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

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INTRODUCTION
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1.1 | OVERARCHING RATIONALE AND RESEARCH QUESTIONS

Earth's climate in the Eocene (c. 56-33.9 Ma) is mostly characterized by “greenhouse” conditions, with a change to “icehouse” conditions at the Eocene–Oligocene transition (EOT; c. 33.9 Ma) (Westerhold et al., 2020; Zachos et al., 2008) (Section 1.2.3). Vegetation patterns are greatly influenced by global or regional climate, as suggested by studies on plant fossils (e.g., macro-: woods, tree-rings, leaves and seeds; and micro-: palynomorphs, cuticles and phytoliths) (e.g., Kershaw, 1983; Li et al., 2018b; Mosbrugger and Utescher, 1997; Wing and Greenwood, 1993; Yuan et al., 2020).

Palynology is used as an effective tool to reconstruct past vegetation and climate and provide an indication of past floristic diversity (Section 1.2.1), particularly during critical time intervals with climatic events, such as the “greenhouse” Eocene and the cooling EOT. For example, palynological records from the Tibetan Plateau may reflect the Middle Eocene Climatic Optimum (MECO; c. 40 Ma) with a transient warming event (e.g., Yuan et al., 2020), and regional aridification in the late Eocene (e.g., Dupont-Nivet et al., 2008; Hoorn et al., 2012; Yuan et al., 2020) suggested by compositional changes of environment-indicative taxa. In another continent, South America, palynological diversity fluctuations correlate well with the global temperature changes, particularly at the EOT, when both show a dramatic decline (Jaramillo et al., 2006).

South and Southeast (SE) Asian regions host five (Indo-Burma, Western Ghats and Sri Lanka, Sundaland, Wallacea, and Phillipines) of the 25 biodiversity hotspots around the globe (Myers et al., 2000), suggesting an extremely important conservation priority. Myanmar, the second largest country in SE Asia, is located at the Indo-Burma biodiversity hotspot, with c. 12,340 species of spermatophytes (based on Kress et al., 2003; Yang et al., 2020). Past biodiversity, including plant diversity and vegetation dynamics, is of great importance for understanding present-day plant composition and vegetation patterns, but also for planning future biodiversity conservation strategies. Paleobotanical and palynological studies in South and SE Asia have been widely reported, in particular for Eocene (Section 1.2.2). However, previous quantitative studies on the vegetation, environment and climate change, with paleobotanical and palynological evidence from Myanmar are rare (sections 1.3.1, 1.3.2 and 1.3.3).

The Central Myanmar Basin (CMB) comprises two backarc sub-basins (Shwebo and Pegu) and two forearc sub-basins (Chindwin and Minbu), with a complete sedimentary
record (Licht et al., 2019). Palynological studies in the CMB can inform us about the sporomorph (pollen and spore) diversity, and by comparing with other Eocene tropical sites in the region (e.g., the middle Eocene Nanggulan Formation in central Java; Lelono, 2000) we can obtain a regional understanding of past forest composition. Additionally, with the analysis on the composition of the palynofloras and climate tolerances of each taxon, the palynological studies can suggest vegetation patterns and climate dynamics (Section 1.2.1). Sporomorphs can also provide clues on biogeographic changes through time. In the case of Myanmar, this could provide evidence on the evolution of the Burma Terrane (BT), such as its role in the plant dispersals between the India Plate, mainland and SE Asia, its position in the Eocene and the timing of the BT-Asia collision, and also depositional environments. All these can be compared with previous geological results (e.g., Licht et al., 2019; Westerweel et al., 2019, 2020).

Preliminary evidence shows that palms (Arecaceae) were abundant and diverse in the late Eocene CMB palynoflora. These occurrences, combined with other records, provide an excellent opportunity to further investigate the diversification and biogeographic histories of palms. Given that most of the diversification and historical biogeographic stories are based on phylogenies (Section 1.2.4), the rich palm pollen records will provide new calibration points, and a deep time context for palm evolutionary studies. Furthermore, this will expand our understanding of the evolution of tropical rainforests.

In 2016 I had the opportunity to join the Myanmar Paleoclimate and Geodynamics Research group (MyaPGR, https://myapgr.blog), led by Dr. Alexis Licht (e.g., Licht et al., 2014b, 2019, 2020) from the Centre de Recherche et d'Enseignement de Géosciences de l'Environnement (CEREGE), France. In the context of this project the following four research questions (RQs) were posed, which form the basis of this thesis.

(1) **RQ.1:** What is the composition of the late Eocene palynoflora in the CMB and what can it tell us about the role of the BT for plant dispersal between India and Asia?

(2) **RQ.2:** How did the vegetation and climate change in the late Eocene CMB, and how does the Burmese paleoflora compare to other contemporary tropical palynofloras in terms of species diversity?

(3) **RQ.3:** Can palynology contribute to our understanding of depositional environments in the late Eocene CMB?
(4) **RQ.4:** How did Arecaceae (palms) composition and diversity and historical biogeography change across time, and what was their relationship with climate and geological changes?

Before discussing and answering the four RQs in the subsequent chapters, I will introduce the study design of this thesis (Section 1.1.1) by briefly presenting the applied materials and methods. Subsequently, I will review and succinctly discuss previous studies on Eocene Asian palynology, climate and environment and calamoid and nypoid palms (Section 1.2). I will also introduce the background and geological setting of the CMB (Section 1.3), including the present-day vegetation and climate, and previous studies on Eocene vegetation and climate. Finally, I will conclude this chapter by clarifying the research objectives, scope and outline of this thesis (Section 1.4).

### 1.1.1 Study design

This thesis is principally formed by two themes covered in five chapters, which all have a close connection (Fig. 1.1). In addition, there is an Introduction (this chapter) and a General discussion and synthesis (Chapter 7).

