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

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Late Eocene vegetation and environmental dynamics under monsoonal climate in central Myanmar


In preparation
ABSTRACT

After the India-Asia collision, the Burma Terrane (BT) acted as a crossroads of plant dispersals between India, mainland Asia, and Southeast Asia. The evidence for this can be found in the palynofloral composition of the late Eocene fluvio-deltaic Kalewa section in the Central Myanmar Basin (CMB). However, the relationship between vegetation, environment and climate changes remains unresolved and could provide important clues on late Eocene climatic conditions. In this study, we quantitatively assessed the past vegetation, climate and environment through the late Eocene Kalewa section in the CMB, with pollen diagrams, bioclimatic analysis and sequence stratigraphy evaluation. We also calculated the palynological diversity and drew inferences with rarefaction analysis by comparing with other four other contemporary tropical palynofloras in the region and beyond (northeastern India, Indonesia, South China and Colombia). Our data suggest that in the Eocene lowland evergreen forests and swamps dominated in the CMB. Additionally, the Kalewa palynological record suggests that paleoenvironmental change is controlled by global sea level change, which drove two transgressive-regressive depositional sequences. Besides, bioclimatic analysis suggests that in the late Eocene, the CMB had a warmer and similarly wet climate with a weaker monsoonal activity than that at present. The dominant lowland evergreen forests, and warm and wet climatic conditions in the CMB could be explained by its near-equatorial and open-to-ocean position at that time, where it was under the strong influence of monsoonal activities and received abundant moisture. Rarefaction analysis shows that in the late Eocene Indonesia has the most diverse palynoflora, which could be due to its near-equatorial location and perhumid climate. Myanmar has the second highest diversity of species, which could be explained by its near-equatorial position, and its role as a crossroads for plant dispersals. Therefore, our study confirms the presence of monsoonal climate in the late Eocene Myanmar, which together with geological changes greatly impacted the vegetation pattern and depositional environments in this region.
3.1 | INTRODUCTION

Monsoons are defined by annual surface wind inversion and contrasting wet summers and dry winters (Wang and Ding, 2008). Today Asian monsoons are the most intricate monsoon system around the globe (Spicer, 2017) and mainly formed by the South Asia Monsoon (SAM) and East Asia Monsoon (EAM) (Molnar et al., 2010). The SAM affects India, southern Tibet, Myanmar and Thailand, while the EAM influences most of Japan and China (e.g., Molnar et al., 2010). These monsoons are located at low latitudes and driven by seasonal migrations of the Intertropical Convergence Zone (ITCZ). Based on field observational evidence, the initiation of the SAM and EAM have been suggested to as early as the early Miocene (Guo et al., 2002; Morley, 2012) or the late Oligocene (Sun and Wang, 2005). More recently, middle to late Eocene monsoons have been suggested based on quantitative reconstructions (e.g., Herman et al., 2017; Jacques et al., 2011b; Licht et al., 2014b; Su et al., 2020). These Eocene monsoons would also have been driven by seasonal migrations of the ITCZ (Spicer, 2017), and their existence has been corroborated by modeling results (e.g., Huber and Goldner, 2012). However, observational and modeling results should be taken cautiously as the criteria for the presence of a monsoonal circulation may differ (Tardif et al., 2020).

Paleobotany has been an effective tool when quantifying monsoonal intensity. Climate-Leaf Analysis Multivariate Program (CLAMP, http://clamp.ibcas.ac.cn), using fossil leaf morphological traits, is the most common method, and has been applied to reconstruct monsoonal signals from the Asian Paleogene, such as in the middle Eocene (c. 47 Ma) central Tibet (Su et al., 2020), India (Bhatia et al., 2021; Shukla et al., 2014), the middle Eocene–early Oligocene of South China (Herman et al., 2017; Spicer et al., 2016) and even early to middle Eocene in the Antarctic (Jacques et al., 2011b). In the Minbu sub-basin, southern Central Myanmar Basin (CMB), a monsoonal climate, which may be favored by Eocene greenhouse conditions, was suggested for the late middle Eocene Pondaung Formation, based on low oxygen isotope values with strong seasonality in gastropod shells and mammal teeth (Licht et al., 2014b). Coexistence and wood anatomical approaches that were applied on fossil woods from the same formation also corroborates the existence of this monsoonal climate (Licht et al., 2015).

In the Chindwin sub-basin, northern CMB, the presence of a long and well-exposed Cenozoic geologic record in Kalewa, has enabled the Myanmar Paleoclimate and
Geodynamics Research group (MyaPGR) to constrain the sediment ages (U-Pb zircon dating, Licht et al., 2019; magnetostratigraphy, U-Pb apatite dating, and apatite fission track dating, Westerweel et al., 2020; palynostratigraphy, Huang et al., 2020). The late Eocene paleoenvironments at the Kalewa site have been well documented from sedimentological (Licht et al., 2019; Westerweel et al., 2020), and palynological studies (Huang et al., 2020; Huang et al., in revision). The palynological composition of the late Eocene of Kalewa suggests a predominance of palms and mangrove elements. Moreover, the Burma Terrane (BT) acted as a crossroads of plant dispersals between India, mainland Asia, and Southeast (SE) Asia after the India-Asia collision (Huang et al., in revision). However, a comprehensive evaluation of the sporomorph composition is needed to quantitatively investigate the early history of vegetation, depositional environments and monsoonal climates.

In this study, we present the palynological data with comprehensive sporomorph diagrams to reconstruct vegetation changes throughout the late Eocene Kalewa section in the CMB (Fig. 3.1A-B). We also evaluate the data in a sequence biostratigraphic framework to unravel the dynamics of the depositional environments through the section. Additionally, we apply bioclimatic analysis to quantitatively reconstruct the climate based on the main climatic variables. Furthermore, we applied the rarefaction method to analyze the sporomorph diversity in the late Eocene Yaw Formation, and compared this with four other contemporary tropical sporomorph assemblages. This provided us with an estimate on how beneficial the combined climate and geological factors were in stimulating plant diversity. These analyses together will enable us to understand the relationship between vegetation, depositional environment, plant diversity with climate and geological driving factors in the late Eocene CMB.

