae) (Germeraad et al., 1968).

Source ecology: perhumid forest trees.

Stratigraphic distribution: *Retistephanocolpites williamsi* first occurred from the Paleocene of Africa (Germeraad et al., 1968) and India, and then diversified in the early Eocene in India (Plate VI, 2 in Morley, 2000). Possible variants within this morphotype are illustrated schematically by Krutzsch (1989). In the Sunda region *R. williamsi* variants first occur in the middle Eocene (Morley, 1998), and subsequently occur in the late Eocene Yaw Formation in Kalewa (CMB). It has also been recorded in the latest early Oligocene Lanzhou Basin in China (Miao et al., 2013). In Myanmar, it was also found in the early Miocene Letkat Formation in the CMB (Soe Moe Lwin et al., 2017). This is an 'out-of-India' taxon.

Genus: ***Cicatricososporites*** Pflug et Thomson 1953

Type species: *Cicatricososporites dorogensis* (Potonié) Thomson et Pflug 1953

Cicatricososporites eocenicus (Selling 1944) Jansonius et Hill 1976

Plate II, 27-28

Synonym: *Schizaea eocenica* Selling 1944.

Description: LM: monolete spore, radial, anisopolar; in equatorial view oblate; laesura obscured; exine up to 1.0 μm thick; sculpture striate.

Dimensions: greatest dimension 20.0-40.1 μm (nm = 5).

Botanical affinity: Schizaeaceae (Selling, 1944).

Source ecology: probably ferns of swamps and riversides.

Stratigraphic distribution: Rarely in Europe (Krutzsch, 1959), in SE Asian records include those from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), the late Eocene Tanjung Formation in central Borneo (Kristyarin et al., 2016), and the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Gemmatosporis*** Krutzsch 1959

Type species: *Gemmatosporis gemmatoides* Krutzsch 1959

Journal Pre-proof

Gemmatosporis gemmatoides Krutszch 1959

Plate II, 29-30

Description: LM: monolete spore, radial, anisopolar; in equatorial view oblate; laesura weak; sculpture psilate with sparse gemmae, gemmae diameter up to 2 μm.

Dimensions: greatest dimension 37.8-44.5 μm (nm = 3).

Botanical affinity: This spore type is tentatively attributed to *Cyclophorus* based on the presence of gemmae, but the match is not clear-cut, and it may be from an extinct fern.

Source ecology: presumably ferns of terrestrial wet environments.

Stratigraphic distribution: This spore type is common in the Oligocene Sunda Shelf, where it has sometimes been used as a zonal marker in unpublished palynological zonation schemes (Ho, 1978; Ramli, 1988; Yakzan et al., 1996). It is also recorded from the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Cyclosorus*** Link 1833

Type species: *Cyclosorus gongylodes* (Schkuhr) Link 1833

Cyclosorus type

Plate II, 31

Description: LM: monolete spore, radial, anisopolar; in equatorial view kidney-shaped; laesura up to 24.0 μm long; sculpture psilate with short echini.

Dimensions: greatest dimension 40.4-46.0 μm (nm = 2).

Botanical affinity: *Cyclosorus* (Thelypteridaceae).

Source ecology: It is mainly thought to be derived from ferns growing in wet terrestrial environments such as swamps (Morley et al., 2019), but also occur in wet forests (Morley, 1982).

Stratigraphic distribution: It commonly occurs in the Oligocene and younger sediments in the Sunda region (Morley et al., 2021). It is also recorded from the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Acrostichum*** L. 1753

Type species: *Acrostichum aureum* Krutzsch 1875

Acrostichum type

Plate II, 34

Journal Pre-proof

Description: LM: trilete spore, radial, anisopolar; amb near circular, to convexly subtriangular, with straight or slightly convex sides; laesurae up to 16.1 μm in length, reaches 1/2-2/3 toward the round apices; sculpture psilate to microgranulate; exine 1.5 μm thick.

Dimensions: greatest dimension 42.5-52.1 μm (nm = 4).

Botanical affinity: *Acrostichum* (Pteridaceae).

Source ecology: ferns of disturbed mangroves (Morley et al., 2019) or disturbed floodplain settings but also in ephemeral freshwater floodplains in mid Cenozoic of Spain (Moreno-Domínguez et al., 2016) and the enclosed non-marine Palaeogene basins surrounding Vietnam (Morley et al., 2019).

Stratigraphic distribution: The oldest occurrence in SE Asia is from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000) and the late Eocene Yaw Formation in Kalewa (CMB), This spore type occurs widely from the middle Eocene onward throughout the SE Asian region. Outside SE Asia this spore type is often mentioned as *Leiotriletes adriennis* Krutzsch by European workers, or *Biretisporites luonensis* Playford by Australian workers. The concept of the taxon needs a review.

Genus: ***Anthocerisporis*** Krutzsch 1963

Type species: *Anthocerisporis europaeus* Krutzsch 1963

Anthocerisporis sp.

Plate II, 32-33

Description: LM: trilete spore, radial, anisopolar; amb circular to convexly subtriangular, with distinct trilete mark extending to the equator with a characteristic 'Y' mark at the apices; sculpture shallowly reticulate or psilate, with spines, spines up to 1.7 μm long with tapered, truncated, and bifurcated or trifurcated apices; exine 0.7-1.3 μm thick.

Dimensions: greatest dimension 27.8-40.5 μm (nm = 5).

Botanical affinity: *Phaeoceros* (Anthocerotaceae) (Warny et al., 2012).

Source ecology: The ecology of Anthocerotaceae (hornworts), from the perspective of their spore record, is enigmatic, but greatly clarified by the recent study of Warny et al. (2012). The group are low lying herbs and epiphytes typically growing on stones and leaves, or wood along rivers in permanently wet places. They will not tolerate drying out, nor inundation by brackish water (Warny et al., 2012). Their common occurrence across SE Asia and West Africa in sediments preferentially deposited under periods of seasonal climate, but rarity during periods of

wet climate is enigmatic. For instance, in the Late Pleistocene Sankarang 16 deep sea core, from offshore Southwest Sulawesi, spores of Anthocerotaceae are common during MIS 2-4 age of sediments, but rare during MIS 1 and 5 (Morley and Morley, 2010). The enigma is explained by hornworts growing in open permanently wet seasonal swamps bordering slow-moving rivers in areas of seasonal climate, but being shaded out in areas characterised by peat swamp formation in areas of perhumid climate.

Stratigraphic distribution: Spores of the ancient group of bryophytes, the hornworts, have a very long geological record, being recorded widely from Cretaceous and older sediments under names such as *Foraminisporis* Krutzsch. In the Cenozoic they are particularly characteristic of sediments deposited under seasonal tropical climates, such as would have been the case in Myanmar in the late Eocene Yaw Formation in Kalewa (CMB), and also in the Pliocene (Plate VII, 22 in Morley, 2000). In equatorial Africa they display a greatly increased abundance from the late Miocene onward (Morley et al., 2003).

Genus: ***Crassoretitriletes*** Germeraad et al. 1968

Type species: *Crassoretitriletes vanraadshooveni* Germeraad et al. 1968

Crassoretitriletes vanraadshooveni Germeraad et al. 1968

Plate II, 35

Description: LM: trilete spore, radial, anisopolar; amb near circular; laesura indiscernible, covered by sculpture; exine thick, up to 2.0 μm; sculpture entirely coarsely reticulate with undulating muri, muri up to 1.0 μm wide, lumina up to 1 μm wide.