The first theme of the thesis includes chapters 2 to 4, and documents the late Eocene Kalewa palynoflora based on an analysis of sporomorphs that were extracted from rock samples collected in the Central Myanmar Basin. The results of this analysis were used to reconstruct the past vegetation, climate and environment. Light- and scanning electron microscopy with single-grain analysis (Halbritter et al., 2018; Zetter, 1989) was used to observe sporomorph morphology. Multivariate analyses including principal components analysis (PCA) and Pearson correlation, and rarefaction method on the palynoflora were employed to analyze paleoecology of selected taxa and paleoenvironment, and species richness respectively. Tilia software (Grimm, 1991) with a cluster analysis program CONISS (Grimm, 1987), and bioclimatic analysis (Thompson et al., 2012) were used to investigate the vegetation and climate change through the studied section. This part was in collaboration with Dr. Alexis Licht who founded the MyaPGR group in 2016, with a research focus the evolution of central Myanmar.

The second theme includes chapters 4 to 6, and focuses on the pollen morphology, diversification and biogeographic histories of palm subfamilies Calamoideae and Nypoideae. Light-, scanning- and transmission electron microscopy was used to observe
and describe the pollen morphology. Statistical morphometric analysis was applied to define species and their relationships to other Mauritiinae. Fossil and modern data on their global geographic distribution were collected and mapped with the tectonic software GPlates based on previous plate models (Matthews et al., 2016; Westerweel et al., 2019) or with Getech paleomaps. Sample-in-bin and range-through species richness was calculated with fossil occurrences to analyze the diversification history. Environmental niche modeling with paleoclimate data mainly using Maxent was also employed to predict the past distributions. This is for the comparison with the geographic distributions using fossil data and to relate it with past climate change. My collaborators (Dr. Giovanni Bogotá-Ángel from the Universidad Distrital Francisco José Caldas, Colombia, and Dr. Jun Ying Lim from the Nanyang Technological University, Singapore) and I contributed equally to this part, of which the Mauritiinae palm chapter (Chapter 4) was coordinated and corresponded by my principal supervisor Dr. Carina Hoorn from the University of Amsterdam, The Netherlands.

Fig. 1.1. Two research themes in this thesis. Chapters 2-4 focus on the late Eocene vegetation, environment and climate in central Myanmar, which is part of the projects in the Myanmar Paleoclimate and Geodynamics Research group (MyaPGR). Chapters 4-6 aim at the pollen morphology, diversification and historical biogeography of the ancestral palm lineages. Chapter 4 bridges the two themes of the thesis. Left photo (credit: Huasheng Huang) was taken in the 2016
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CMB fieldwork, while right photo (credit: Rodrigo Bernal González) are *Mauritia flexuosa* trees (details see Fig. 1.2).

1.2 | CURRENT UNDERSTANDING OF STUDIES ON (1) EOCENE ASIAN PALYNOLOGY, CLIMATE AND ENVIRONMENT, AND (2) CALAMOID AND NYPOID PALMS

Below I will introduce the background and research objectives of this thesis (Section 1.4) and explain how they relate to the research questions posed in Section 1.1. Before documenting the late Eocene Kalewa palynoflora and unravel the vegetation and climate history during this time interval, I will firstly introduce the approaches to reconstruct the past vegetation and climate with palynology as a tool (Section 1.2.1). Then I will review the previous Eocene palynological studies in South and SE Asia, and briefly summarize the plant migration between India and SE Asia based on the palynological evidence (Section 1.2.2). Eocene Asian climate and environment will also be reviewed to better understand the late Eocene climate and environment in central Myanmar (Section 1.2.3). Diversification and biogeographic histories of palm subfamilies Calamoideae and Nypoideae are the topic of the section of this thesis. Finally I will briefly introduce (sub-)tribe compositions of calamoid and nypoid palms and review the previous studies on their pollen fossil analogues, and biogeographic and diversification histories (Section 1.2.4).

1.2.1 | Palynology as a tool to reconstruct past vegetation and climate

Many observational (i.e., non-modeling) proxies have been used to reconstruct past vegetation (with plant remains, e.g., sporomorphs, phytoliths and macrofossils) and climate (e.g., ice cores, tree-rings, corals, stomata index, sporomorphs, stable isotopes and charcoals). Among these, sporomorphs (pollen and spores) are the focus of this thesis. The study of sporomorphs is called palynology, which can provide information about the vegetation and climate of the surrounding regions, due to their high resistance to chemical degradation, widespread occurrence, large productivity, and continuous records with large numbers of specimens being stored in sediments. Palynology has been widely used as a tool to reconstruct the past vegetation and climate (e.g., Ivanov et al., 2007; Kershaw, 1983;
Kershaw and Nix, 1988), and also provide an indication of past floristic diversity (e.g., Jaramillo et al., 2006, 2010). I will introduce below the approaches with palynology as a tool that have been used to reconstruct past vegetation and climate separately.

The most direct way to reconstruct the past vegetation is through determining the nearest living relative (NLR) of a fossil pollen taxon. Then the paleoecology of the fossil taxon can be revealed by unravelling the ecology of its NLR. Thus after investigating the composition of a palynoflora, the vegetation can be reconstructed with different groups situated in different niches. However, this direct and qualitative approach does not always work, particularly when the ecology of its NLR is unknown or ambiguous. Some researchers reconstructed the past vegetation by comparing the similarity of the paleoflora with modern plant functional types (PFTs) with referring to published database (the so-called PFT approach in François et al., 2017, e.g., Hoorn et al., 2012; Ni et al., 2010; Tang et al., 2020; Zhao et al., 2020b), or grouping the temperature preferences of the NLRs (e.g., Jiménez-Moreno, 2006; Li et al., 2009; Li et al., 2015). Another approach is the Integrated Plant Record (IPR) vegetation analysis, a semi-quantitative technique, combined with other fossils (e.g., from leaf, carpological and wood assemblages) (Kovar-Eder and Kvaček, 2003), which was applied to reconstruct and map regional zonal vegetation in several studies (e.g., Bondarenko et al., 2017; Kovar-Eder et al., 2008; Teodoridis et al., 2011). When using sporomorphs, a pollen diagram can be constructed with cluster analysis applied to the dataset (e.g., with the software Tilia coupled with the program CONISS; Grimm, 1987, 1991), this forms an approximation of the vegetation dynamics, together with environmental change indicated by paleoecology of the whole palynoflora.

