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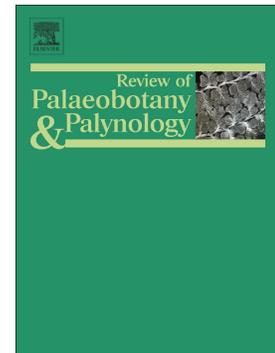


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***Grimmipollis burmanica* gen. et sp. nov.: New genus of the soapberry family  
(Sapindaceae) from the late Eocene of central Myanmar**

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**ABSTRACT**

As a crossroads for plant dispersal between Laurasia and Gondwana since at least the late Eocene, the Central Myanmar Basins have yielded rich and diverse fossil pollen. Here we report *Grimmipollis burmanica*, a new genus and species in the soapberry family (Sapindaceae) from the upper Eocene Yaw Formation in the Central Myanmar Basins. We also investigate its similarity of pollen sculpture with other selected genera using hierarchical cluster analysis, and its source paleoecology with pollen diagrams. *Grimmipollis* pollen grains are characterized by parasyncolporate apertures with an apocolpial field at each side, distinct margins along the colpi, arcuate, tuberculate and rope-shaped mesocolpial ridges, and prominent, verrucate or fossulate apocolpia. These features distinguish this genus from other syncolporate and parasyncolporate types in the extant Sapindaceae genera, and fossil pollen genera. As most syncolporate and parasyncolporate types occur in the tribe Cupanieae, *G. burmanica* is likely derived from an extinct Cupanieae and thus a rainforest tree species. The hierarchical cluster analysis confirms our establishment of *Grimmipollis*, and reveals it is morphologically close to *Meyeripollis*. The sedimentary environment from which these pollen grains were retrieved suggests that *G. burmanica* could be a member of seasonal swamp forest.

**Keywords:** Cupanieae; Morphology; Paleobotany; Paleoecology; Paleogene; Palynology

## 1. Introduction

Sapindaceae, the soapberry family, is the largest family in the order Sapindales, including 138 genera and c. 1,900 species (<http://www.theplantlist.org/1.1/browse/A/Sapindaceae/>), which mostly are trees and shrubs, and less often treelets and lianas, with a distribution predominantly in tropical or subtropical zones (Acevedo-Rodríguez et al., 2011). These genera and species belong to four subfamilies (Xanthoceroideae, Hippocastanoideae, Dodonaeoideae, and Sapindoideae) and more than 10 tribes (Acevedo-Rodríguez et al., 2011, following Harrington et al., 2005). Cupanieae, the largest tribe in Sapindaceae, contains c. 46 genera, and has a pantropical distribution in Australasia, Asia, South America and Madagascar (Harrington et al., 2005; Buerki et al., 2020). Cupanieae species in Southeast Asia are rain forests trees (Yap, 1989).

The morphology of extant Sapindaceae pollen has extensively been studied (for most of the genera in the family, Muller and Leenhouts, 1976, Acevedo-Rodríguez et al., 2011; *Mischocarpus*, van der Ham, 1977; *Pometia*, *Cubilia*, *Otonophelium* and *Litchi*, van den Berg, 1978; *Guioa*, van der Ham and van Heuven, 1989; tribe Nephelieae, van der Ham, 1990; *Lophostigma*, Acevedo-Rodríguez, 1993; *Cnesmocarpon*, *Jagera* and *Trigonachras*, Adema and van der Ham, 1993; tribe Paulinieae, Ferrucci and Anzótegui, 1993; *Serjania*, van der Ham and Tomlik, 1994; *Arytera*, van Bergen et al., 1995; *Gongrodiscus*, Turner and van der Ham, 1996; Sapindaceae pollen types in Brazilian forest fragments, Bellonzi et al., 2020). Muller and Leenhouts (1976) classified the apertural types of extant Sapindaceae pollen into 12 groups and regarded the spherical tricolporate type A with long colpi and small endoapertures as a basic type. Gonçalves-Esteves et al. (2021) concluded that tri(tetra)-colporate, which is most common, tri(tetra)-colporate, parasyncolporate, syncolporate or hemisyncolporate apertural types were found in Sapindaceae. Syncolporate and parasyncolporate types only occur in the subfamily Sapindoideae, and most commonly in the tribe Cupanieae (Acevedo-Rodríguez et al., 2011). Besides variation in the apertural types, variation also occurs in polarity, shape, size and ornamentation of the exine (Muller and Leenhouts, 1976; Acevedo-Rodríguez et al., 2011).