Dimensions: greatest dimension 39.0-46.0 μm (nm = 2).

Botanical affinity: *C. vanraadshooveni* is identical to spores of *Lygodium scandens* (synonym: *L. microphyllum*) in the family Schizaeaceae.

Source ecology: *L. scandens* is a climbing fern, often festooning trees on forest margins and on swamps.

Stratigraphic distribution: This distinctive spore type has a remarkable distribution, with the oldest records from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000) and the Eocene of Queensland (Foster, 1982). It is also recorded here from the late Eocene Yaw Formation in Kalewa (CMB). It displays a sudden appearance in the middle Miocene of equatorial Africa (Germeraad et al., 1968), where the parent plant continues to occur up to the

present. However, in the Neotropics, it displays an initial appearance in the late Miocene (~7 Ma) (Silva-Caminha et al., 2010; Jaramillo et al., 2017).

Genus: ***Dandotiaspora*** Sah, Kar et Singh 1971 emend.

Type species: *Dandotiaspora dilata* (Mathur) Sah, Kar et Singh 1971

Dandotiaspora sp.

Plate III, 31-33

Description: LM: trilete spore, radial, anisopolar; amb triangular-subcircular; laesurae 13.0-17.0 μm in length; Y-rays straight, enclosed with thickened and raised labra, extending ca. 3/4 radius, bifurcating at tips; exine 1.0-2.2 μm; sculpture psilate. SEM: sculpture psilate.

Dimensions: greatest dimension 50.3-56.5 μm (nm = 3).

Botanical affinity: possibly *Matonia* (Matoniaceae).

Source ecology: unknown.

Stratigraphic distribution: Records of *Dandotiaspora* include those from the late Paleocene Lakadong Sandstone in India (Chakraborty, 2004) the early to late Eocene in the CMB (Reimann and Aye Thaung, 1981), the early to middle Eocene Giral lignite mine in India (Khanolkar and Sharma, 2019), the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), the late Eocene Yaw Formation in Kalewa (CMB), and the Miocene Hmawgyi Chaung in Myanmar (Reimann and Aye Thaung, 1981). The parent plant of *Dandotiaspora* is thus an 'out-of-India' taxon.

Remarks: It has been used as a marker fossil for lower Eocene sediments in India (Singh et al., 1979) and in the middle Eocene in central Java (Lelono, 2000).

Genus: ***Pterisisporites*** Sung et Zheng 1976

Type species: *Pterisisporites undulatus* Sung et Zheng 1976

Pterisisporites sp.

Plate III, 34-36

Description: LM: trilete spore, radial, anisopolar; amb triangular-obtuse, with straight or slightly convex sides; laesurae margin discontinuous, laesurae 7.3-18.4 μm long; single cingulum 2.0-7.0 μm thick, narrower at the apices. SEM: sculpture coarsely verrucate along laesurae; exospore proximally verrucate.

Dimensions: greatest dimension 35.3-46.0 μm (nm = 5).

Botanical affinity: *Pteris* (Pteridaceae).

Source ecology: ferns in tropical to subtropical regions, preferring well drained settings in areas of perhumid climate (Holttum, 1953).

Stratigraphic distribution: *Pterisisporites* is widely represented in the low latitude Cenozoic sediments. They are poorly described in the literature, and this is unfortunate because most extant *Pteris* spp. can be differentiated on spore morphology alone, and thus many *Pterisisporites* spp. would be expected to have stratigraphic utility. The oldest records from SE Asia are from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), and subsequently from the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Saxosporis*** Krutzsch 1963

Type species: *Saxosporis duebenensis* Krutzsch 1963

Saxosporis sp.

Plate II, 37-38

Description: LM: trilete spore, radial, anisopolar; amb oblate; laesurae faint; exine thin; sculpture densely echinate with conical elements, echini up to 2.4 μm.

Dimensions: greatest dimension 20.5-30.4 μm (excluding echini, nm = 5).

Botanical affinity: Anthocerotaceae, especially species of *Anthoceros* (Warny et al., 2012).

Source ecology: the same as that of *Anthocerisporis* sp. See above.

Stratigraphic distribution: the late Eocene Yaw Formation in Kalewa (CMB).

Genus: ***Selaginella*** P.Beauv. 1805

Type species: *Selaginella spinosa* P.Beauv. 1805

Selaginella vaginata Spring type

Plate II, 40

Description: LM: trilete spore, radial, anisopolar; amb triangular-obtuse-slightly convex; laesurae distinct till the equator; sculpture coarsely reticulate with sparse echini; echini up to 2.6 μm.

Dimensions: greatest dimension 22.0 μm (excluding echini, nm = 1).

Botanical affinity: Spores with a reticulum and echinae or baculi were placed into the *S. vaginata* group by Morley (1976).

Source ecology: very wet environments.

Stratigraphic distribution: *Selaginella* spores are widely distributed in low latitude Cenozoic sediments but rarely given attention. Morley (1976) divided fossil *Selaginella* spores into four

groups based on the work of Knox (1949). The oldest record of *Selaginella* in SE Asia is from the middle Eocene Nanggulan Formation in central Java (Lelono, 2000), followed by the late Eocene Yaw Formation in Kalewa (CMB). *Selaginella* spores are scattered throughout the younger Cenozoic (Morley et al., 2021).

3.2. Late Eocene vegetation composition in the CMB

Based on the sporomorph types recorded during this study, the vegetation in the late Eocene CMB is thought to have included perhumid/moist, evergreen, seasonally dry forests; swamp forests along rivers, with herbaceous swamps and marshes, possibly associated with floodplain lakes; coastal vegetation including mangroves, and montane forests. The ecological attribution of pollen types which grew in these different vegetation types, and their absence-presence data are listed in Table S4. The main vegetation types based on the evaluation of the botanical affinities of the pollen and spore flora recovered from the CMB are detailed below.

3.2.1. Coastal vegetation including mangroves/back-mangroves

The presence of *Spinizonocolpites prominatus*, derived from the mangrove palm *Nypa* (Huang et al., 2020), together with the sonneratioid *Florschuetzia* cf. *trilobata*, and *Racemonocolpites hians* (*Onagrospermа*) are all indicative of mangroves and back-mangrove vegetation. The mangrove fern *Acrostichum* is likely to be a part of this community, occurring in disturbed or open areas within the intertidal zone, but also in freshwater swamps. Furthermore, the presence of several *Discoidites* spp., suggests the occurrence of diverse *Brownlowia* spp. or related taxa either growing behind true mangroves or bordering freshwater rivers. The mangroves would have grown on muddy deltas which form at river mouths. In interdeltaic areas, coastal forests are suggested by the presence of *Marginipollis*, derived from the coastal tree *Barringtonia*, and also *Casuarina*. *Proxapertites* spp. correlate with mangrove pollen (Huang et al., 2020), the parent plant of which may have also contributed to back-mangroves and coastal vegetation. Intertidal settings may also have been the source of scattered dinocysts.