Several approaches have been employed to quantitatively reconstruct past climate with palynology as a tool, which all employ an NLR approach. The most widely-used one is the Coexistence Approach (CoA), which was developed by Mosbrugger and Utescher (1997). It is based on the assumption that fossil taxa have similar climatic ranges to those of their NLRs (e.g., used in Hoorn et al., 2012; Ivanov et al., 2007; Wu et al., 2018; Yao et al., 2009; Zhao et al., 2020a), usually with climatic tolerances from the PALAEOFLORA Database (http://www2.geo.uni-bonn.de/Palaeoflora/Palaeoflora_home.htm), but sometimes from the climatic records within distribution areas of the NLRs (e.g., Yao et al., 2009). The CoA has been widely applied to the reconstruction of paleoclimate through the Cenozoic in Eurasia and North America (see the references above, and numerous paleobotanical studies, e.g., Jacques et al., 2011a; Li et al., 2018b; Xia et al., 2009). However, there exist some
uncertainties in the CoA, such as, different distributions and climatic tolerances between fossils and NLRs, as well as uncertainty in climate threshold of NLRs. An improved method derived from the CoA, bioclimatic analysis (BA) (Thompson et al., 2012), has also been performed in several studies (e.g., Li et al., 2015; Reichgelt et al., 2013; Tang et al., 2020), which is similar to the CoA, but differs in determining the climatic range of each taxon. It mainly includes three steps illustrated in Li et al. (2015): (1) identify the NLRs of the sporomorphs in a palynoflora; (2) evaluate climatic profiles based on the climatic values of the occurrences of the NLRs; (3) define the most possible climatic ranges for the palynoflora.

Information on the distribution of taxa are usually obtained from the Global Biodiversity Information Facility (GBIF, www.gbif.org), sometimes also from regional species distribution database (e.g., the Chinese Virtual Herbarium, www.cvh.org.cn). Corresponding climate variables were derived from the WorldClim database (www.worldclim.org) with the bioclimatic envelope model in the R package “dismo”. To increase the accuracy of the BA estimate, 10th and 90th percentiles are used to delimit the climatic envelops (e.g., Li et al., 2015; Tang et al., 2020; Thompson et al., 2012). A recent paper used an improved BA, which combined the NLR approach with the probability density function method to statistically constrain the most likely climatic co-occurrence envelop (Klages et al., 2020).

1.2.2 | Eocene palynological studies in South and SE Asia

Eocene palynological studies based on continental or offshore sediments have been widely reported from South and SE Asia, particularly India and the Sunda Shelf (i.e., Peninsular Malaysia and Indonesia). Eocene palynological studies in Myanmar are rare and will be summarized in Section 1.3.2. Studies from South Asia and other SE Asian countries will be separately summarized below.

South Asian Eocene palynological studies have been widely carried out in India. These reports are mainly concentrated on the early Eocene Rajpardi lignite in Gujarat (e.g., Kumar, 1996; Samant and Phadtare, 1997), early Eocene deposits from the Kutch Basin, western India (e.g., Dutta et al., 2011; Mathews et al., 2013; Verma et al., 2020), early Eocene Vastan lignite mines in the Cambay Basin (e.g., Mandal and Guleria, 2006; Rao et al., 2013; Tripathi and Srivastava, 2012), early Eocene sediments (e.g., the Akli Formation) from the
Barmer Basin (e.g., Tripathi and Srivastava, 2010; Tripathi et al., 2009), late Eocene Kopili Formation in Assam (e.g., Saxena and Trivedi, 2009; Trivedi and Ranhotra, 2015; Trivedi and Saxena, 2000), and late Eocene Barail Group, northeastern India (e.g., Handique et al., 1992; Mandal, 1997). The abundance of early Eocene palynofloras confirms that the early Eocene bears the richest and most diverse palynofloras in the Indian Paleogene (Morley, 2000). At this time, optimum climate conditions favored the proliferation of angiosperms and the India subcontinent was covered by dense and multistoried rainforests, while in the late Eocene, warm and perhumid conditions supported diverse rainforest vegetation (Morley, 2000). Compared to the rich Indian Eocene palynological records, to my knowledge only one Eocene palynological study from Pakistan has been reported by Vimal (1952), investigating a sporomorph assemblage from the Eocene lignites of the Dandot coalfields, West Punjab, Pakistan. This may be mainly due to the political and scientific isolation of Pakistan with other parts in the globe. It is also worth mentioning that Frederiksen (1994) published an outstanding paper on the middle to late Paleocene Pakistani palynofloras with excellent descriptions on diverse angiosperm pollen. He suggested the occurrence of Normapolles pollen in the late Paleocene of Pakistan corroborates the hypothesis of intermittent filtered migrations from Eurasia to the Indo-Pakistan island before the middle Eocene India-Asia collision.

SE Asian Eocene palynological studies have been mostly reported from the Sunda Shelf and Vietnam, with the addition to Myanmar (Section 1.3.2). In Malaysia, Muller (1968) studied an Eocene palynoflora from the Kayan Formation (formerly Plateau Sandstone) in Sarawak, and assigned some important new genera and species (e.g., Spinizonocolpites (Nypa) and Dicolpopollis malesianus (Calamus type)), which have been widely found in other sites. In Indonesia, palynological studies have mostly been carried out in Java (e.g., the middle to late Eocene Nanggulan Formation in central Java in Harley and Morley, 1995; Lelono, 2000; and Takahashi, 1982; the late Eocene Walat Formation in west Java in Rachman et al., 2021), Sulawesi (e.g., the middle Eocene Mallawa Formation in south Sulawesi in Morley, 1998; the middle Eocene Ngimbang Formation in subsurface offshore south Sulawesi in Morley, 2014), and West Papua (the early Eocene Waripi Formation from Irian Jaya in Morley, 1998). The middle Eocene palynoflora in the Nanggulan Formation of central Java is the richest Eocene palynoflora between the Gippsland Basin (Australia) and India (Lelono, 2000). The middle to late Eocene SE Asian palynological evidence, coupled with the existence of coaly lithologies, suggests a
flourishing, diverse vegetation and a moist, warm climate, characterized by dryland vegetation consisted of tall, dense, closed-canopy rainforests of modern aspect (Morley, 2000). In Vietnam, Eocene sediments have only been documented palynologically by Morley et al. (2019), including deposits from the late to middle Eocene offshore Ca Coi and late Eocene Tra Cu formations.