3.2 | REGIONAL SETTING

3.2.1 | The present-day climate in Myanmar

The India-Asia collision produced the highest mountains on Earth, including the Tibetan Plateau, the Himalayas and the Sino-Burman Ranges (SBR) (Boos and Kuang, 2010; Prell and Kutzbach, 1992; Xie et al., 2006), which together form a thermal and orographic
barrier. This led to an enhanced North Pacific subtropical anticyclone and southwesterly monsoon streams transporting moisture to Asia (Lee et al., 2015). Myanmar is not only

**Fig. 3.1. Regional and local maps showing geology, geography and paleogeography.** (A) The sampled sub-sections of the Yaw Formation on the Kalewa section near Kalewa Township, modified after Westerweel et al. (2020). Different colors from left to right are middle Eocene Pondaung, late Eocene Yaw, Oligocene Letkat, middle Miocene Natma and late Miocene Shwetamin formations. Sampling positions and formation distribution in Kalewa, located at the Chindwin sub-basin of the Central Myanmar Basin. (B) The position of the sampled section in SE Asia and Myanmar with related geographic areas and tectonic units, with base map from https://mapswire.com/. (C) Paleogeography of the Burma Terrane at 40 Ma, modified after Westerweel et al. (2020). Red square shows the Kalewa section. Abbreviations: BB = Bay of Bengal, BT = Burma Terrane, CB = Chindwin sub-basin, EAB = Eastern Andaman Basins, GA = Gangdese Arc, GB = Greater Burma, IAT = India-
Australia Transform, IBR = Indo-Burman Ranges, LT = Lhasa Terrane, MB = Minbu sub-basin, SB = Sibumasu, SF = Sagaing Fault, SL = Sundaland, TTA = Trans-Tethyan Arc, WPA = Wuntho-Popa Arc.

influenced by the South Asia monsoon system as described above, but also its climate is modulated by the El Niño-Southern Oscillation and Indian Ocean Dipole events (Ashok et al., 2010). Among these, the Asian summer monsoon is the predominant climate system and approximately 90% of the total rainfalls occur during the summer monsoon, with the monsoon season from mid-May to mid-October (Htway and Matsumoto, 2011). The highest precipitation values are reached along the Arakan and Tenasserim Ranges (Fig. 3.2B). At the same time though, these ranges cause the monsoon to lose its intensity along the eastern flank of the Arakan Range (Fig. 3.2B) leading to a rain-shadow effect in central Myanmar (de Terra, 1944).

In Myanmar there are three climatic regions: (1) the dry belt in central Myanmar with a mean precipitation (MAP) of less than 1000 mm given their sheltered location leeward of the Arakan Range (Fig. 3.2B), which is insufficient to allow forest growth; (2) regions presenting 1000 to 2000 mm of MAP hosting most monsoon forests; (3) regions presenting over 2000 mm of MAP hosting evergreen tropical forests (Stamp, 1925). Based on Köppen-Geiger climate classification maps (Beck et al., 2018), Myanmar is characterized by tropical monsoon, tropical wet and dry or savanna, hot semi-arid, and monsoon-influenced humid subtropical climate types (Fig. 3.2C). The Kalewa study area, situated in the eastern fringe of the IBR, occupies a tropical wet and dry or monsoon-influenced humid subtropical climate under the strong influence of the South Asian Monsoon, which belongs to the regions (2) as mentioned above (Fig. 3.2C). Based on the climate data of nearby five nearby climate stations (Kalewa, Kalamyo, Minkin, Mawlaik and Varr), the Kalewa study area occupies a MAP of c. 900-1700 mm, of which Kalewa climate station suggests 1641.3 mm (Lai Lai Aung et al., 2017).

3.2.2 | Geological context

The Kalewa study site is situated in the CMB and comprises an almost continuous succession of Cenozoic sedimentary rocks that were mostly deposited in fluvio-deltaic environments (Licht et al., 2013, 2019) (Fig. 3.1A-B). The study area is limited to the east
by the SBR, comprising the Yunnan highlands, the Shan Plateau and the Tenasserim Range, all belonging to the local units of the Sibumasu Terrane (Fig. 3.2A; Metcalfe, 2013). At the western side, the basin is separated from the Bengal Fan by the IBR (Maurin and Rangin, 2009). During the late middle Eocene to early Oligocene, the CMB was open to the Indian Ocean, and was the locus of SW-directed deltas (Licht et al., 2013, 2019), most probably sourced in the Himalayan collision zone (Westerweel et al., 2020). By 40 Ma, the BT was at a near-equatorial position and situated along the Neotethyan margin (Fig. 3.1C; Westerweel et al., 2019, 2020). The hyper-oblique convergence of the Indian plate along the Burmese margin from at least the late Bartonian (c. 39-38 Ma), and their collision with

Fig. 3.2. Regional vegetation, topographic and climate maps. (A) Modern vegetation in India and SE Asia, from Morley (2018a), which simplified from Ashton (2014). (B) Topography of Myanmar with the base map was modified from Hel-hama (2013). (C) Köppen-Geiger climate in Myanmar, after Beck et al. (2018). Ranges of SAM and TA were obtained from Spicer et al. (2017), which refers to Wang and Ho (2002). Red square shows the Kalewa section. Abbreviations: Am = Tropical monsoon climate, Aw = Tropical savanna climate with dry-winter characteristics, Bsh = Hot semi-arid climate, Cwa = Dry-winter humid subtropical climate, Cwb = Dry-winter subtropical highland climate, Dwb = Monsoon-influenced warm-summer humid continental climate, Dwc = Monsoon-influenced subarctic climate, Et = Tundra climate, SAM = South Asia Monsoon, TA = Transitional area influenced by South Asia, East Asia and Western North Pacific monsoons.
the Asian margin, resulted in the emergence of the inner wedge of IBR (Licht et al., 2019; Westerweel et al., 2020). By 37 Ma, the main southward drainage systems formed in the CMB, resulting in the modern low plains in central Myanmar (Licht et al., 2019).

The Cenozoic sedimentary sequence exposed at Kalewa is formed by the Pondaung Formation followed by the Yaw Formation, both of Eocene age and deposited in fluvio-deltaic environments. Sediments were supplied by the exhuming volcanic rocks from the Himalayan collision zone in the north (Westerweel et al., 2020). The Yaw Formation is mainly formed of sandstones and mudstones, bearing some plant fossil fragments and several tens of intercalations of lignite layers. The sediments were deposited in an onshore fluvio-deltaic to deltaic environment, reflecting an overall transgression (Licht et al., 2013), which could be caused by increased subsidence or by eustatic variations and tectonic processes (Licht et al., 2019; Westerweel et al., 2020). The uppermost horizon of the Yaw Formation is unconformably overlain by a thick-bedded fluvial, whitish yellow sandstone called Letkat Formation (lower part called Tonhe Formation in Westerweel et al., 2020), which presents erosional features characteristic of incised fluvial channels and its base can be regarded as a sequence boundary (Moe Zat and Day Wa Aung, 2018).

3.3 | MATERIALS AND METHODS

3.3.1 | The study section

The Kalewa section is a 627.5 m-thick sedimentary sequence that is exposed at the western side of the Kalewa Township, Sagaing Region, NW Myanmar (23°14′ N, 94°15′ E) (Figs. 3.1-3.2). In this study we included two additional samples situated below this section (23°15′ N, 94°15′ E). The Kalewa section is located at the south of Chindwin Basin, which belongs to the CMB (Licht et al., 2019; Fig. 3.1). Paleomagnetic analysis of the sediments and U-Pb dating of a tuff layer provided an age of c. 38-37 Ma (Fig. 3.3; Licht et al., 2019; Westerweel et al., 2020), which is also supported by the palynological evidence discussed below and in Huang et al. (2018, 2020). The lowest two samples show an age of c. 40-38 Ma (Licht et al., 2019).