3.2.2. Lowland swamp and terra firma *vegetation*

In the lowlands, palms and Sapotaceae are likely to have been two of the most important families. Palms are diverse in the palynoflora and occupy different ecological niches (Huang et al., 2020). *Dicolpopollis*, derived from *Calamus*, are climbing rattans, and most likely occurred in wet swamps, and perhaps analogous to the 'rattan brakes' of Stamp (1925). *Palmaepollenites kutchensis* may also be derived from swamp trees or shrubs but also could have been derived from plants growing in other vegetation. The parent plant of *Longapertites*, possibly ancestral to *Eugeissona*, may also have been representative of the perhumid forest. Sapotaceae are diverse with at least five pollen types (identification key provided in Appendix S2) dominantly from the subfamily Sapotoideae, encompassing the tribes Sideroxyleae, Mimusopeae, and Isonandreae, which suggests that this family has diversified in the early Eocene of SE Asia. This is likely related to the India-Asia collision and the warmer climate with higher temperature and humidity. Its abundance also suggests that Sapotaceae has been an important component of the lowlands in SE Asia since at least the early Eocene. Our records are dominated by pollen of the subfamily Sapotoideae, especially the tribes Isonandreae (e.g., *Palaquium* type) and Mimusopeae (e.g., *Mimusops* type). The pollen type *Meyeripollis naharkotensis* is thought to be derived from lowland swamps.

Additional perhumid forest indicators are *Anacolosidites*, the parent plant of which occurs in peat swamps in areas such as in Sumatra (Anderson, 1976), *Cupanieidites flaccidiformis*, possibly from *Mischocarpus*, which occurs today in evergreen forests and coastal swamps, and diverse *Lanagiopollis* species, the parent plants of which are *Alangium* sect. *Conostigma*, trees of evergreen tropical forests. Seasonal dry forests may be suggested by the common presence of *Margocolporites* spp. (suggesting Caesalpinoideae), *Berlinia* type and *Pinus* pollen (cf. Morley et al., 2019). Pollen of *Cupuliferoipollenites* spp., is common, and its abundance suggests a local source and that it may have been growing in relatively lowland settings, as was the case during the last glacial maximum in northern Thailand (Penny, 2001). *Shorea* woods from the late middle Eocene Pondaung Formation in the CMB (Licht et al., 2015) are comparable to *S. robusta*, a deciduous tree found across northern India, and its occurrence in red-beds would be consistent with this. However, the majority of *Shorea* spp. are evergreen rain forest trees and the scattered *Shorea* type pollen recorded here is more likely from an evergreen species.

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Among the pteridophytes and bryophytes, the hornworts within the Anthocerotaceae include *Anthocerisporis* and *Saxosporis*. These bryophytes probably grew in permanently wet swampy settings on stones, leaves and wood as discussed in above section 3.1, possibly within fern-dominated swamps surrounding ephemeral lakes. Spores referred to as *Verrucatosporites usmensis* (derived from the climbing fern *Stenochlaena palustris*) and *Crassoretitriletes vanraadshooveni* (derived from the climbing fern *Lygodium scandens*), may have been elements of swamps and riversides forming thickets, as is their current habit in the Sunda region (Morley and Morley, 2013). Sometimes monolete spores are very abundant, and these spore maxima may reflect fern dominated swamps, as occur in the Oligo–Miocene of the Sunda region (Morley and Morley, 2013). Other 'terrestrial wet' taxa include *Cyclosorus* type spores and these may also have been elements of freshwater swamps. Some ferns, such as *Pteris* and the Schizaeaceous ferns that produced *Cicatricosisporites* spp. may have been derived from well drained terrestrial areas. Algae, including colonial freshwater algae such as *Spirogyra*, *Mougeotea*, *Pediastrum* and *Botryococcus* occur in low numbers and were most likely derived from lakes associated with the river floodplain.

3.2.3. Uplands

Montane forests are indicated by the presence of several pollen taxa, specimens of which are invariably poorly preserved, which would be consistent with transportation from a distant source. They fall into three groups: a) conifer *Inaperturopollenites hiatus* (Taxodiaceae); b) probable evergreen angiosperms such as *Liquidambarpollenites stigmosus* (*Liquidambar* or *Altingia*), *Triatriopollenites engelhardioides* (Engelhardioideae), *Celtispollenites* (*Celtis*), *Ericipites* (Ericaceae), *Saurauia* type pollen and Magnoliaceae; c) temperate deciduous trees, including *Acerpollenites* (*Acer*), *Nyssapollenites* (*Nyssa*), *Alnipollenites verus* (*Alnus*), *Betulapollenites* (*Betula*), *Multiporopollenites maculosus* (*Juglans*), *Triatriopollenites myricoides* (*Myrica*), *Intratriporopollenites instructus* (*Tilia*) and *Polyporopollenites carpinoides* (*Carpinus*). The common representation of pollen from Fagaceae is thought to suggest a relatively lowland origin (see above). Two montane vegetation types growing in the hinterland of the pollen catchment are suggested and include montane evergreen forests, and montane deciduous forests. Deciduousness in a tropical montane setting suggests a seasonally cold climate, possibly in upper montane

forests as suggested by Morley and Morley (2018), and it is possible that the evergreen elements were growing at a lower altitudes, perhaps in lower montane forests.

3.3 Gondwanan versus *Laurasian components in the palynoflora of the late Eocene BT*

Our results of analysis on absence-presence data (Table S4) show that the number of Gondwanan elements, or taxa with Gondwanan ancestors (34), is similar to that from Laurasia (33) (Table 1). All taxa of montane forests (e.g., *Alnipollenites*) are Laurasian boreal components. Most of the taxa of perhumid/wet forests (e.g., *Palmaepollenites kutchensis*, *Cupanieidites*, *Lanagiopollis* and *Longapertites*) are from Gondwana, and several such as *Anacolosidites* and *Ilexpollenites*, may be viewed as 'cosmopolitan' as they occur at an early date in both hemispheres. Most taxa from seasonal dry forests (e.g., *Margocolporites*) are also from Gondwana, while *Pinuspollenites* is a Laurasian boreal element.

Table 1. Here.

4. Discussion

4.1. Eocene vegetation in the CMB and contrast with present-day vegetation

In the late middle to late Eocene, the CMB was located near-equatorially (Westerweel et al., 2019) and formed a quasi-enclosed estuary open to the proto-Bengal Bay while the IBR was subject to emergence and initial uplift (Licht et al., 2019). The abundant precipitation was likely due to monsoonal activity (perceived by Licht et al. (2014b) based on the markers of highly seasonal precipitations) and favoured the development of seasonal evergreen forests. At the time, the CMB and its adjacent areas included three depositional settings, ranging from lower deltaic plain (LDP), upper deltaic plain (UDP) to floodplains beyond the coastal plain (Fig. 3). Coastal forests (in interdeltaic areas) and mangroves/back-mangroves occupied the LDP during this time interval. However, in the UDP, riparian forests along rivers and open-forested seasonal wetlands inland in the late middle Eocene Pondaung Formation (Licht et al., 2015) (Fig. 3A), while extensive swamp and gallery forests, and evergreen forests occurred along rivers and inland

respectively in the late Eocene (Fig. 3B). In the late middle Eocene the upstream area was drier, with *Schima*-dominated forests in mid-altitude (>1000 m) occurring above the dry dipterocarp forests on and along the WPA (Licht et al., 2015). The *Schima*-dominated forests and dipterocarp forests could be lower montane evergreen forests, and deciduous forests in lowlands respectively. Instead, in the late Eocene the area was dominated by seasonal dry, deciduous, evergreen piedmont and montane forests (Fig. 3). The vegetation contrast between the late middle Eocene and the late Eocene could be due to wetter climate in the late Eocene, or taphonomic biases. More specifically, in the late Eocene, palms such as *Spinizonocolpites* (*Nypa*), *Dicolpopollis* spp. (*Calamus* type), and *Longapertites* spp. (probable *Eugeissona*) were common as back-mangrove, and in swamps and evergreen forests respectively (Huang et al., 2010). At the time, Sapotaceae were diverse including the dominant *Mimusops* and *Palaquium* types. The two genera are also dominant with five and four species respectively within Sapotaceae in the present-day Myanmar (Kress et al., 2003). Palms together with the abundance of Sapotaceae pollen types are indicative for a wet climate, which could be attributed to the near-equatorial position of the BT in the late Eocene.