Eocene palynological evidence from India and SE Asia supports distinct floristic exchange between them. Prior to the India-Asia collision, when in the early Eocene, parts of the Indian Plate hosted a perhumid climate (i.e., largely aseasonal with regards to moisture availability; Morley, 2000, 2018a; Thornthwaite, 1948), and a flora dominated by palms, Sapotaceae, Malvaceae, Meliaceae and Myrtaceae among others. As India approached Asia, plants dispersed from the Indian Plate into SE Asia in two stages (Morley, 2014). The first stage initiated around the early/middle Eocene boundary (c. 47.8 Ma) and was characterized by the appearance of *Palmaepollenites kutchensis*, *Alangium* section *Conostigma* and *Durio* type pollen in SE Asia. *P. kutchensis* may disperse via the BT to SE Asia at this stage. The common occurrence of Restionaceae at this stage probably suggests a distinctly seasonal climate (Morley, 2018a). At the time, megathermal rainforest taxa were fully established across SE Asia and straddled three parallel latitudinal zones (Morley, 2007), including some of the most characteristic and common components of the present-day SE Asian forests. The second stage was after c. 45 Ma, when climate became more perhumid in SE Asia with the reduction of Restionaceae, the appearance of *Gonystylus* and *Ctenolophon*, and palms becoming more abundant (Morley, 2018a), with pollen diversity increasing dramatically (Lelono, 2000).

### 1.2.3 | Eocene climate and environment in Asia

During the Eocene (c. 56-33.9 Ma), earth's climate generally cooled from a “greenhouse” condition (in most of the Eocene) to a “icehouse” condition (near the end of the Eocene), with a likely intermediate late Eocene phase sometimes referred to as “doubthouse”, characterized by the formation of an incipient polar ice-sheet. Climatic events in this period mainly include the Early Eocene Climatic Optimum (EECO; c. 52-50 Ma), the Middle Eocene Climatic Optimum (MECO; c. 40 Ma), and global cooling at the Eocene–Oligocene transition (EOT; c. 33.9 Ma) (Westerhold et al., 2020; Zachos et al., 2008).
The EECO is a period characterized by long-term global warmth, and represents one of the periods of highest global temperature in the past 70 million years (Zachos et al., 2001). The MECO is the most noticeable as a short-lived warming event in the Eocene, firstly identified in ocean drilling cores by Bohaty and Zachos (2003), which is related to short-lived shoaling of the calcite compensation depth (e.g., Lyle et al., 2005; Pälike et al., 2012). At the EOT, earth's climate dramatically cooled, due to a major expansion of the Antarctica ice-sheets (DeConto and Pollard, 2003; Liu et al., 2009) and a decrease in atmospheric CO₂ concentration (Pearson et al., 2009). Below, I will briefly summarize earlier studies on the Asian paleoenvironments that relate to the three aforementioned climatic events.

Regional mountain uplift and sea retreat may have played an important role in shaping Asian environments and caused monsoonal intensification in the Eocene (e.g., Bosboom et al., 2014a, b; Dupont-Nivet et al., 2007, 2008; Li et al., 2018a), while global cooling was also found to be a major contributor to the Asian mid-latitude interior aridification at this time (Li et al., 2018a). Asian interior aridification has been reported from the EECO towards the MECO by several studies (e.g., Bosboom et al., 2011, 2014a, b; Dupont-Nivet et al., 2007, 2008; Sun and Windley, 2015; Wang et al., 2016; Wasiljeff et al., 2020; Xiao et al., 2010; Yuan et al., 2020). Increased moisture was found to be driven by westerlies modulated by proto-Paratethys Sea incursions during the EECO and middle to late Eocene (c. 46-41 Ma and 40-37 Ma) (Meijer et al., 2019). In contrast to the increased moisture caused by westerlies, right after the MECO (c. 40 Ma), the global cooling, which reduced moisture supply to the Asian interior continent, and the eustatic fluctuations driving the westward retreat of the shallow epicontinental proto-Paratethys Sea, were proposed to have caused the Asian continental aridification (Bosboom et al., 2014a). Subsequently, two step-wise changes of the Asian continental environment preceding the EOT were reported by Abels et al. (2011), including a regional aridification event at c. 36.6 Ma linked to a coeval retreat of the Tarim Sea, and a significant increase of clastic sedimentation at c. 34.7 Ma reflecting a seasonal drying trend. They interpreted that these changes may relate to increased climate variability preceding the greenhouse to icehouse transition at the EOT. At the EOT, Dupont-Nivet et al. (2007) found that global cooling – a major contributor – and uplift of Tibetan Plateau after the India-Asia collision, caused the Asian continental aridification.
Apart from the commonly-reported Asian interior aridification, monsoons, associated with marked seasonal variations in precipitation, have been widely proposed from Asia in the Eocene based on observational evidence in the last decades (e.g., Licht et al., 2014b; Shukla et al., 2014; Spicer et al., 2016, 2017; Su et al., 2020). The seasonal migration of the Intertropical Convergence Zone (ITCZ) is proposed to mainly drive the Eocene Asian monsoons (including those in India, Tibet and South China) (Spicer et al., 2016, 2017). The proposed middle to late Eocene (c. 40-34 Ma) monsoon in central Myanmar (Licht et al., 2014b), indicated by strong seasonality and modern-like monsoonal rainfall. This Eocene monsoon was also likely induced by the migration of the ITCZ, unlike the modern South Asia monsoon which is enhanced by topography. However, modeling result shows that precipitation seasonality should be used with caution in suggesting the existence of a monsoonal circulation (Tardif et al., 2020).