3.3.2 | Samples and palynological processing
In 2016 and 2017, 83 rock samples were collected at Kalewa from fine-grained sandstones and mudstones of the Yaw Formation. Of these, 81 samples belong to the 627.5 m-thick Kalewa section (Fig. 3.3), while two samples are respectively at ~250 m and ~500 m.

Fig. 3.3. Sedimentary log of the late Eocene Kalewa section, Central Myanmar Basin. It shows the lithology and pollen sampling layers, modified from Licht et al. (2019). The magnetostratigraphy...
indicates the age modified from Westerweel et al. (2020). In the Paleosol column, black lines indicate histosols. Abbreviations: vfs = very fine sand, fs = fine sand, ms = medium sand, cs = coarse sand, B = Boulder. Star indicates two additional samples of the Yaw Formation located at ~250 and ~500 m. The latter forms the base of the Yaw Formation.

below the base of this section and representing the base of Yaw Formation.

Two palynological processing methods were performed to ensure maximum recovery. One set of samples was processed for the quantitative study. The processing was as follows: 1.3 grams sample was boiled in 10% sodium pyrophosphate. Then 10% HCl, and sieves with 5 μm and 212 μm meshes were used. The sample was heated in acetolysis mixture to 100 °C. Bromoform treatment was applied to separate any remaining inorganic fraction to produce residue. A second set of selected samples were processed mainly for microphotography. The processing method was as following: 30 grams of sample were treated with 10% HCl, washed and dried, and then treated with 40% HF, followed by a heavy liquid separation to separate the organic and remaining inorganic fractions. All resulting residues were mounted on a slide in glycerin and sealed with paraffin for light microscope (LM). Residues were further used for analysis with LM and scanning electron microscopy (SEM) at the Department of Palaeontology, University of Vienna, Austria. Details were presented in Huang et al. (2020).

3.3.3 | Palynological analysis and microphotography

In total, 56 samples were productive for pollen analysis with a pollen count of around 100 specimens or more. The identification of specimens was carried out using the palynological literature from South America, China, Thailand, India and Vietnam, and particularly from regions in the proximity of the Kalewa section, such as Assam (India) and Tibet (China) (e.g., Germeraad et al., 1968; Jaramillo and Dilcher, 2001; Jardine, 2011; Morley, 1998, 2013; Sah and Dutta, 1966; Saxena and Trivedi, 2009). All pollen grains from Kalewa were counted using a LEICA DM LB2 light microscopy (LM), and a Zeiss Axiophot Microscope at the Institute for Biodiversity and Ecosystem Dynamics (IBED). Pollen count data are shown in Table S3.1 in Supporting Information (SI). Pollen diagrams were made in Tilia 2.1.1 (Grimm, 1991) with cluster analysis program CONISS (Grimm, 1987).
LM micrographs were produced with a FUJIFILM X-M1 digital camera (Fujifilm Holdings Corporation, Tokyo, Japan) connected with a LM Zeiss Axiophot Microscope (Carl Zeiss, Oberkochen, Germany) under the 630× magnification (with oil) at the IBED. We also investigated the morphological details of the sporomorphs under a scanning electron microscopy (SEM) JEOL JSM-6400 at the Department of Palaeontology, University of Vienna, Austria, with the single-grain analysis method (Halbritter et al., 2018; Zetter, 1989). The micrographs were then processed in the software CorelDRAW 2019 (Corel Corporation, Ottawa, Canada). Each palynomorph under LM was referenced using the “England Finder” coordinates with the number slides.

3.3.4 | Sequence biostratigraphy

Depositional sequences can be identified from the examination of microfossil distribution patterns, which is termed sequence biostratigraphy. This method was developed using foraminifera and nannofossils by Armentrout (1991, 1996) and Shaffer (1987) and extended to take into account palynomorph distributions by Morley (1996) and Morley et al. (2021). In this study, systems tracts were suggested on the basis of palynomorph assemblages. They were then dated by reference to the magnetostratigraphy for the succession as established by Westerweel et al. (2020), and then the succession of depositional sequences was compared to the predicted succession for the late Eocene from the ICS website (ICS, 2020) which is a modification of the scheme of Hardenbol et al. (1998).

3.3.5 | Bioclimatic analysis

We applied a bioclimatic analysis (BA, e.g., Kershaw, 1997; Reichgelt et al., 2013) to quantitatively derive the paleoclimatic information from the Yaw Formation data. BA is a method that compares the mutual climate range (MCR), using the climatic envelopes of the nearest living relatives (NLRs) of fossil taxa to derive the climate ranges in which the majority of an assemblage could co-occur (e.g., Eldrett et al., 2009; Kershaw, 1997; Reichgelt et al., 2013; Thompson et al., 2012), which is slightly different from the coexistence approach (CoA, Mosbrugger and Utescher, 1997) on how climatic range of each taxon is determined. BA defines the overlapping zone based on the 10th and 90th
percentiles, to exclude climatic outliers statistically and objectively (Greenwood et al., 2003, 2005).

The montane taxa, which are all anemophilous and occur in very low percentages, and can mislead the interpretation of the local or regional climate, and for this reason they should be removed in the MCR analysis (e.g., BA, Li et al., 2015; Tang et al., 2020; CoA, Xie et al., 2019). We followed this standard of removing the anemophilous taxa following Li et al. (2015), and applied this to Pinus and Betula pollen types, which are less than 25% and 4% respectively, and also Alnus, Carpinus, Juglans and Taxodium pollen types, the former three with percentages less than 4%, and the latter one less than 25%. Local elements such as algae, aquatics (Myriophyllum, Jussiaea and Liliaceae types) and xerophytic taxa (Ephedra types) were also excluded from the analysis, as this could mislead the interpretation of the regional climate.

Occurrence data of the NLRs were obtained from the GBIF (Global Biodiversity Information Facility, www.gbif.org). These data were processed to delete duplicated and misplaced points following the methods of Palazzesi et al. (2014) and Zizka et al. (2019). Corresponding climate variables were extracted from the WorldClim Version 2 (https://worldclim.org/version2, 30 seconds in resolution). The modern climate variables in the study area were also derived from WorldClim Version 2 with a resolution of 30 seconds, as the meteorological data is out of our reach and could be incomplete.

In the BA we estimated 10 quantitative climatic variables: (a) temperature (°C), including annual mean temperature (MAT), maximum temperature of warmest month (MTWM), minimum temperature of coldest month (MTCM), mean temperature of warmest quarter (MTWQ) and mean temperature of coldest quarter (MTCQ); (b) precipitation (mm), including mean annual precipitation (MAP), precipitation of wettest month (PWETM), precipitation of driest month (PDRYM), precipitation of wettest quarter (PWETQ) and precipitation of driest quarter (PDRYQ). The monsoon intensity index (MSI) was calculated with the equation of Li et al. (2015), a modified version of van Dam (2006) and Xing et al. (2012): MSI = (PWETM–PDRYM)/MAP*100. To our knowledge, this is the first time that BA is applied on paleovegetation datasets from SE Asia.