At present, the CMB is situated at a different latitude (ca. 16-27° N) from the Eocene (ca. 0-10° N; Westerweel et al., 2020) and principally hosts moist deciduous forests (Ashton, 2014). We suggest the difference of vegetation between in the late Eocene with present-day, occurred due to the northward drift of the BT, the two-stages uplift of the IBR together with the uplift of the Himalayas creating a rain shadow in the CMB, and later Neogene global cooling and drying.

Fig. 3. Here.

4.2. The BT as a crossroads of floristic exchange in the Cenozoic

4.2.1. A Gondwanan origin for the BT?

The BT was thought by some to be a part of Laurasia (e.g., Mitchell, 1993; Sevastjanova et al., 2016) while others propose it was part of Gondwana (e.g., Yao et al., 2017). Fossils from the Burmese amber suggest that the BT has a Gondwanan origin (e.g., Zhang et al., 2018; Poinar, 2018; Liu et al., 2020). Poinar (2018) illustrated some remarkable angiosperm flowers with

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Gondwanan affinities from amber obtained from the mines of the Hukawng Valley. The beautiful flowers include *Palaeoanthella huangii* (Monimiaceae), *Endobeuthos paleosum* (Dilleniaceae) and *Tropidogyne pentaptera* (Cunionaceae). Samples from the same locality were also analysed for pollen by Davies (2001) (unpublished document in Cruikshank and Ko, 2003) and these have yielded Gondwanan *Araucaria* pollen, but also common *Sequoia*, which is of Laurasian origin. However, the identification of *Sequoia* should be taken with caution, as some Cupressaceae genera from the southern hemisphere can also produce *Sequoia*-like pollen, and fossils in so many inclusions in Cretaceous Burmese ambers have a Gondwanan origin (e.g., Zhang et al., 2018; Poinar, 2018). Prior to any collision with either India or Asia, the BT was part of an isolated island arc and bore several Gondwanan elements, but also possible Laurasian taxa that should be further evaluated. The abundant Gondwanan elements (e.g., *Lanagiopollis* spp.; Table 1) and 'out-of-India' taxa (Fig. 4) in the late Eocene Kalewa palynoflora together with the early Eocene occurrences of *Palmaepollenites kutchensis* and *Barringtonia* type pollen (Reimann and Aye Thaung, 1981) from the CMB could support growing evidence about the Gondwanan origin of the BT.

4.2.2. The late Eocene north BT-Asia collision is supported by a montane connection between the BT and Asia

Prior to collision with either India or Asia, the BT was part of an isolated island arc lying between southern Gondwana and Asia. The timing of the collision between the BT with the Asian margin is of great importance to understand the role of the BT as part of the Trans-Tethyan Arc (Westerweel et al., 2019). Klaus et al. (2016) observed that dispersal events from mainland Asia to India increased at 41 Ma. Thus we propose a continuous dispersal corridor for the India-Asia biotic interchange not earlier than 41 Ma. The BT may thus have played an important role in such a corridor.

In this study, we found numerous Laurasian plant taxa, indicated by the presence of scattered, but diverse Laurasian montane pollen. This suggests a montane connection between Myanmar and Asia to the north before the uplift of the Himalayan Range along the northern edge of the Indian Plate. Then the montane connection between the BT and India was established after the late Eocene, when these taxa dispersed to India. These taxa (i.e., 'out-of-Asia' taxa) include

Alnipollenites verus (*Alnus*), *Intratriporopollenites instructus* (*Tilia*), *Liquidambarpollenites stigmouis* (*Liquidambar* or *Altingia*) and *Polyporopollenites carpinoides* (*Carpinus*) (Fig. 4) and the Normapolles pollen *Trimagnaporites mixis*. The palynofloras of the Paleocene to middle Eocene Paunggyi, Laungshe, Tilin, Tabyin and Pondaung formations in the CMB will need to be analysed to determine when the montane connection between the BT and mainland Asia was first established (Fig. 5A).

4.2.3. Lowland connection between the Indian Plate and BT in the late Eocene

Many taxa, such as *Palmaepollenites kutchensis* (a member of the palm subfamily Areceae), *Lanagiopollis* spp. (*Alangium* sect. *Conostigma*), *Florschuetzia* cf. *trilobata*, (extinct sonneratioid taxon), *Cupanieidites flaccidiformis* (*Mischocarpus* sp.) and *Retistephanocolpites williamsi* var. (*Ctenolophom parvifolius*) are derived from taxa that were growing in India before the collision of India with Asia, and are thus 'out-of-India' elements, discussed in detail by Morley (2018a) (Fig. 4). In this study we identify several additional taxa that could reflect 'out-of-India' elements, and these include *Racemonocolpites hians* (*Oncosperma*), *Margocolporites* spp. (Caesalpinoideae) and *Echimonoporopollis grandiporus* (parent plant unknown). However, they could have occurred in the BT at the same time as or before their appearance in the Indian Plate via the Kohistan Ladakh Arc. More studies from prior to the late Eocene will be needed to answer this question. These taxa are elements from mangroves, perhumid or seasonally dry lowland forests and swamp trees (details are provided in Table S4). Considering that these elements are all from lowland vegetation, and similar to those of the Eocene Indian floras, their presence in the late Eocene CMB provides further evidence for a connection of the BT with Indian Plate at that time.

We also found that some of the pollen taxa from the late Eocene Kalewa palynoflora have also been recorded in India only in younger sediments (i.e., 'out-of-Asia' taxa in Fig. 4; Morley, 2018a), as plant dispersals from mainland Asia to Myanmar may have occurred independently of the India-Asia collision. These are essentially lowland alluvial swamp elements. They include *Pandaniidites* spp. (*Pandanus*), *Discoidites* spp. (Brownlowoideae), *Corsinipollenites* spp. (*Jussieua*), *Ranunculacidites operculatus* (*Alchornea*), *Ilexpollenites* spp. (*Ilex*) and *Retibrevitricolpites* cf. *triangulatus* (parent plant unknown). This suggests that lowland alluvial swamp habitats that bore these taxa had already been established on the BT by the late Eocene,

but a dispersal path for these taxa to India was not in place until the early Miocene. It is suggested that the dispersal corridor was created by the formation of the Siwaliks and their precursors (i.e., the fluvial deposits that preceded the Siwaliks), beginning approximately in the early Miocene (Johnson et al., 1985; White et al., 2002), formed as a result of the uplift of the Himalayan Range (e.g., Harrison et al., 1992; Valdiya, 2002; Ding et al., 2017) (Fig. 5B).