1.2.4 | Previous studies on calamoid and nypoid palms

Biogeography and diversity of lineages can be directly inferred from the fossil record (Crisp and Cook, 2011; Quental and Marshall, 2010), compared with molecular phylogenies alone, which has significant uncertainty (Louca and Pennell, 2020; Quental and Marshall, 2011). The palm family (Arecaceae) is a model group for evolutionary studies in tropical rainforests (Baker and Dransfield, 2016; Couvreur and Baker, 2013; Reichgelt et al., 2018), and has an abundant pollen fossil record (Harley, 2006; Dransfield et al., 2008). This can help to further understand its biogeographic and diversification histories, and form an important indication of plant turnover following climate change, which may shed light on the evolution of tropical rainforests. Two of the ancestral palm lineages, subfamilies Calamoideae and Nypoideae (Baker and Couvreur, 2013a), are the subject of this thesis (mainly Chapter 6), of which Mauritiinae (Calamoideae: Lepidocaryeae) is the subject of Chapter 5. Calamoideae consists of three tribes (i.e., Eugeissoneae, Lepidocaryeae and Calamieae), which include 10 subtribes, 17 genera, and c. 550 species, while Nypoideae is a monophyletic subfamily and only contains one species, Nypa fruticans (Kuhnhausser et al., 2021). Below, I will now introduce the previous studies on their pollen fossil analogues, and biogeographic and diversification histories.

Eugeissoneae comprises the sole genus, Eugeissona, including six species (Kuhnhausser et al., 2021) (see one of its species in Fig. 1.2A), which is confined to the
Malay Peninsula and Borneo (Dransfield et al., 2008). Its unequivocal fossil analogues are *Quilonipollenites* pollen types, which have only been reported from India (Phadtare and Kulkarni, 1984). Most *Longapertites* pollen types are also possible fossil analogues (Morley, 2000). The taxon has extensive fossil records from the Paleocene–Eocene and displays considerable morphological variation from psilate to reticulate (Frederiksen, 1994). However, some *Longapertites* pollen types, such as *L. dupliclavatus* and *L.* sp. aff. *L.* *Sahnii* in Frederiksen (1994) are dupliclavate, and have probably an affinity to Asparagaceae or Liliaceae or possibly other palm subfamilies, as previously noted in Harley and Baker (2001). *Longapertites* sp. cf. *L.* *discordis* in Frederiksen (1994) is also more similar to a Liliaceae pollen type. *Quilonipollenites* and *Longapertites* are characterized by their extended monosulcus with thick walls (Morley, 2000; Phadtare and Kulkarni, 1984).

*Lepidocaryeae* has three subtribes, Ancistrophyllinae, Raphiinae and Mauritiinae (see one of its species in Fig. 1.2B) (Kühnhäuser et al., 2021). So far, only the fossil pollen types of Mauritiinae, which widely occurs in north South America (Dransfield et al., 2008), have been reported (e.g., van Hoeken-Klinkenberg, 1964). These fossil pollen types are assigned to three form-genera, *Mauritiidites*, *Grimsdalea* and *Echidiporites*, and mostly featured by the monosulcus. They are widely reported from South America (e.g., van Hoeken-Klinkenberg, 1964) and Africa (e.g., Eisawi and Schrank, 2008).

**Fig. 1.2. Trees of the four studied palm lineages in this thesis.** (A) *Eugeissona utilis* Becc., a group of tree palms restricted to the Malay Peninsula and Borneo. (B) *Mauritia flexuosa* L.f., one of the commonest species in Amazonia, with an estimated 1.5 billion individuals (ter Steege et al., 2013). (C) *Calamus longipinna* K.Schum. et Lauterb., showing the cirri, extensions of the leaf that possess
hook-like structures that allow the plants to attach themselves to neighboring vegetation. (D) *Nypa fruticans* Wurmb, a common mangrove species in many parts of the Indo-Pacific, often forming large monodominant stands (Tomlinson, 1986). Photo credits: William J. Baker (A) (C) (D) together with cover images of chapters 4-7, and Rodrigo Bernal González (B) together with cover image of Summaries in English, Dutch and Chinese.

**Calameae**, sister to Eugeissoneae (Kuhnhäuser et al., 2021), contains six subtribes (i.e., Korthalsiinae, Salaccinae, Metroxylinae, Pigafettinae, Plectocomiinae and Calaminae). *Calamus*, including 415 species, is the sole genus in Calaminae (Kuhnhäuser et al., 2021), and the largest palm genus (Dransfield et al., 2008) (see one of its species in Fig. 1.2C). It is widely distributed in the humid tropics of Africa, India, Burma, and South China throughout the Malay Archipelago to Queensland and Fiji, with greatest diversity in the Sunda Shelf area, and a second center of diversity in New Guinea (Dransfield et al., 2008). Within the subtribe Calaminae and even tribe Calameae, only fossil pollen types of *Calamus*, in the manner of the form-taxon *Dicolpopollis* spp., have been reported, which have distinct disulcate aperture (Harley and Morley, 1995). *Dicolpopollis* has been found in all continents except South America and Antarctica (e.g., Asia: Potonié, 1960; Europe: Zetter and Hofmann, 2001; Australasia: Playford, 1982; Africa: Sowunmi, 1981; North America: Frederiksen, 1984).

*Nypa fruticans*, the sole species in *Nypoideae*, occurs from Sri Lanka, the Ganges Delta to Australia, the Solomon Islands and the Ryukyu Islands (Fig. 1.2D) (Dransfield et al., 2008). Its pollen fossil analogues are *Spinizonocolpites* pollen types, which have a pantropical distribution (e.g., Africa: Pan et al., 2006; Asia: Hoorn et al., 2012; Europe: Lenz et al., 2020), and was very diverse in the past (e.g., Frederiksen, 1994; Lenz et al., 2020; Srivastava and Prasad, 2015). *Spinizonocolpites* pollen types are characterized by their zonasulcate aperture and finely reticulate wall covered by scattered baculate or echinate spines (Frederiksen, 1980; Morley, 2000; Muller, 1968).