Fossil pollen types of Sapindaceae have also been extensively reported, including the widely distributed form-genus *Cupanieidites*, with affinity to the tribe Cupanieae. *Cupanieidites* is derived from the proposed

ancestors of the tribe Paullinieae, which originated in the Late Cretaceous of Africa and dispersed to India, the Americas and Australia (see the review in Huang, 2021; Huang et al., 2021) and Europe (e.g., Krutzsch, 1959a, b, 1961, 1969). For instance, *Cupanieidites flaccidiformis* (with affinity to *Mischocarpus*) was found in the Paleocene of Pakistan (Frederiksen, 1994), the middle Eocene of south Sulawesi, Indonesia (Morley, 1998) and late Eocene of central Myanmar (Huang et al., 2021). Other fossil pollen records include *Alectryon*-type from the middle Eocene of Germany (Hofmann and Gregor, 2018), *Cardiospermum*, *Paullinia* and *Serjania* from the late Eocene of Panama (Graham, 1985, 1987), *Paullinia* and *Serjania* from the early to middle Miocene of Mexico (Chavez et al., 1993), and *Pometia* from the Miocene of Borneo (Muller, 1964).

The Central Myanmar Basins (CMB), situated between the Indo-Burma Ranges and Sino-Burman Ranges (Fig. 1A), comprises most of Myanmar and has been a crossroads for plant dispersal between Laurasia and Gondwana since at least late Eocene, principally driven by the India-Asia collision and its tropical and proto-monsoonal climate (Huang, 2021; Huang et al., 2021). This crossroads may persist until the modern day, and thus renders Myanmar as a global biodiversity hotspot (Myers et al., 2000) with c. 12,340 spermatophyte species (according to Kress et al., 2003, and Yang et al., 2020). The CMB yields highly diverse palynofloras from the Eocene onwards (Potonié, 1960; Reimann and Aye Thaug, 1981; Soe Moe Lwin et al., 2017; Huang et al., 2020, 2021; Huang, 2021), including among many others a diversity of Arecaceae (Huang et al., 2020) and Sapotaceae (Huang et al., 2021) pollen types.

In this study, we investigate the (para)syncolporate sapindaceous fossil pollen from the upper Eocene Yaw Formation in the CMB with light microscopy (LM) and scanning electron microscopy (SEM). We compare these fossil pollen with the pollen in the extant genera of Sapindaceae and (para)syncolporate fossil pollen form-genera to discuss its taxonomic position. We further seek to unravel its source paleoecology by comparing its distribution in relation to paleoecological and systems tract interpretation as presented in Huang et al. (2023).

## 2. Material and Methods

### 2.1. Geological Setting

The CMB include four wide Late Cretaceous–Cenozoic Basins: the Chindwin and Shewbo Basins to the north, and the Minbu and Pegu Basins to the south. The Chindwin and Minbu Basins are in a forearc position, while the Shewbo and Pegu Basins are in a backarc setting, separated by the Wuntho-Popa Arc (WPA; Fig. 1A; Bender, 1983; Pivnik et al., 1998; Licht et al., 2019). In the late Eocene, the CMB (1) had a near-equatorial position (Westerweel et al., 2019, 2020); (2) was open to the Bay of Bengal and located at the margin of Eurasia (Licht et al., 2013); (3) was predominantly sourced from the WPA and northern Myanmar (Westerweel et al., 2020); (4) formed a crossroads for plant dispersal between Laurasia and Gondwana (Huang et al., 2021).