In summary, we found that: 1) Taxa of mangrove, perhumid and seasonally dry lowland forests might have immigrated into Myanmar from India prior to the late Eocene. However, these taxa could also have occurred in the BT, at the same time as or before their appearance on the Indian Plate, dispersing via the Kohistan Ladakh Arc. No matter in which condition, in the late Eocene a lowland connection existed between the Indian Plate with BT; 2) Lowland alluvial swamp elements dispersed from Myanmar to India until the early Miocene, possibly following the uplift and erosion of the Himalayan Range, and the formation of extensive floodplains in northern India which probably bore widespread alluvial swamps.

Fig. 4. Here.

4.2.4. Floristic comparison between SE Asia and Myanmar in the middle to late Eocene

Sporomorph assemblages from the middle to late Eocene Nanggulan Formation (Lelono, 2000), and offshore South Sulawesi (Morley, 2014), show many similarities with the assemblage from the Yaw Formation in the Kalewa section. The main differences are that there are far fewer montane elements in assemblages from Java and South Sulawesi. There are fewer seasonal climate elements and assemblages are more diverse after the above-mentioned middle Eocene plant dispersals. The rarity of upland elements is due to the low relief of the river catchments feeding sediments to the southern margin of Sundaland (Witts et al., 2012). Montane elements of Laurasian affinity increase in representation northward and are a common component of assemblages derived from the Natuna Arch, Con Con Swell and Indochinese uplands (Morley and Morley, 2018). The reduced representation of seasonal climate elements, and increased assemblage diversity relates to the more equatorward position of the southern Sundanian margin at this time (Morley, 2000).

Fig. 5. Here.

5. Conclusions

In this study, we reported at least 141 sporomorph types from the late Eocene CMB, 56 of which were described in terms of morphology and discussed in terms of their botanical affinity, source ecology, and biogeography. Two new form-species (*Discoidites angulosus* Huang, Morley et Hoorn sp. nov. and *Anacolosidites reticulatus* Morley, Huang et Hoorn sp. nov.) were described according to their different characters compared to other species; five Sapotaceae pollen types belonging to subfamilies Sapotoideae and Chrysophylloideae were described for the first time.

The late Eocene Kalewa palynoflora principally comprised elements of evergreen and gallery forests (including perhumid taxa, such as *Alangium*, *Ctenolophon*, and *Mischocarpus* and various Sapotaceae) and swamps in the upper deltaic plain, and seasonally dry forests in *terra firma* areas beyond, possibly with *Pinus*, Caesalpinioideae and Fagaceae. The lower deltaic plain bore deltas with mangroves, which includes *Nypa* and other elements, and coastal forests in interdeltaic areas may have included *Pandanus* and *Casuarina*. Montane forests were present on mountains in the hinterland and are thought to have included evergreen montane forests with Engelhardioideae and Magnoliaceae, and deciduous forests with *Alnus*, *Carpinus*, *Juglans* and *Tilia* suggesting a seasonally cold climate at higher altitudes. The habitat of the late Eocene flora was probably created by the plate collision (e.g., the middle Eocene India-Asia collision and late Eocene northern BT-Asia collision) and monsoonal climate. Its difference from the present-day moist deciduous forests might be due to the northward drift of the BT, the two-stages uplift of the IBR together with the uplift of the Himalayas creating a rain shadow in the CMB, and later Neogene global cooling and drying.

The palynofloras support tectonic reconstructions that require a late Eocene montane connection between the BT and Asian uplands to the north before the uplift of the Himalayan Range along the northern edge of the Indian Plate, and are consistent with a dramatic migration of Gondwanan lowland elements from India as it collided with Asia during the Eocene as previously summarised by Morley (2000, 2018a). However, there was also a previously unrecognised dispersal of lowland swamp elements into India from the beginning of the Miocene. The

occurrence of abundant Gondwanan and 'out-of-India' elements in the late Eocene provide growing evidence about a Gondwanan origin for the BT, while a montane connection between the BT and Asia supports the late Eocene northern BT-Asia collision. Considering the plant dispersals between the India Plate, BT, mainland and SE Asia discussed above, we proposed that the BT played a major role as a corridor and crossroads between Laurasia and Gondwana for plant dispersals, from no later than the late Eocene to early Miocene. Studies on the Paleocene to middle Eocene formations in the CMB should clarify the earlier phases of plant migration prior to and during the initial collision of the India Plate with the BT, and also of India Plate and the BT with Asia.

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Appendix A. Supplementary data

Supplementary material 1

Supplementary material 2

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Captions of figures, plates, and tables

Fig. 1. The present-day vegetation of Southeast Asia and India, and the localities of the Central Myanmar Basin and the Kalewa section. The map shows vegetational types that can easily be differentiated palynologically, modified after Morley (2018a), who simplified the map after Ashton (2014).

Fig. 2. Topographic map showing the main localities of Myanmar, Central Myanmar Basin, Indo-Burman and Sino-Burman ranges, Wuntho-Popa Arc (WPA), Chindwin (Cb), Minbu (Mb), Shwebo (Sb), Pegu (Pb) and Hukawng (Hb) sub-basins, and Kalewa section (1) and Minbu section (2). Ranges of the CMB, Cb, Mb, Sb and Pb, and Hb are from Licht et al. (2014b, 2019) and Morley et al. (2020) respectively. Base map was modified from Hel-hama (2013).

Fig. 3. Schematic landscape models from the late middle Eocene Pondaung Formation supported by fossil woods (A, Licht et al., 2015) to the late Eocene Yaw Formation with evidence from palynomorphs (B, this study) in the Central Myanmar Basin. Yellow stars indicate the studied sections.

Fig. 4. Stratigraphic distributions of ‘out-of-India’ and ‘out-of-Asia’ elements occurring in the Central Myanmar Basin, including the taxa in Morley (2018a). Ranges of Myanmar taxa were also based on Reimann and Aye Thaung (1981) and Soe Moe Lwin et al. (2017). Black dashed line indicates the time of India-Asia land connection at 41 Ma (Klaus et al., 2016). ‘Out-of-India’ taxa existed in India before the collision with Asia, while ‘out-of-Asia’ taxa have a longer range in Myanmar (and elsewhere in Asia) than in India. Note that for the ‘out-of-India’ taxa, the

shorter ranges in Myanmar do not necessarily indicate the dispersals from India. Their occurrences in Myanmar could also be at the same time as or before their appearance in the Indian Plate via the Kohistan Ladakh Arc. Geological time scale was modified after Cohen et al. (2020).

Fig. 5. Two important plant dispersal events identified by this study. A. Montane taxa dispersed from mainland Asia to the Wuntho-Popa Arc but not to Peninsula India in the late Eocene (route 1); B. Lowland alluvial swamp taxa dispersed to Peninsular India due to the formation of the Siwaliks and their precursors until the early Miocene as a result of the uplift of the Himalayan Range (route 2). The ranges of plate blocks and palaeo-coastlines were drawn after Westerweel et al. (2020) and Morley (2018a). The lowland in the Tibetan Plateau was based on Su et al. (2020). Abbreviations: GI = Greater India, not reconstructed; BT = Burma Terrane; IBR = Indo-Burman Ranges; WPA = Wuntho-Popa Arc.