So far, the biogeography of calamoid and nypoid palms has only been studied through molecular phylogenies (e.g., Baker and Couvreur, 2013a), but as yet their abundant fossil record has never been systematically assessed. Baker and Couvreur (2013a) proposed a Laurasian origin in the Late Cretaceous for all five subfamilies based on molecular phylogenies. However, *Spinizonocolpites*-type pollen with affinity to *Salacca* (Calamoideae: Calameae) proposed by the authors was found in the Early Cretaceous
Patagonia, Argentina (Martínez et al., 2016). Baker and Couvreur (2013a) concluded that the early range expansion of Calamoideae into Africa and South America is in the Cretaceous (80 Ma). They also concluded that: (1) **Eugeissoneae** diverged from the remaining Calamoideae at the crown node (i.e., 80 Ma) of Calamoideae in Eurasia; *Eugeissona* (*Quilonipollenites* pollen types) occurs in India from the middle Eocene until the Miocene, and subsequently went extinct; (2) **Calameae** and **Lepidocaryeae** diverged from each other in the Campanian (77 Ma), the former in Eurasia and the latter in Africa; Mauritiinae expanded into South America in the Maastrichtian (66 Ma), which may be alongside island chains; Calaminae expanded westwards into the Pacific in the middle Eocene (c. 45 Ma) and then migrated into Eurasia and became extinct in the Pacific; (3) **Nypoideae** diverged from other palms at 94 Ma, became most abundant in the early Eocene and since that time has contracted in its present-day distribution. However, these results may not be very reliable as without the abundant fossil record. Environmental niche modeling together with paleoclimate data is used to predict the past distribution of plants (e.g., Meseguer et al., 2015). Biogeography inferred by past distribution information resulted from pollen fossil record, integrated with the predicted past distribution obtained by paleoclimate and climatic niche models, may help to understand the relationship with past climatic events (e.g., global cooling at the EOT).

Besides the molecular phylogenies, which are based on the extant taxa, there are only few studies based on pollen record on the change of species richness of calamoid and nypoid palms through time (e.g., Frederiksen, 1994; Pan et al., 2006; Srivastava and Prasad, 2015). These studies can provide strong evidence on their diversification history. Frederiksen (1994) studied the middle to late Paleocene palynofloras, including diverse *Longapertites* (probably *Eugeissona*) and *Spinizonocolpites* (*Nypa*), from Pakistan with a large sample set, suggesting that they were more diverse in the middle Paleocene than in the late Paleocene. Pan et al. (2006) summarized the African pollen and macrofossil records of *Longapertites* (probably *Eugeissona*), *Spinizonocolpites* (*Nypa*), *Mauritiidites* (Mauritiinae), *Grimsdalea* (Mauritiinae) from the Late Cretaceous through the Pleistocene, and found they were abundant in the Paleogene and absent in the Neogene and Pleistocene. Srivastava and Prasad (2015) investigated the species diversity of *Spinizonocolpites* pollen (*Nypa*) across the Paleocene–Eocene transition (PET) with sediments from the eastern Khasi hills, South Shillong Plateau, Meghalaya, India. They found that species diversity is higher at the PET (late Thanetian–early Ypresian) favored by high precipitation and good water runoff, than
in the Eocene (late Ypresian) due to the low rainfall. However, the global species diversification history of calamoid and nypoid palms across the Cenozoic, which may have connection with the past global climatic events, have not yet been completely documented, particularly in recent years with fast growing pollen records.

1.3 | THE CENTRAL MYANMAR BASIN

1.3.1 | Geological context

In terms of geology, Myanmar is situated on the BT (also named West Burma Block) and the Shan Plateau on the Sibumasu Terrane (also named Sibumasu Block) (Fig. 1.3A). The CMB is situated in the east of the Indo-Burman Ranges (IBR), and forms part of the BT and includes two forearc sub-basins (i.e., the Chindwin sub-basin in the north and the Minbu (also called Salin) sub-basin in the south) and two backarc sub-basins (i.e., the Shwebo sub-basin in the north and the Pegu sub-basin in the south) divided by the Wuntho-Popa Arc (WPA) (Fig. 1.3A). The WPA is considered as the eastern continuation of the Tibetan Gangdese Arc (Ma et al., 2014; Wang et al., 2014) and comprises isolated Quaternary volcanoes (Mounts Popa) and crater lakes (Lakes Taungtalon, Loimye and Monywa) spreading over a ~1000 km north-south trend in western Myanmar, and pre-Quaternary igneous rocks (Licht et al., 2020).

The CMB was a quasi-closed estuarine system and open to the Bay of Bengal in the late Eocene (Licht et al., 2019), most probably sourced in the Himalayan collision zone (Westerweel et al., 2020). (Fig. 1.3B). At the time the BT was located at a near-equatorial position (Westerweel et al., 2019, 2020) (Fig. 1.3B), when the northern extent of the BT collided with the Asian margin (Westerweel et al., 2020). The IBR was subject to its initial uplift in the late Eocene, and with its second uplift in the Mio-Pliocene (Licht et al., 2019). The BT was part of a Trans-Tethyan Arc and has moved at least 2,000 km northwards together with the India Plate since the late Eocene (Westerweel et al., 2019, 2020).

The study area (c. 23°14′ N, 94°15′ E) forms part of the southwestern Chindwin sub-basin (Fig. 1.3A), and is situated at c. 4 km, northwest of the Kalewa Township in the Sagaing Region, northwestern Myanmar (Fig. 1.3C). The Chindwin sub-basin is considered an en echelon pull-apart sub-basin, which is partly attributed to the rapid subsidence (c. 1.0
m per thousand years) in the process of the deposition of the Yaw Formation (Licht et al., 2019). Samples were collected from four sub-sections (i.e., MA, MB, MC and MD, herein together called the Kalewa section; Fig. 1.4) during the winter fieldwork seasons in 2016 and 2017.