3.3.6 Rarefaction on sporomorphs diversity
We compared the sporomorph diversity in the late Eocene Kalewa section with contemporary palynofloras from four sites that also were also formed in depositional systems, comparable to the studied sediments in Kalewa. Sample information and palynological data for the four sites and Kalewa site are provided in Tables S3.3-S3.7 in SI. The summary of the depositional environments and vegetation types of the four sites is as follows: (1) The late Eocene Kopili Formation in North Cachar Hills, Assam, India, were deposited in coastal and freshwater swamps and ponds (Saxena and Trivedi, 2009). The flora is characterized by a tropical-subtropical, warm-humid climate with heavy precipitation. Pteridophytes, mangroves and other coastal elements such as palms, predominate in these sediments. (2) The middle to late Eocene Nanggulan Formation from the Watupuru River, central Java, Indonesia, deposited in a transgressive succession and containing rich and diverse sporomorphs (Lelono, 2000). (3) The Zhenjiang section in Maoming Basin, Guangdong, China includes the Youganwo and Huangniuling formations (Aleksandrova et al., 2015). The late Bartonian Youganwo Formation was formed in an intermittently swamped lacustrine-fluvial plain to a freshwater lake setting, favoring the development of wet tropical forests with evergreen taxa. The Priabonian Huangniuling Formation was deposited in a broad fluvial plain setting bearing seasonal-tropical forests. (4) The selected sites in Colombia are situated in the Catatumbo and eastern Cordillera-Llanos foothill basins, where sediments accumulated in a fluvial or coastal plain setting (with samples from c. 38-36 Ma time interval) (Jaramillo et al., 2006).

For application of the rarefaction method (e.g., Birks and Line, 1992) to determine sporomorph diversity, we refer to Jardine et al. (2018). Taxonomic richness (number of sporomorphs) was standardized on both coverage and sample size by unified interpolation and extrapolation (Chao and Jost, 2012; Colwell et al., 2012). Expected richness was calculated using abundance data within samples and using incidence data from pooled samples within geological ages (Gotelli and Colwell, 2001). For within-sample richness, a coverage level of 0.8 was calculated to include most samples on the sections. Expected richness at the coverage level of 0.9 and sample sizes of 160 and 220 was also applied to explore the impact of coverage versus sample size. For within-age richness, we pooled within-sampling localities without the impact of the different geographic extent. We assessed within-sample evenness through the time series with the $E_{var}$ evenness metric of Smith and Wilson (1996). The Chao1 richness estimator was used to estimate total richness (Chao and Jost, 2012). R v.3.6.1 (R Core team, 2019) was used to perform diversity
rarefaction (sampling standardization and Chao1 metric calculation) with the iNEXT package (Hsieh et al., 2014).

3.4 | Results and interpretation

3.4.1 | Age of the Yaw Formation based on palynology

The presence of *Proxapertites operculatus* and *Meyeripollis naharkotensis* but without *Magnastriatites howardi*, throughout the succession suggests reference to palynological zone E8 using the SE Asian palynological zonation scheme presented in van Gorsel et al. (2014) and recently updated in Morley (2020). The E8 zone was interpreted to range from 36-35 Ma, based on long-ranging larger foraminifera and regional correlation (Pieters et al., 1987), but bearing in mind the age obtained from magnetostratigraphy of 38.4-37 Ma, the age of zone E8, needs to be adjusted.

3.4.2 | Vegetation dynamics reconstructed from quantitative palynological analysis

The late Eocene Kalewa sedimentary record yielded more than 141 sporomorph types. Characteristic sporomorphs are shown in Figs. 3.4-3.5, with numbers of sample/residue and England Finder positions shown in Table S3.2 in SI. The 141 sporomorph types were derived from plant taxa growing in mangroves/back-mangroves, coastal forests; swamp forests along rivers, with herbaceous swamps and marshes, possibly associated with floodplain lakes; perhumid/wet, evergreen, seasonally dry forests and montane forests, from a swampy coast setting to dry *terra firma* forests inland (Huang et al., in revision). Pollen diagrams are presented in Figs. 3.6-3.7 and are divided into the following six pollen zones (K1-6) (Table 3.1) which are thought to reflect vegetation changes based on visual observation coupled with cluster analysis.

3.4.3 | Bioclimatic analysis of the sporomorph assemblage

The results from the bioclimatic analysis are based on 11 climatic variables of the Kalewa section and are shown in Table 3.2 and Figs. S3.1-S3.10 in SI, including the present climate
variables in the study site. The MAT is higher than the present-day level, while and MAP is similar to that, indicating a warmer and similarly wet climate. MTWM, MTWQ, PWETM

Fig. 3.4. Light microscopy (LM) micrographs of representative sporomorphs from the late Eocene Kalewa section, Central Myanmar Basin. (1) (2) Margocolporites spp. (3) (4) Sapotaceae. (5) Meyeripollis naharkotensis. (6) Proxapertites operculatus. (7) Gothanipollis sp. (8) Palmae-pollenites kutchensis. (9) Dicolpopollis kalewensis. (10) Longapertites retipilatus. (11) Verrucatosporites usmensis. (12) Cupanieidites flaccidiformis. (13) Monolete spore. (14) Trilete spore. (1) (3-5) (7) (12) are from Huang et al. (in revision), and (8) (10) are from Huang et al. (2020).
Fig. 3.5. Scanning electron microscopy (SEM) micrographs of representative sporomorphs from the late Eocene Kalewa section, Central Myanmar Basin. (1) Proxapertites operculatus. (2) Spinizonocolpites prominatus. (3) Dicolpopollis kalewensis. (4) Longapertites retipilatus. (5) Margo-colporites sp. (6) Lanagiopollis emarginatus. (7) Discoidites sp. (8) Anacolosidites reticulatus. (9)
Euphobiaceae type. (10) Sapotaceae type. (11) Verrucatosporites usmensis. (12) Striatricolpites catatumbus. (13) Dandotiaspora sp. (14) Cicatricosisporites dorogensis. (2-4) are from Huang et al. (2020), and (5-6) (8) (12-13) are from Huang et al. (in revision).

and PWETQ are lower than the present-day level, while MTCM, MTCQ, PDRYM and PDRYQ are higher than that. The MSI is lower than the present-day level. Bioclimatic analysis results for each sample were shown in Table S3.8 in SI and Fig. 3.8, suggesting three “dry-wet” climatic cycles from base to top. These cycles are also clearly displayed from the examination of groupings within the terra firma pollen component, which shows that intervals with a drier climate are indicated by maxima of “seasonally dry trees and shrubs” which correspond to maxima of deciduous montane trees (Fig. 3.6).