Plate I. Light microscopy (LM) micrographs of selected pollen grains from the late Eocene Kalewa section, Central Myanmar Basin. 1. *Echimonoporopollis grandiporus*; 2. *Pandaniidites* sp.; 3-4. *Racemonocolpites hians*; 5. *Kestonioidites* ?*punctulosus*; 6. *Pinuspollenites* sp.; 7. cf. *Shorea* type; 8. *Discoidites angulosus* sp. nov.; 9. *Discoidites* cf. *borneensis*; 10. *Discoidites* cf. *pilosus*; 11. *Discoidites* sp.; 12. *Marginipollis* sp.; 13-15. *Perfotricolpites* cf. *digitatus*; 16. *Psilatricolpites* sp.; 17. *Retitricolpites* sp.; 18. indeterminate type; 19-20. *Casuarinites* sp.; 21. *Corsinipollenites* sp.; 22. *Trimegnaporites mixis*; 23. *Proteacidites* sp.; 24. *Triatriopollenites engelhardtioides*; 25. *Avicennia* type; 26. *Berlinia* type; 27-28. cf. *Berlinia* type; 29-30. *Campnosperma* type; 31-32. *Cupanieidites flaccidiformis*; 33-34. *Cupanieidites* sp.; 35-38. *Cupuliferoipollenites* sp.; 39. Ericaceae type; 40. *Florschuetzia* cf. *trilobata*; 41. *Gothanipollis* sp.; 42. *Ilexpollenites* sp.; 43. *Lanagiopollis nanggulanensis*; 44. *Lanagiopollis emarginatus*; 45. *Retitricolporites* sp.; 46. *Iugopollis* sp. 47. *Malvacipollis* ?*diversus*; 48-51. *Margocolporites* spp.; 52-54. *Meyeripollis naharkotensis*.

Plate II. Light microscopy (LM) micrographs of selected palynomorphs from the late Eocene Kalewa section, Central Myanmar Basin. Pollen (1-26): 1-3. *Cupanieidites* sp.; 4-5. *Retibrevitricolpites* cf. *triangulatus*; 6-7. cf. *Scollardia* sp.; 8. *Striasyncolpites* sp.; 9-15.

indeterminate types; 16. *Tetracolpites* sp.; 17. *Lanagiopollis nanggulanensis*; 18. *Alnipollenites verus*; 19. *Myriophyllum* type; 20. *Anacolosidites luteoides*; 21. *Anacolosidites reticulatus* sp. nov.; 22. *Anacolosidites trilobatus*; 23. *Heterocolpites* sp.; 24. *Retistephanocolpites williamsi* var.; 25. *Heterocolpites combretoides*; 26. *Ephedripites* sp.; spores (27-40): 27-28. *Cicatricososporites eocenicus*; 29-30. *Gemmatosporis gemmatoides*; 31. *Cyclosorus* type; 32-33. *Anthocerisporis* sp.; 34. *Acrostichum* type; 35. *Crassoretitriletes vanraadshooveni*; 36. *Cicatricosisporites* sp.; 37-38. *Saxosporis* sp.; 39. *Schizaeoisporites digitatoides*; 40. *Selaginella* type; algae (41-49): 41-42. *Concentricystes circulus*; 43. indeterminate dinocyst; 44-45. *Mougeotia* type; 46. *Pediastrum* cf. *palaeogenites*; 47. *Spirogyra* sp.; 48-49. indeterminate fungal spores; 50. foraminiferal lining; 51. peltate trichome from leaf fragment, probably belonging to same taxon of *Triatriopollenites engelhardtioides* or *Multiporopollenites maculosus* within the family Juglandaceae.

Plate III. Light microscopy (LM) and scanning electron microscopy (SEM) micrographs of selected sporomorph types from the late Eocene Kalewa section, Central Myanmar Basin. Each three micrographs are from the same pollen grain or spore with the first one under LM and the other two under SEM. 1-3. *Cupanieidites* sp.; 4-6. *Discoidites* cf. *pilosus*; 7-9. *Striatopollis catatumbus*; 10-12, 16-18. *Lanagiopollis emarginatus*; 13-15. *Ranunculacidites operculatus*; 19-21. *Margocolporites* sp.; 22-24. *Anacolosidites reticulatus* sp. nov.; 25-27. *Verrucatosporites usmensis*; 28-30. *Cicatricosisporites* sp.; 31-33. *Dandotiaspora* sp.; 34-36. *Pterisisporites* sp. Scale bars: whole grain = 11 μm, close-up = 1 μm.

Plate IV. Light microscopy (LM) micrographs of selected *Sapotaceoidaepollenites* pollen grains from the early Eocene–early Oligocene Central Myanmar Basin. 1, 5-6. type 2; 2-4, 13. type 1; 7-10, 12, 14. type 3; 11, 15-18. type 4.

Plate V. Light microscopy (LM) micrographs of selected *Sapotaceoidaepollenites* pollen grains from the late Eocene Kalewa section, Central Myanmar Basin. 1-5. type 1; 6-10. type 3; 11-13. type 4; 14-16. type 5.

Plate VI. Scanning electron microscopy (SEM) micrographs of selected *Sapotaceoidaepollenites* pollen grains from the early Eocene–early Oligocene Central Myanmar Basin (except for 3-4). 1-

2, 5-6, 9-10, 13-14. type 1; 3-4, 11-12. type 2, and 3-4 is a late Holocene pollen grain from the herbarium of the University of the West Indies, Jamaica; 7-8, 15-16. type 4. Scale bars: whole grain = 5 μm, close-up = 1 μm.

Plate VII. Scanning electron microscopy (SEM) micrographs of selected *Sapotaceoidaepollenites* pollen grains from the late Eocene Kalewa section, Central Myanmar Basin. 1-8, 15-16. type 4; 9-14. type 3. Scale bars: whole grain = 5 μm, close-up = 1 μm.

Table 1. Gondwanan *versus* Laurasian components from the late Eocene Kalewa section, Central Myanmar Basin.