Fig. 1.3. Maps showing regional and local geology. (A) Myanmar and surrounding regions at present. (B) Myanmar and surrounding regions at 40 Ma. (C) The study area near Kalewa in the

Sediments near Kalewa mainly comprise of the middle Eocene Pondaung, late Eocene Yaw, Oligocene Letkat, middle Miocene Natma, and late Miocene Shwetamin formations (Fig. 1.3C; Westerweel et al., 2020). I focus on the late Eocene Yaw Formation as it is the most palynologically productive formation. The Yaw Formation consists of four distinct sedimentary facies including the following anoxic deposits and reflecting a quasi-closed estuarine system: (1) massive organic-rich black mudstones and siderite-rich carbonate layers; (2) deltaic tidal siltstones and sandstones; (3) continental sediments with thick sandstones; and (4) lignite layers (Licht et al., 2019). The underlying Pondaung Formation was deposited in a fluvial-deltaic setting which opened towards the proto-Bay of Bengal (Aung Naing Soe et al., 2002), and had an estimated age of late middle Eocene (c. 40-39 Ma) (Licht et al., 2019). A 6 km-thick coarse-grained fluvial facies, from older to younger including the Tonhe, Letkat, Natma, Shwethamin and Irrawady formations overlay the Yaw Formation (Bender, 1983). Of these, the Tonhe Formation is formed by thick packages of especially coarse-grained sandstones and conglomerates, with thick sets of trough cross-bedding and planar bedding, alternating with paleosols (Westerweel et al., 2020). It may be of a late Oligocene–early Miocene age suggested by the presence of *Florschuetzia semilobata* as part of a rich palynoflora (Soe Moe Lwin et al., 2017). The age of the Yaw Formation was estimated to be c. 37-36 Ma based on dates by a tuff layer (Licht et al., 2019), magnetostratigraphy, U-Pb apatite dating, and apatite fission track dating (Westerweel et al., 2020). Because of this, an unconformity was presumed to exist between
the Yaw and Tonhe formations, which may be related to the first collision of the India Plate and the northern BT with the Asian margin (Westerweel et al., 2020).

**Fig. 1.4.** Fieldwork photos in the 2016 winter season. (A) (B) (C) Parts of the MB sub-section, with a white arrow indicating the layer of sample 16MBP049.

**1.3.2 | The present-day vegetation and previous paleobotanical and palynological studies in Myanmar**

Ashton (2014) classified the Burmese vegetation into five types (Fig. 1.5B), which are explained here following a Burmese topographic map (Fig. 1.5A). Montane vegetation covers the high-altitudinal areas in the north (i.e., on the southwestern margin of the East Tibetan Plateau), northeast (i.e., on the Shan Plateau) and along the IBR and the Sino-
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Burman Ranges (SBR). Dry deciduous forests occur around the Pegu Range in the central Myanmar, which is the “dry belt” proposed in Stamp (1925). Moist deciduous forests occupy most areas of the CMB (Fig. 1.5B), in the west of the SBR and east of the IBR. Semi-evergreen forests inhabit the mid-altitudinal regions of the SBR and IBR, Arakan and Tenasserim ranges. Seasonal evergreen forests grow in the mid-altitudinal areas of northern and northeastern Myanmar, and coastal lowlands of the south Tenasserim Range and Arakan Range. The study area is located where the Myittha River meets the Chindwin River (Fig. 1.5B). This area has moist deciduous forests (Fig. 1.5B; Ashton, 2014), which includes dry teak forests (Kress et al., 2003).

The study of vegetation history is of great importance to reconstruct past floristic composition, climate and environment. The vegetation history of Myanmar has only been documented by a few studies based on fossil woods, suggesting the long-term presence of seasonal and mixed-semievergreen forests in the Neogene (Gottwald, 1994; Prakash, 1965, 1971; Prakash and Bande, 1980) and a multi-ecosystem in the late middle Eocene (Licht et al., 2014a, 2015). This multi-ecosystem includes littoral forests on the lower deltaic plain, riparian forest and open-forested seasonal wetlands in the upper deltaic plain and dry dipterocarp forests in upstream areas. Other paleobotanical studies include the numerous reports of different plant organs in the Cretaceous Burmese amber (also known as Burmite) from the well-known locality, Hukawng Valley, northern Myanmar, including mostly flowers (e.g., Poinar, 2018), leaves (e.g., Schneider et al., 2016) and fruits (e.g., Xing and Gu, 2020). However, leaf fossils which are helpful for reconstructing past vegetation, have not been reported so far, although some leaf fragments were found in the CMB (Licht et al., 2019). Palynological studies include samples mostly from sediments (e.g., Potonié, 1960; Reimann and Aye Thaung, 1981), rarely from the Burmite (e.g., Bao et al., 2019; Grimaldi et al., 2019). Previous palynological studies on sedimentary deposits will be summarized below.

Potonié (1960) firstly reported an Eocene palynoflora from the Thitchauk coalmine in the Chindwin sub-basin, northwestern Myanmar, and compared it with the Cenozoic palynofloras from middle Europe. Also in the same sub-basin, Reimann and Aye Thaung (1981) published Eocene–Miocene palynofloras from a large sample set and discussed their palynostratigraphy and paleoenvironments. Subsequently Engelhardt and Wrenn (1994) reported some pollen taxa and dinocysts from the early to late Eocene upper Laungshe, Tilin and Tabyin formations in the Minbu sub-basin, which indicate paleoenvironments
ranging from fluvial/deltaic to inner neritic. More recently, Soe Moe Lwin et al. (2017) discussed the paleoenvironments on the basis of some sporomorphs from the Miocene Takam Hka Formation in the Hukawng sub-basin, and the early Miocene Letkat Formation in the Chindwin sub-basin. The above-mentioned studies either report palynomorphs or discuss their stratigraphic/paleoenvironmental implications, but none are concerned with the composition and evolution of the vegetation. With palynofloras, we need to comprehensively evaluate the botanical affinities and source ecology of the recovered sporomorphs, and then determine the vegetation types they reflect. Along with accurate age constraints for the studied sections, we will be able to unravel the vegetation history in central Myanmar (Chapter 2).

Fig. 1.5. The present-day topographic, vegetation and climate maps of Myanmar. (A) Topography, with base map from Hel-hama (2013). (B) Vegetation, after Ashton (2014). (C) Climate, showing the Köppen-Geiger climate from Beck et al. (2018). Red square indicates the study area. Abbreviations: (B) Ddf = dry deciduous forests, scrub, savanna, Mdf = moist deciduous forests, Mv = montane vegetation, Sef = seasonal evergreen forests, Sf = semi-evergreen forests. (C) 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.