3.4.4 | Palynological diversity in the late Eocene tropics

Within-sample diversity results are provided in Tables S3.9-S3.13 in SI and Figs. 3.9 and S3.11-S3.25. Some of the confidence intervals on the Chao1 estimated richness are very large, which has been left off in Fig. 3.9 and included in Figs. S3.11, S3.14, S3.17, S3.20 and S3.23 in SI that shows the large confidence intervals are tied to count size. When the richness of the count size is with higher certainty, Chao1 estimated richness increases and the confidence intervals become bigger. When constructing the richness and evenness at different levels, both for coverage and for the sample-size based richness, they show similar results (Figs. S3.12, S3.15, S3.18, S3.21 in SI).

In the Myanmar section, there is a positive correlation between evenness and expected richness. Yet this is less pronounced with Chao1 estimated richness. In the Indian and Indonesian sections, evenness also has a close concordance with expected richness and Chao1 estimated richness, all of which do not show a noticeable change. In the Chinese section, evenness correlates more similarly with Chao1 estimated richness than expected richness and generally do not show a change, while the latter has higher richness at the bottom. In the Colombian section, richness and evenness do not have a correlation and change; evenness in all samples are low and almost have no variation.
Fig. 3.6. Pollen diagram on *terra firma* taxa of the Kalewa palynoflora. The pollen sum excludes indeterminate pollen and pollen taxa with unknown affinity, algae and pteridophytes, and is formed
by the total count of all taxa shown here. Pollen zone boundaries were positioned using cluster analysis via CONISS program.

Fig. 3.7. Sporomorph diagram for the late Eocene Kalewa section, Central Myanmar Basin. It is with data grouped according to vegetation type and based on the total terra firma sum (left) and total sporomorph sum (right) but excluding algae. Groups are arranged from mangrove/back-mangrove area, coastal to inland settings. Spores are displayed to the right of the terra firma summary diagram, and divided into terrestrial wet, terrestrial dry, climbing, monolete smooth, trilete smooth, trilete ornamented, the representation of indeterminate (including poorly preserved) pollen is also shown. Percentages of Acrostichum, mangroves/back-mangroves and spores are presented outside the terra firma pollen sum and are thus shown as ratios of their counts to the pollen sum in the terra firma summary diagram. Percentages of taxa with unknown affinity and indeterminate pollen are the ratios of their counts to the pollen sum of that in the terra firma summary diagram plus themselves. Pollen zone boundaries were positioned through cluster analysis via CONISS program.

Generally, within-sample richness in the Indonesian section is highest, while that in Myanmar is second highest and similar to Colombia. All of three are higher than that in India and China. The four sections except the Colombian one, have a positive correlation between richness and evenness, while the Colombian section has a very low and non-richness-correlated evenness.

3.4.5 | Sequence-biostratigraphic evaluation
The Yaw palynological succession suggests cyclical vegetation changes, with periods of increased perhumid taxa during wetter/warmer periods and increased seasonally dry and montane taxa during drier/cooler intervals. There is also a close relationship with the abundance of mangrove/back-mangrove elements and changes in the character of swamp vegetation on the floodplain and periods of warmer/wetter climate. For instance, the warmer/wetter period of zone K2 coincides with a mangrove pollen maximum and a maximum of *Dicolpopollis* spp., whereas in zone K6 there is a *Dicolpopollis* spp. maximum.

Table 3.1. Summary of pollen zones.

<table>
<thead>
<tr>
<th>Pollen zone</th>
<th>Assemblage</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>K6</strong> (519.2-627.5 m, c. 37.5 Ma)</td>
<td>Pollen have the highest percentages in this zone among the five zones with spores occurring in low percentages. Hinterland assemblages are dominated by <em>Dicolpopollis</em>. Mangrove/back-mangrove pollen and spores of the mangrove fern <em>Acrostichum</em> occur in low percentages.</td>
</tr>
<tr>
<td><strong>K5</strong> (436.7-519.2 m, c. 37.7-37.5 Ma)</td>
<td><em>Meyeripollis naharkotensis</em> and spores of hornworts (Anthocerotales) are common.</td>
</tr>
<tr>
<td><strong>K4</strong> (364.6-436.7 m, c. 37.8-37.7 Ma)</td>
<td><em>Meyeripollis naharkotensis</em> and Sapotaceae pollen are common. Pollen of swamp trees dominate.</td>
</tr>
<tr>
<td><strong>K3</strong> (249.4-364.6 m, c. 38.0-37.8 Ma)</td>
<td>Monolete spores are abundant. Spores of hornworts (Anthocerotales) occur in low percentages.</td>
</tr>
<tr>
<td><strong>K2</strong> (162.5-249.4 m, c. 38.2-38.0 Ma)</td>
<td>Mangrove pollen (<em>Proxapertites</em> and <em>Spinizonocolpites</em>) and pollen of the swamp rattan (<em>Dicolpopollis</em>) are common. Spores of the climbing fern <em>Stenochlaena palustris</em> are relatively abundant.</td>
</tr>
<tr>
<td><strong>K1</strong> (5.8-162.5 m, c. 38.2 Ma, including the two samples below the Kalewa section)</td>
<td>Terrestrial dry spores are common, including mostly scattered <em>Cicatricosisporites</em> spp., indicative of a well-drained environment. Seasonally dry forest elements including <em>Pinus</em> (indicated by <em>Pinuspollenites</em> spp.) and <em>Berlinia</em> type are also common. Mangroves occur in low numbers. The common occurrence of <em>Psilatricolpites cf. operculatus</em> suggests the presence of <em>Alchornea</em> swamp.</td>
</tr>
</tbody>
</table>

without mangroves, probably due to its more proximal depositional setting. The synchronicity of a period of warmer climate coupled with a mangrove pollen maximum
suggests that glacio-eustacy may be driving the recorded vegetation changes and that the assemblages may be reflecting systems tracts (Morley, 1996; Morley et al., 2021). The age of the Yaw succession has been accurately determined from U-Pb zircon dating (Licht et al., 2019) and paleomagnetism (Westerweel et al., 2020) and comparison of the timing of climate and facies changes with the global sequences of the ICS coastal onlap curve (ICS, 2020) shows a very close agreement (Fig. 3.10). Based on this comparison, the possibility that the Yaw succession represented by zones K2-5 corresponds to the PaBart-1 depositional sequence (ICS, 2020) needs to be given consideration. From examination of the high resolution δ¹⁸O and δ¹³C isotope curves (Westerhold et al., 2020), it seems likely that the late Eocene cyclicity seen here may be driven by 1.2 Ma tilt astronomical cycles since several have a duration of 1.1 or 1.2 Ma.

Table 3.2. Bioclimatic analysis results on sporomorphs from the late Eocene Kalewa section, Central Myanmar Basin. Its modern levels were estimated based on its coordinates via the WorldClim Version 2 database (https://worldclim.org/version2). Note that as situated in the foothills of the Indo-Burman Ranges (IBR), Kalewa area is a transitional region between the central dry belt and the IBR. Based on information from adjacent climate stations, its MAP should be 900-1700 mm, of which Kalewa climate station shows 1641.3 mm (Lai Lai Aung et al., 2017).