Gondwanan component (34)	**Laurasian component (33)**
1. West: *Berlinia* type, *Heterocolpites* spp., *Lagerstroemia* type, Leguminosae type, *Margocolpites* spp., cf. *Planchonia* type, *Heterocolpites combretoides*, *Myrtaceidites* spp., *Sapotaceoidaepollenites* spp., *Corsinipollenites* spp., *Palaquium* type, *Restioniidites* ?*punctulosus*, *Striatopollis catatumbus*, *Pandaniidites* spp., *Avicennia* type, *Florschuetzia* cf. *trilobata*;	1. Boreal: *Acerpollenites* spp., *Alnipollenites verus*, *Betulapollenites* spp., *Celtispollenits* spp. *Ericipites* spp., *Inaperturopollenites minutus*, *Inaperturopollenites instructus*, *Liquidambarpollenites stigmosus*, Magnoliaceae, *Multiporopollenites maculosus*, *Nyssapollenites* spp., *Pinuspollenites* spp., *Polyporopollenites carpinoides*, *Triatriopollenites engelhardtioide*, *Triatriopollenites myricoides*;
2. Indian: *Lanagiopollis* spp., *Retistephanocolpites williamsi* var. Lecythidaceae, *Marginipollis* spp.;	2. Boreotropical: cf. *Saurauia* type, Fagaceae, *Calophyllumpollenites* spp., *Cricotriporites* spp., *Cupuliferoipollenites* spp., Euphorbiaceae type, Rubiaceae type, *Campnosperma* type, cf. *Amanoa* type, cf. *Gluta* type, *Ranunculacidites operculatus*;
3. African: Apocynaceae type, *Tugopollis* sp. (Madagascar), Meliaceae type;	
4. Australasia: *Casuariidites cainozoicus*;	
5. Others: *Cupanieidites flaccidiformis* (Africa?), *Longapertites* spp., *Mimosa* type, cf. *Shorea* type, *Cupanieidites* spp., *Proteacidites* spp., Sapindaceae type (Africa?), *Striasyncolpites* spp. (Africa?), *Liliacidites* spp., *Perfotricolpites* cf. *digitatus* (east?).	3. Others: cf. *Canarium* type (boreotropical?), cf. *Santiria* type (boreotropical?), *Gothanipollis* spp., Loranthaceae type, *Urtica* type, *Cepalomappa malloticarpa*, *Myriophyllum* type (North America?).

Journal Pre-proof

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Highlights

- New palynological data from the late Eocene Central Myanmar Basin (CMB).
- Seasonal evergreen forests ruled under seasonal wet climate in the late Eocene CMB.
- Palynological data support a late Eocene north Burma Terrane (BT)-Asia collision.
- Plate collision and tropical climate created the late Eocene flora in the CMB.
- The BT was a crossroads for plant dispersals between Gondwana with Laurasia.

Journal Pre-proof

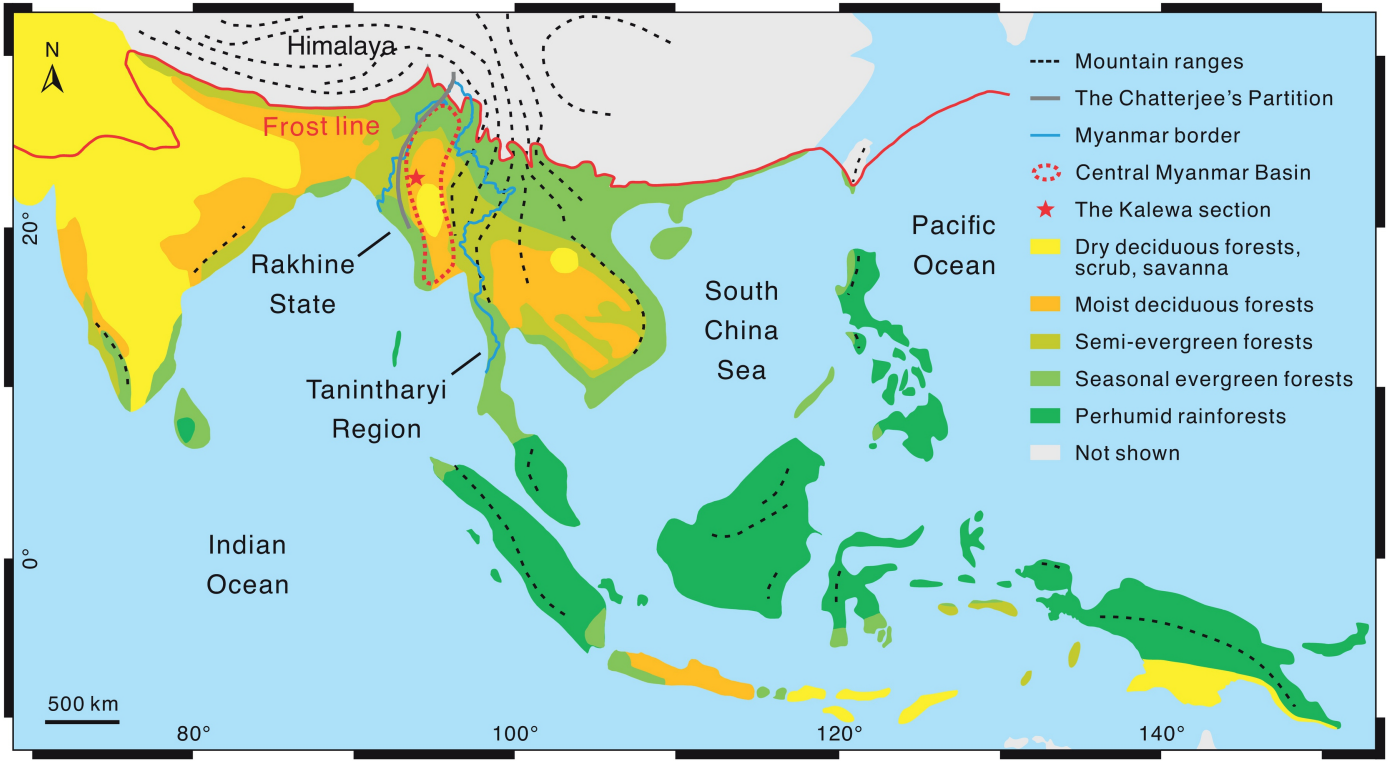

N
Himalaya
Frost line
Rakhine State
Tanintharyi Region
Indian Ocean
South China Sea
Pacific Ocean
20°
0°
80°
100°
120°
140°
500 km
Mountain ranges
The Chatterjee's Partition
Myanmar border
Central Myanmar Basin
The Kalewa section
Dry deciduous forests, scrub, savanna
Moist deciduous forests
Semi-evergreen forests
Seasonal evergreen forests
Perhumid rainforests
Not shown

Figure 1

N
95°
100°
Himalaya
East Tibetan Plateau
Hb
Yunnan highlands
25°
Cb
1
Sb
WPA
Indo-Burman Ranges
Sino-Burman Ranges
2
Mb
20°
Pb
Bay of Bengal
Central Myanmar Basin
15°
Andaman Sea
Thailand Bay
10°
200 km