The Kalewa section is situated in the Kalewa Township, Sagaing Region in northwestern Myanmar, and located at the southern margin of the Chindwin Basin (Fig. 1A; 23°14' N, 94°15' E). This c. 650-m thick section comprises the Yaw Formation (Fig. 1B). This Formation consists of four prominent sedimentary facies associations (FA): organic-rich lacustrine mudstones (FA2), deltaic tidal siltstones and sandstones (FA3), thick continental sandstones (FA4), and lignite layers from past swamps (FA1), reflecting a quasi-closed estuarine depositional system (Fig. 1B; Licht et al., 2019; Westerweel et al., 2020). The underlying upper middle Eocene Pondaung Formation was deposited in a fluvial deltaic setting and opened towards the proto-Bay of Bengal (Aung Naing Soe et al., 2002; Licht et al., 2014). The overlying Tonhe Formation possibly with an age of late Oligocene–early Miocene (indicated from the spores in Soe Moe Lwin et al., 2017), is formed of thick packages of coarse-grained sandstones and conglomerates (Westerweel et al., 2020). 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), and palynostratigraphy (Huang et al., 2020).

## 2.2. Preparation of Fossil Pollen

We collected 81 samples from mudstones and sandstones in the upper Eocene Yaw Formation along the Kalewa section. These samples have been documented and published in terms of fossil palm pollen (Huang et

al., 2020), floristic composition (Huang et al., 2021), climate and sequence biostratigraphy (Huang et al., 2023). Two processing methods were applied to extract as many and well-preserved pollen grains as possible: (1) 1.3 grams of rock sample was boiled in 10% sodium pyrophosphate, followed by the 10% hydrochloric acid (HCl), sieving, acetolysis mixture and bromoform-treatment; (2) 30 grams of rock sample was treated with 10% HCl and 40% hydrofluoric acid (HF), followed by a heavy liquid separation and sieving. Final residues were mounted on a slide in glycerin and sealed with paraffin for LM observation and microphotography. Residues were also used for LM and SEM analysis at the Department of Palaeontology (DoP), University of Vienna, Austria. For details on processing refer to Huang et al. (2020). All pollen slides and residues are stored at the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, and SEM stubs are deposited at the DoP.

### 2.3. Microphotography

All LM micrographs in Plate I were taken with Fujifilm X-E2 and a Zeiss Universal microscope with 63× Plan Neofluar NA1, 25 oil at the IBED, applying Nomarski Differential Interference Contrast (DIC) following Bercovici et al. (2009). Stacking of micrographs with different layers through manual Z-making in Helicon Focus and Photoshop CC provide a fully focused image. LM micrographs in Plates II–IV were taken by the camera ProgRes Speed XT<sup>core</sup> 5, linked with the LM Nikon Eclipse 80i; SEM micrographs in Plates II–IV were taken with the SEM JEOL JSM-6400. Plates II–IV were made with InDesign CC (Adobe, California, US).

### 2.4. Pollen Analysis

We compared the pollen type with the pollen micrograph database of Sapindaceae held by the third author (RvdH). We applied single-grain analysis (Zetter, 1989; Halbritter et al., 2018) to investigate the details of pollen sculpture at the DoP. LM and SEM pollen terminology follows Punt et al. (2007) and Halbritter et al. (2018), respectively. We measured the pollen with the software ImageJ (National Institute of Health, USA)

(pollen information and measurement results are provided in Supplementary Material 1, Tables S1 and S2). With presence-absence data matrix (Supplementary Material 1, Tables S3 and S4), we applied hierarchical cluster analysis (HCA, with Ward's method and Euclidean distance) on PAST 4.10 software (Hammer et al., 2001) to determine similarity of pollen sculpture among genera. We constructed the pollen diagram with the Tilia v.3.0.1 software (Grimm, 1991). Software-produced images were processed with CorelDRAW 2019 (Corel Corporation, Ottawa, Canada).

### 3. Results

#### 3.1. Systematic and descriptive palynology

*Kingdom:* PLANTAE Haeckel, 1866

*Division:* SPERMATOPHYTA Willkomm, 1854

*Subdivision:* MAGNOLIOPHYTA Cronquist et al., 1966

*Order:* SAPINDALES Juss. Ex Bercht. and Juss., 1820

*Family:* SAPINDACEAE Juss., 1789

*Subfamily:* SAPINDOIDEAE Burnett Brummett, 1835

*Tribe:* CUPANIEAE Blume, 1847

*Genus:* *Grimmipollis* Huang, McJannet et Hoorn gen. nov.