<table>
<thead>
<tr>
<th>Climate variables</th>
<th>Kalewa (late Eocene)</th>
<th>Kalewa (Modern)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual mean temperature (MAT)</td>
<td>25.4-25.6</td>
<td>24.4</td>
</tr>
<tr>
<td>Max temperature of warmest month (MTWM)</td>
<td>31.4-31.7</td>
<td>32.2</td>
</tr>
<tr>
<td>Min temperature of coldest month (MTCM)</td>
<td>18.9-19.1</td>
<td>14.2</td>
</tr>
<tr>
<td>Mean temperature of warmest quarter (MTWQ)</td>
<td>25.7-25.8</td>
<td>28.1</td>
</tr>
<tr>
<td>Mean temperature of coldest quarter (MTCQ)</td>
<td>24.6</td>
<td>18.9</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual precipitation (MAP)</td>
<td>1635-1637</td>
<td>1683</td>
</tr>
<tr>
<td>Precipitation of wettest month (PWETM)</td>
<td>282-293</td>
<td>338</td>
</tr>
<tr>
<td>Precipitation of driest month (PDRYM)</td>
<td>47-54</td>
<td>3</td>
</tr>
<tr>
<td>Precipitation of wettest quarter (PWETQ)</td>
<td>763-792</td>
<td>901</td>
</tr>
<tr>
<td>Precipitation of driest quarter (PDRYQ)</td>
<td>209-225</td>
<td>18</td>
</tr>
<tr>
<td>Monsoon intensity index (MSI)</td>
<td>14-15</td>
<td>20</td>
</tr>
</tbody>
</table>
Fig. 3.8. **Climate results of each sample on the late Eocene Kalewa section, Central Myanmar Basin.** These include the mean annual precipitation (MAP), mean annual temperature (MAT) and monsoon intensity index (MSI). Note that MAPs display three “dry-wet” climatic cycles from the bottom to the top, corresponding well with the six pollen zones.

The succession represented by zone K1, where assemblages suggest a seasonally dry climate, and cooler temperatures, are consistent with late highstand (HST) or lowstand (LST) deposition (for reference see model by Morley et al., 2021). For zone K2, assemblages suggest a wetter and warmer climate, and increased mangrove pollen indicates increased marine influence, which would be consistent with deposition in a more aggradational setting within the transgressive systems tract (TST). For the succession spanning zones K3, K4 and K5, most assemblages suggest a slightly drier and cooler climate, and mangrove pollen reaches a minimum, which would be consistent with deposition in a prograding TST setting. The youngest interval, represented by zone K6, yielded assemblages suggesting a warmer and wetter climate, and common *Dicolpopollis kalewensis*, and shows similarities with zone K2, but without common mangrove pollen. This interval would be consistent with a facies and climatic setting similar to K2, but in a more proximal setting due to the reduced mangrove pollen recovery. This package would therefore be consistent with proximal deposition within the TST.
Fig. 3.9. Rarefaction results of the five contemporary sections in the tropics. These show the within-sample diversity (richness and evenness) of the late Eocene samples from the Central Myanmar Basin (Myanmar), Assam (India), central Java (Indonesia), Maoming Basin (China) and Colombia. Horizontal in expected richness are bootstrapped 95% confidence intervals.
Fig. 3.10. Sequence-biostratigraphic evaluation on the late Eocene Kalewa section, Central Myanmar Basin. Comparison of magnetostratigraphy, a summary sporomorph diagram from Fig. 3.7, and the PaBart-1 sequence of ICS coastal onlap curve (ICS, 2020), shows the close agreement between the age of the main Yaw Formation sequence (38.2-37.5 Ma) and the PaBart-1 sequence and coastal onlap curve of ICS (2020). The PaBart-1 sequence ranges in age from 39.1-37.4 Ma. The PaBart-1 maximum flood at 38.2 Ma is also very close to the top of zone K2, which reflects the transgressive systems tract, dated at 38.0 Ma and would reflect the position of the maximum flood in the Kalewa succession.

The zone K1/2 boundary has an age of 38.2 Ma based on magnetostratigraphy, which would be consistent with the position of the transgressive surface in PaBart-1, which must fall between the sequence boundary (SB) at 39.0 Ma and maximum flood (MF) at 38.2 Ma. The underlying zone, K1, would then form part of the lowstand or late highstand of the previous sequence PaLu-4. The zone K2/3 boundary would reflect the maximum flood, dated at 38.0 Ma based on magnetostratigraphy, and comparing to 38.2 Ma according to ICS (2020). The zone K5/K6 boundary has a magnetostratigraphic age of 37.5 Ma, exactly consistent with the age for the PaPr-1 SB. The overlying interval, consisting of zone K6, would then form the TST of the overlying sequence PaPr-1. This model implies that there was limited deposition on the delta plain at times of sea level lowstands. It is possible that
channel sands at 80 m and 140 m may be lowstand feeder channels, but these were not sampled. Other than for this interval times of lowstand would have been represented by unconformities on the delta plain coinciding with the positions of sequence boundaries.

Fig. 3.11. Schematic dip cross-section through the prograding delta of the Yaw Formation. Position of the transect (A to B) is shown in Fig. 3.12.

3.5 | DISCUSSION

3.5.1 | Sequence biostratigraphy helps construction of a landscape model and provides a temporal perspective of vegetation change

By evaluating the palynological record within the framework of the succession of systems tracts, the development of vegetation on the delta plain and in the hinterland within a temporal perspective can be significantly visualized (Figs. 3.11-3.12). Deposition within the PaLu-4 late HST or PrBart-1 LST would have been mostly in a seaward position on a prograding delta plain explaining the presence of just limited mangroves, together with swamp forest, with *Alchornea* and herbaceous fern swamps, and the climate at the time would have been the driest of the whole formation, with lowland *terra firma* vegetation including *Pinus*, suggestive of some vegetation types in central Thailand today (Ratnam et al., 2016). Myrtaceae pollen is common in this interval and could have been derived from either *terra firma* or swamp trees.

Then with rising sea levels at the beginning of the PaBart-1 TST, mangroves would have been well represented, and with a change to a wetter climate, rattan swamps, reflected by a maximum of *Dicolopollis kalewensis*, would have been extensive on the aggrading coastal plain. The swamp vegetation would also have included common *Campnosperma*
and *Mischocarpus*, together with the parent plant of *Longapertites* spp. (possibly *Eugeissona*), the parent plant of *Palmaepollenites kutchensis* and the climbing fern *Stenochlaena palustris*, and also hornworts, such as *Phaeoceros*. The presence of undifferentiated palm pollen suggest that Arecaceae would also have been prominent elements of the vegetation. There is very little pollen suggesting seasonally dry vegetation indicating that this was the period of wettest climate. In this succession, montane pollen is at a minimum, and this would be consistent with warmer climates, with montane vegetation occurring at higher altitudes in upland areas and with reduced areal representation.