Figure 2

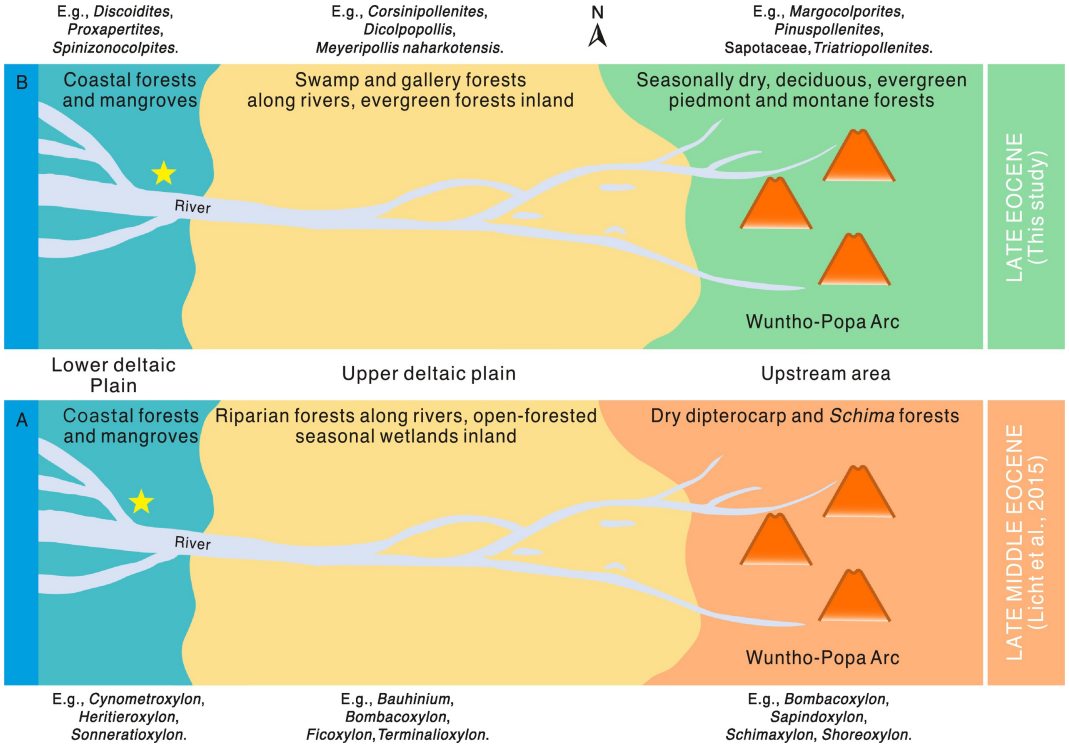
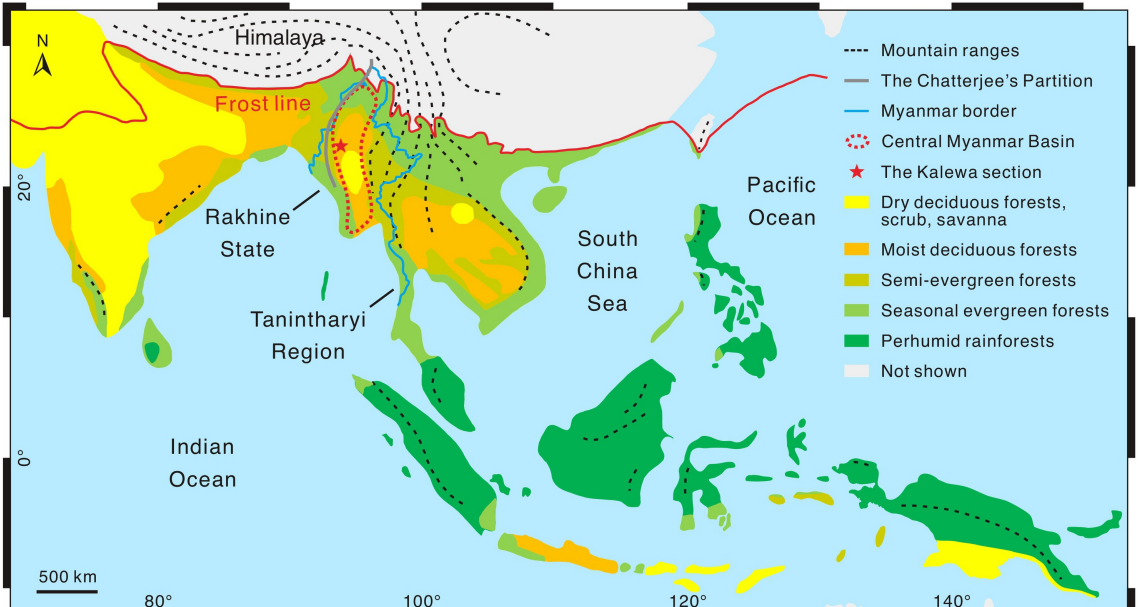

E.g., *Discoidites*, *Proxapertites*, *Spinizonocolpites*.
E.g., *Corsinipollenites*, *Dicolpopollis*, *Meyeripollis naharkotensis*.
N
E.g., *Margocolporites*, *Pinuspollenites*, Sapotaceae, *Triatriopollenites*.
B
Coastal forests and mangroves
Swamp and gallery forests along rivers, evergreen forests inland
Seasonally dry, deciduous, evergreen piedmont and montane forests
River
Wuntho-Popa Arc
LATE EOCENE (This study)
Lower deltaic Plain
Upper deltaic plain
Upstream area
A
Coastal forests and mangroves
Riparian forests along rivers, open-forested seasonal wetlands inland
Dry dipterocarp and *Schima* forests
River
Wuntho-Popa Arc
LATE MIDDLE EOCENE (Licht et al., 2015)
E.g., *Cynometroxylon*, *Heritieroxylon*, *Sonneratioxylon*.
E.g., *Bauhinium*, *Bombacoxylon*, *Ficoxylon*, *Terminalioxylon*.
E.g., *Bombacoxylon*, *Sapindoxylon*, *Schimaxylon*, *Shoreoxylon*.

Figure 3


N
Himalaya
Frost line
Rakhine State
Tanintharyi Region
Indian Ocean
South China Sea
Pacific Ocean
20°
0°
500 km
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140°
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Myanmar border
Central Myanmar Basin
The Kalewa section
Dry deciduous forests, scrub, savanna
Moist deciduous forests
Semi-evergreen forests
Seasonal evergreen forests
Perhumid rainforests
Not shown

Figure 4

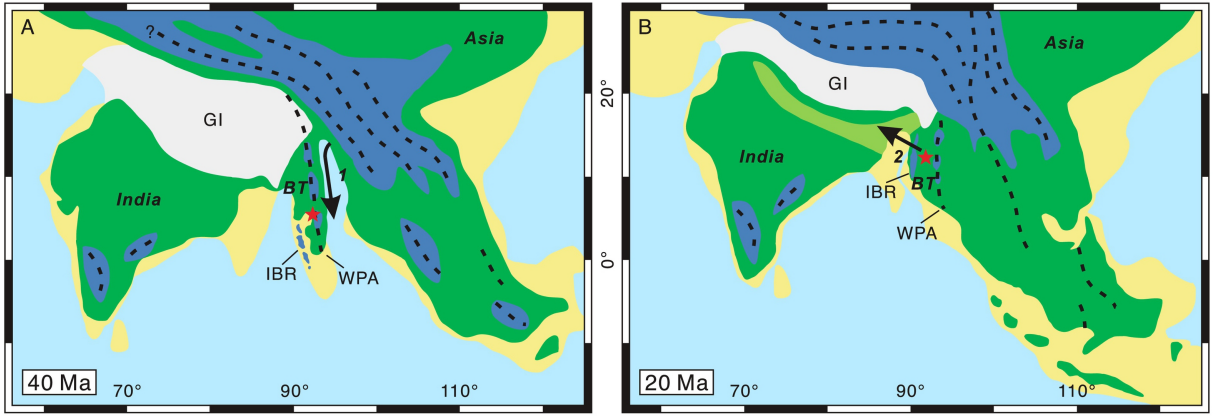
A
?
Asia
GI
India
BT
1
IBR
WPA
40 Ma
70°
90°
110°
20°
0°
B
Asia
GI
India
2
BT
IBR
WPA
20 Ma
70°
90°
110°
The Kalewa section
Upland
Lowland
Alluvial swamp in Siwaliks and their precursors
Plates
Ocean
Mountain range

Figure 5