(格林氏粉属, gé lín shì fěn shù)

*Etymology:* The generic name “*Grimmipollis*” is named after and in honor of the influential American paleoecologist and palynologist Dr. Eric Grimm (1951–2020), for his immense contributions to palynology, particularly on developing the software Tilia (Grimm, 1991; including the program CONISS, Grimm 1987), which was also applied in this study, and the Neotoma database (Williams et al., 2018).

*Generic diagnosis:* Triparasyncolporate, mesocolpial ridges arcuate, granulate, rugulate, tuberculate (prominently verrucate) and rope-shaped, apocolpial fields verrucate or fossulate, mesocolpia granulate and rugulate, margins well developed along the colpi, apocolpia prominent, colpi wide.

*Type species:* *Grimmipollis burmanica* Huang, Morley et Hoorn sp. nov.

***Grimmipollis burmanica*** Huang, Morley et Hoorn sp. nov.

(缅甸格林氏粉, miǎn diàn gé lín shì fěn)

Plates I–IV

*Holotype:* IBED-T 40.976 (Plate IA).

*Paratypes:* IBED-T 40.974 (Plate IB), IBED-T 41.222/1 (Plate IIA), IBED-T 41.227 (Plate IIC), IBED-T 40.968 (Plate IIIA), IBED-T 41.222/2 (Plate IIIC), IBED-T 41.189 (Plate IVA), IBED-T 41.222/3 (Plate IVC).

*Stratigraphic horizon:* Upper Eocene Yaw Formation, Central Myanmar Basins (Fig. 1B).

*Type locality:* Western side of the Kalewa Township, Sagaing Region, Myanmar (23°14' N, 94°15' E).

*Age:* Late Eocene, c. 37–36 Ma (Licht et al., 2019; Westerweel et al., 2020; Huang et al., 2021).

*Repository:* Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, the Netherlands, and Department of Palaeontology, University of Vienna, Austria. Information about the numbers of sample/residue and England Finder coordinates of the pollen micrographs in the Figures are provided in Supplementary Material 1, Table S1.

*Etymology:* The specific epithet “*burmanica*” refers to the origin (Burma, former name of Myanmar) of the fossil pollen.

*Specific diagnosis:* Outline convex-triangular to near-circular in polar view, pollen size category small, triparasyncolporate, mesocolpial ridges arcuate, granulate, rugulate, tuberculate and rope-shaped, apocolpial fields verrucate or fossulate, mesocolpia granulate and rugulate, margins well developed along the colpi, apocolpia prominent, colpi wide.

*Description:* Pollen grains isopolar monads, outline convex-triangular (e.g., Plates IA, IIIA) to near-circular (e.g., Plates IB, IVD) in polar view; pollen size category small, equatorial diameter 12.6–19.0  $\mu\text{m}$ ; triparasyncolporate, angulaperturate, ectocolpus long, wide and connected around the poles, forming apocolpia,

pori circular and situated equatorially, 0.4–1.7  $\mu\text{m}$  in diameter; apocolpia triangular (e.g., Plate IVE) or severely corroded (Plate IVF), sculpture verrucate or fossulate (SEM), size 3.0–8.0  $\mu\text{m}$ , verrucae up to 0.8  $\mu\text{m}$  in diameter (SEM); mesocolpia granulate, granules up to 0.8  $\mu\text{m}$  in diameter (SEM), penetrated through by rope-like sculpture (e.g., Plates IIIH, IIIG), forming coarse rugulae, tuberculate rope-like structure 0.5–1.4  $\mu\text{m}$  in diameter (SEM); margins psilate, rugulate and well developed along colpi, 0.4–1.6  $\mu\text{m}$  in diameter, thicker around the pores (SEM); exine with indistinct columellate, 0.3–0.6  $\mu\text{m}$  thick, sexine and nexine indiscernible; pollen wall tectate; pollen sculpture psilate, scabrate to rugulate in LM, verrucate (apocolpia), psilate and rugulate (margins), granulate and rugulate (mesocolpia) in SEM. 18 specimens measured in polar view (Supplementary Material 1, Table S2), as the pollen grains did not occur in equatorial view. Due to their oblate shape, syncolporate/parasycolporate pollen grains whether extant or fossil, appear in preparations much more frequently in polar view than in equatorial view, similarly in family Myrtaceae, and genus *Nymphoides* (family Menyanthaceae).