Delta progradation within the PaBart-1 HST with stabilized sea levels and a change to a slightly drier climate resulted in the reduction of mangrove swamps (although locally tidal channels could have intermittently brought mangrove pollen into the delta plain) and a change to fern-dominated swamps on the delta plain, which were later replaced by swamps dominated by the parent plant of *Meyeripollis naharkotensis*. The initial stage of swamp development with abundant fern swamps also saw a return of *Alchornea*, and *Palaquium* could also have been a significant component of swamp vegetation. In the hinterland, drier climates resulted in the expansion of taxa such as *Caesalpinioideae*, indicated by the presence of *Margocoplorites* spp. and *Berlinia*. Montane pollen shows a distinct increase in abundance, and mainly consists of evergreen elements, with *Engelhardia* and *Magnoliaceae*, and this could reflect the expansion of montane vegetation, with cooler climates with montane forests occurring at lower altitudes. The subsequent stage of development of the PaBart-1 HST, included widespread swamps with the parent plant of *Meyeripollis naharkotensis*, and also bore common *Campnosperma* and *Mischocarpus* and herbaceous swamps with hornworts, such as *Phaeoceros*. *Terra firma* vegetation was characterized by evergreen forests with widespread Sapotaceae, and a slight increase in seasonal climate elements such as *Austrobusxus*, *Caesalpinioideae*, *Berlinia* and *Pinus* suggesting a drier climate. With respect to montane vegetation, this interval is characterized by regular pollen of deciduous angiosperms, such as *Juglans* and *Carpinus*.

The final stage of development of the Yaw succession was a further change to more transgressive conditions and a wetter climate with the PaPr-1 TST. This again resulted in widespread establishment of rattan swamps on the delta plain, indicated by a further maximum of *Dicolpopollis kalewensis*. However, the delta had prograded sufficiently that by this time deposition was beyond the reach of brackish influence, and so there were no mangrove swamps at the sampled locality. Swamp vegetation also included *Palaquium* and...
the parent plant of *Meyeripollis naharkotensis*, as well as an Areceae (Arecaceae: Arecoideae) taxon, which produced *Palmaepollenites kutchensis*. The climate would have been wet, since dry climate elements are missing, and pollen of montane taxa is rare, suggesting that montane vegetation may have been of reduced extent compared to the cooler and drier periods of the LST and late HST. It is of interest that, despite the perhumid climate, fern spores are less frequent than during the underlying succession. This could indicate that swamps during this period were relatively closed, and that the niche available for fern swamps was reduced.

It is noteworthy that whereas systems tract interpretation indicates the presence of the PrBart-1 sequence with a duration of ~0.7-0.9 Ma, depending on how the PaBart-1 lowstand in envisaged, there is an additional climate cyclicity with three dry-wet cycles each with a duration of about 0.35 Ma. $\delta^{18}O$ data from low latitude Ocean Drilling Program sections from the Oligocene of the equatorial Pacific (Pälike et al., 2006) suggests that there is a climate “pulsebeat” during the Oligocene with a cyclicity of 406 kyr which they term the “pulsebeat of the Oligocene”. Studies of non-marine basins form offshore Vietnam at approximately the same paleolatitude as the Kalewa section indicates that the 406 kyr climate cycles drove vegetation change during the late Eocene and Oligocene. *Terra firma* vegetation typically within the range of tall deciduous or semi-evergreen forest, oscillated between intervals with increased representation of *Pinus* during drier periods and increased rainforest elements during wetter periods (Morley et al., 2021; Nguyen et al., 2021). These cycles were very similar to the cycles present in the Yaw Formation, and the possibility needs to be raised that these higher frequency cycles may have been driver of the higher frequency cyclical climate oscillations seen in the Kalewa section.

### 3.5.2 A monsoon-like climate in the late Eocene CMB

Evidence for monsoonal activity during the Eocene of Asia has been shown by several studies (e.g., Sorrel et al., 2017; Spicer et al., 2016). In this study, the presence of the abundant taxa in swamp and *terra firma* areas such as the parent plants of *Anacolosidites*, *Meyeripollis naharkotensis*, *Palmaepollenites kutchensis* and diverse Sapotaceae, suggest a seasonally wet climate. The parent plants of *Malvacidites diversus* and *Pinus* also occur in seasonally dry climatic conditions, away from the depositional area of river flood plains.
Fig. 3.12. Catchment landscape model of the Chindwin sub-basin in the late Eocene CMB. It was modified from the tectonic model in Licht et al. (2019), with yellow arrow suggesting the IBR was still taking uplift, and blue arrow showing the drainage system coming from northeast as in Westerweel et al. (2020). At the time the volcanoes in the Wuntho-Popa Arc were inactive and often buried (Westerweel et al., 2020). Proportions of different vegetation types are also reflected in the reconstruction. Details of the transect (A to B) are shown in Fig. 3.11.

Therefore, we conclude that in the late Eocene CMB, seasonal evergreen forests dominated the terra firma areas with perhumid vegetation in areas of alluvial swamps and with drier areas supporting semi-evergreen and deciduous forests. This generally indicates a vegetation pattern under the impact of a monsoon-like climate in the late Eocene CMB, supporting the existence of monsoonal activity in the middle to late Eocene of Asia with a seasonal wet climate (e.g., Licht et al., 2014b; Su et al., 2020). The existence of this monsoon-like climate in the late Eocene CMB could be due to the near-equatorial position of the late Eocene BT (Westerweel et al., 2019), and was probably driven by the temperature gradients and associated with the seasonal migration of the Intertropical Convergence Zone.
The late Eocene CMB had a warmer (1.0-1.2 °C higher) climate than at present, suggested by the reconstructed MAT (Table 3.2, Fig. S3.1 in SI), which corroborates a global warmer climate depicted in Zachos et al. (2008) based on the δ¹⁸O isotope record. This also could be explained by its near-equator and open-to-ocean position in the late Eocene. Situated in the foothills of the Indo-Burman Ranges and a transitional area between the dry belt and moist deciduous forests, the Kalewa study area falls into the regions presenting 1000-2000 mm of rainfall hosting most monsoon forests stated in Stamp (1925). Although the modern MAP suggested by the WorldClim Version 2 database on the coordinates (23°14′ N, 94°15′ E) is 1682.50 mm, five nearby climate stations (Kalewa, Kalamyo, Minkin, Mawlaik and Varr) show that, the study area occupies a MAP of ~900-1700 mm (Lai Lai Aung et al., 2017). Besides, the adjacent southeastern dry belt in central Myanmar possesses a MAP of ~500-800 mm (Stamp, 1925; Lai Lai Aung et al., 2017). Therefore, Our reconstructed MAP (1634.90-1636.79 mm) suggests a similarly wet climate in the Eocene (Table 3.2), also evidenced by the presence of lignites in the Yaw Formation (Licht et al., 2019), which would have formed under an everwet climate. PDRYM (47-54 mm) and PWETM (282-293 mm, representing 17.2-17.9 % of the annual rainfall) suggest marked seasonality.