1.3.3 | The Burmese present-day climate and previous studies on late Eocene climate

The climate of Myanmar can be classified into eight types (Fig. 1.5C) (Beck et al., 2018), which will be briefly presented below. I will also relate climate to the topographic (Fig. 1.5A) and vegetation (Fig. 1.5B) occurrences. The extremely small northernmost area around the Burmese highest mountain, Hkakabo Razi (Fig. 1.5A), located at the southwestern margin of the East Tibetan Plateau, has three cold climate types (i.e., monsoon-influenced warm-summer humid continental, monsoon-influenced subarctic, and tundra climate). The dry-winter subtropical highland climate characterizes the high-altitudinal area of the IBR and northern mountainous region. Most of the IBR, Shan Plateau, and broad north, forms an area mostly covered by northern seasonal evergreen and semi-evergreen forests, and has a dry-winter humid subtropical climate. Areas with hot semi-arid climate, tropical savanna climate with dry-winter characteristics, and tropical monsoon climate are relatively consistent with those covered by dry deciduous, moist deciduous and southern seasonal evergreen forests.

The Sagaing Region, where Kalewa area is situated, has a dry-winter humid subtropical climate and tropical savanna climate with dry-winter characteristics. It is located in a region with 1000-2000 mm of mean annual precipitation that hosts most monsoon forests (Stamp, 1925).

The study of past climate is of great importance to understand how the climate system works and how it may change in the future. The Eocene climate in the CMB has been the topic of several studies (e.g., Licht et al., 2014b, 2015). Licht et al. (2014b) reported the presence of a monsoon-like climate in the late middle Eocene of the CMB, the south of the Tibetan-Himalayan orogen, compared to its present-day dry-winter humid subtropical climate and tropical savanna climate with dry-winter characteristics. This was based on the signal of strong seasonality from gastropod shells and mammal teeth. Subsequently, the existence of a monsoon-like climate in the late middle Eocene was corroborated by means of quantitative botanical approaches on fossil woods, which pointed at significant rainfall...
and a marked dry season (Licht et al., 2015). The presence of the monsoon-like climate in the Eocene was also demonstrated in other studies in India and China (e.g., India: Shukla et al., 2014; Tibet, China: Su et al., 2020). Climate reconstructions with palynology can provide further evidence on the existence of this monsoon-like climate in the late Eocene CMB (Chapter 3).

1.4 | THESIS OBJECTIVES, SCOPE AND OUTLINE

In this thesis, I studied the composition of the late Eocene Kalewa palynoflora, and based on this I investigated the evolution of the vegetation, environment and climate in the CMB and BT. Moreover, the abundant palm pollen that were found in the late Eocene Kalewa, which served as a bridge (Fig. 1.1) to further palm studies. Then pollen morphology (Mauritiinae) and historical biogeography and diversification (Calamoideae and Nypoideae) of ancestral palm lineages and their relationship with tectonic and climate change were explored, by combining global palm pollen record dataset and paleoclimate and climatic niche models. I addressed the RQs posed in Section 1.1 as follows.

1) In Chapter 2, I documented the composition of the late Eocene Kalewa palynoflora from the CMB with light- and scanning electron microscopy. I described in detail the morphology of important sporomorphs, discussed their botanical affinity, source ecology and historical biogeography. Specifically, I paid attention to the Sapotaceae in terms of its diversity, paleoecology and biogeography. I also determined the vegetation types these sporomorphs reflect and disentangled the driving factors of the formation of this late Eocene palynoflora. Furthermore, I investigated the components of Gondwanan versus Laurasian and “out-of-India” versus “out-of-Asia” elements. Based on this I unraveled the role and evolution of the BT by discussing plant dispersals between the India Plate, BT, mainland and SE Asia. (RQ.1)

(2) In Chapter 3, I assessed vegetation, environmental and climate change in the late Eocene CMB. To achieve this I constructed pollen diagrams with cluster analysis, performed bioclimatic analysis and sequence-biostratigraphic evaluation. Furthermore, I compared the species diversity in the late Eocene Kalewa palynoflora with that of other four contemporary tropical palynofloras with rarefaction method. Based on this dataset, I further corroborated the existence of a
monsoon-like climate in the late Eocene CMB and explored possible driving factors of this climate system. (RQs.1-3)

(3) In Chapter 4, I studied the morphology of the abundant palm and palm-like (PPL) taxa found in the late Eocene Kalewa palynoflora by single grain analysis with light- and scanning electron microscopy. I analyzed the PPL taxa with principal components analysis (PCA) to determine their paleoecology. I also quantified paleoenvironmental change with a pollen diagram using cluster analysis, combined the PPL taxa with mangrove elements. Then I compiled global Eocene records of selected palm pollen taxa and generated maps using GPlates software for spatiotemporal comparisons in species distribution. Finally, I discussed species diversity of selected PPL taxa in the Paleogene SE Asia and sought the driving factors. (RQs.3-4)

(4) In Chapter 5, I contributed equally to the paper. We compiled a comprehensive pollen database for extinct and extant Mauritiinae and mapped their global geographic distribution from the Late Cretaceous to present, using GBIF and fossil data, to discuss the global biogeography of this lineage and its relationship to tectonic and climate change. We also described pollen morphology of fossil and extant species of Mauritiinae palms with light-, scanning- and transmission electronic microscopy. Furthermore, we defined Mauritiinae species and their relationships with statistical morphometric analysis. (RQ.4)

(5) In Chapter 6, I was also equal contributor. We evaluated the role of Cenozoic climate change on the biogeographic and macroevolutionary dynamics of an iconic tropical group of plants, the palms. We focused on four palm lineages (Calaminae, Nypoideae, Eugeissoneae and Mauritiinae) with abundant and long fossil pollen records, each represented by present-day taxa with very different ecologies and varying in extant species richness. For each lineage, we inferred its diversity trajectory and biogeography through time by analyzing its fossil record, and estimated changes in the extent and distribution of climatically suitable habitat using climatic niche models for each epoch of the Cenozoic. (RQ.4)

In Chapter 7, I will present a general discussion and synthesis, and outlook on the research questions based on the results. Subsequently I will bring together all my findings from chapters 2-6 separately as Summaries in English, Dutch and Chinese.