The IBR was uplifted in two stages, namely exposure of its inner wedge in the late Eocene, with its outer wedge forming during the late Mio–Pliocene (Licht et al., 2019). Today the formation of the IBR results in a rain shadow for the CMB, preventing the moisture brought by the South Asia Monsoon (Fig. 3.2A) from the Indian Ocean from reaching the region. Thus it is similarly wet today to the Eocene, although the South Asia Monsoon has intensified since the Eocene, which cannot counteract the influence of the IBR. The reconstruction of monsoon intensity index on the late middle to late Eocene Yaw Formation, however, suggests a weaker monsoon than the modern level (Table 3.2), which still supports the existence of a monsoon-like climate in the Eocene central Myanmar (e.g., Licht et al., 2014b, 2015).

3.5.3  |  Floristic diversity in the late Eocene tropics

The five late Eocene localities that we compared were all situated in the tropics, with deposition in fluvial or coastal plain. With regard to forest composition and depositional environment, the Myanmar section is more similar to the Indian section, probably because
the deposition of both took place in coastal settings, are closely juxtaposed and show a dominance of pteridophytic spores (Huang et al., 2020). Furthermore, they are dominated by seasonal evergreen forests and bear the same conifers (e.g., Pinuspollenites).

Our results suggest that the within-sample richness in the Watupuru section (central Java, Indonesia) is the highest among the five sites. The real species richness would be much higher in the Indian, Chinese and Colombian sections, if more samples were included (Figs. S3.16, S3.19, S3.22 in SI). The rarefaction curve in the Myanmar section indicates that overall, the sampling is complete enough (Fig. S3.13 in SI), which means adding more samples probably would not find many more species.

The highest species diversity in the middle to late Eocene Watupuru section corroborates that the “Nanggulan Formation is the only Eocene sedimentary succession which contains a rich and diverse palynomorph assemblages between the Gippsland basin (in eastern Australia) and India” in Lelono (2000). This high diversity attributes to its near-equatorial position and perhumid climate at that time (Morley, 2000). The high species diversity in late Eocene Myanmar could be due to the India-Asia collision, which accelerated the dispersal of plants between the Indian and Asian plates. The near-equatorial position of the late Eocene BT (Westerweel et al., 2019) in the Paleotropics with a seasonal monsoon-like climate could be another driver. Thus, the BT, acted as a dispersal crossroads (Huang et al., in revision), gained increased species numbers at this time. This corridor may have persisted until the present day, which renders Myanmar as one of the biodiversity hotspots in the world (Myers et al., 2000) with c. 12,340 species of spermatophytes (based on Kress et al., 2003; Yang et al., 2020). The India-Asia collision, along with the Australasian-Sunda collision, resulted in the dramatic increase of plant diversity in SE Asian area, which made this area no longer the backwater of angiosperm evolution (Morley, 2018a), as during the earliest Cenozoic.

3.6 | CONCLUSIONS

In this study, we investigated vegetation and environmental changes and plant diversity under monsoonal climate in the late Eocene Yaw Formation on the Kalewa section, CMB. We conclude that:

(1) Vegetation and environmental changes are evaluated within the framework of two transgressive-regressive depositional successions, and three wet-dry climate cycles. The
late Eocene Kalewa region was characterized by lowland evergreen forests, due to its near-equatorial and coastal plain position, where it could obtain abundant moisture from monsoons. The vegetation was evaluated within a framework of, six pollen zones, which are characterized by fern and *Alchornea* swamps, *Proxapertites* mangroves and rattan swamps, fern swamps, *Meyeripollis* swamps, *Meyeripollis* swamps and rattan swamps from the bottom to the top of the section. The succession was evaluated from a sequence-biostratigraphic perspective that allowed vegetation change to be visualized within the dynamic perspective of transgressions and regressions driven by sea level change. During times of rising sea levels, the climate was wetter, and coastal vegetation communities extended further landward, whereas during periods of sea level stillstand, and subsequent fall, the climate was drier and deltas prograded seaward, resulting in the presence of more fluvial facies at the depositional locality. Based on the very precise magnetostratigraphy for the Kalewa section, the main part of the succession coincides very closely with a global sea level oscillation, termed the PrBart-1 sequence, and this suggests that the sea level changes which drove deposition are due to glacio-eustacy. Superimposed on the succession of depositional sequences, there is an additional wet-dry climate cyclicity, which based on magnetostratigraphy has a cycle of about 350 kyr and it is tentatively suggested that this may relate to 406 kyr eccentricity-driven climate cycles, which were prominent in driving late Eocene vegetation change in nearby Nam Con Son Basin offshore Vietnam.

(2) Monsoonal climate existed in the late Eocene CMB evidenced by indicative taxa and quantitative analysis. Bioclimatic analysis indicates that in the late Eocene, the CMB was warmer (MAT: 25.4-25.6 °C) and similarly wet (MAP: 1635-1637 mm) than that at present (MAT: 24.4 °C; MAP: 1683 mm estimated by climate database, 1641.3 mm from Kalewa climate station, and 900-1700 mm for the Kalewa region from adjacent five climate stations). This is probably because of the near-equatorial and open-to-ocean position of the late Eocene CMB and the establishment of the IBR on the western side of the CMB since the Eocene, which prevents the moisture by the South Asia Monsoon. The Asian monsoons have intensified since the Eocene suggested by the MSI. Different proxies (e.g., leave fossils and stable isotopes) will need to be integrated together with palynological data to better understand the evolution of the vegetation and climate in the Eocene of SE Asia.

(3) Rarefaction analysis performed on five Eocene tropical sites in terms of within-sample richness, evenness, and coverage and sample size-based interpolation and extrapolation suggests that the middle to late Eocene Javanese Watupuru palynoflora has
the highest species richness than the other four contemporary tropical sites which were from
the Yaw Formation in Myanmar, the Kopili Formation in Assam, the Maoming Basin in
South China, and the Catatumbo and eastern Cordillera-Llanos foothills basins in Colombia.
The high diversities for the Watupuru section relates to its near-equatorial position and
perhumid climate. The Kalewa section has the second highest richness and evenness, while
the others have low similarly richness. However, these results could be biased due low
numbers of samples from the Indian, China and Colombia sites. The high floristic diversity
in the late Eocene CMB could be due to the India-Asia collision, which provided
opportunities for the dispersal of plants between India and SE Asia during the Eocene,
coupled with its near-equatorial position.

3.7 | ACKNOWLEDGEMENTS

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3.8 | SUPPORTING INFORMATION

Supporting Information can be found online in figshare doi: 10.21942/uva.14308091.