*Botanical affinity:* Extinct and with affinity to Cupanieae, largest tribe of Sapindaceae; and see discussion below.

#### 4. Discussion

##### 4.1. Placement of *Grimmipollis burmanica* in Sapindaceae and comparisons with the extant parasycolporate pollen genera of the family

For the assignment of the studied fossil pollen at the family level, qualitative characters are more important than quantitative characters (e.g., pollen size), because the latter may change during the process of deposition, particularly sediment compaction. Additionally, even within a genus of Sapindaceae, pollen grain size may vary considerably. At the very first glance, our pollen type seems to belong to Myrtaceae with its parasycolporate aperture with arcuate colpi. However, its rounded shape and ornamentation of the exine (verrucate or fossulate

apocolpial field and granulate and tuberculate mesocolpia) does not match any myrtaceous morphotype (Thornhill and Macphail, 2012).

The tuberculate condition is also seen in some Leguminosae, such as *Humboldtia*, but the syncolporate aperture configuration is missing in this family. Pollen grains of *Pachydiscus gaultherioides* (= *Periomphale gaultherioides* in van Steenis, 1978; = *Periomphale pancheri* in Gardner, 1978) in the family Alseuosmiaceae (with micrographs from Carlos Jaramillo, Smithsonian Tropical Research Institute) resemble our fossil pollen; however, although it has margins along the colpi, it is syncolpate and has no tuberculate ridges. Pollen grains of the Madagascan endemic family Sarcolaenaceae generally are united in tetrahedral tetrads, and seem parasyncolporate (Nilsson et al., 1996). However, the tetrads range from c. 40 to 120 µm in diameter, with psilate ornamentation (including margins). The most comparable Sarcolaenaceae types occur in *Leptolaena*, *Sarcolaena*, *Xyloolaena* and *Rhodolaena*; nevertheless, the constituent grains are tricolporate without apocolpial fields (Carlquist, 1964; Nilsson et al., 1996).

The combination of a syncolporate apertural pattern, coupled with the tuberculate exine (as in *Magonia* from tribe Harpullieae) supports the placement of the fossil pollen into Sapindaceae. Margines form just part of ornamentation and are a common feature of Sapindaceae, but do not form an independent character. Therefore, the presence of the prominent margins of the fossil pollen along the colpi is not generally an argument for its affinity. There are some connections between the mesocolpia and the margins; namely, margins are not distinctly separated from the mesocolpia. In Sapindaceae, the ornamentation is denser around the colpi. However, the distinct margins along the colpate apertures are rare in Sapindaceae.

We compared our fossil pollen with the extant pollen archive in Sapindaceae, including 134 genera, almost covering the whole family (138 genera). We listed parasyncolporate pollen types (33 genera) and compared these types with our fossil pollen in terms of sculpture. Parasyncolporate pollen types only occur in the subfamily Sapindoideae, and mostly in the tribe Cupanieae including 28 genera; most genera of this tribe have a Southeast Asian distribution (Table 1). Other parasyncolporate pollen types occur in the tribes Nephelieae (*Alectryon*), Schleichereae (*Schleichera*) and several genera incertae sedis (*Castanospora*, *Tristira* and

*Tristiropsis*) (Table 1). None of the pollen of these 33 genera is comparable to our fossil pollen in terms of sculpture, with most of them having rugulate ornamentation of exine (Table 1).

The four genera which are not in the archive are: (1) *Chonopetalum* (not placed in a tribe), with a single species in central and eastern Africa; (2) *Euchorium* (subfamily Dodonaeoideae), with a single species in Cuba (pollen not parasyncolporate); (3) *Haplocoelopsis* (tribe Cupanieae), with a single species in equatorial Africa (e.g., Guinea); (4) *Namataea* (tribe Lepisantheae, subfamily Sapindoideae), with a single species in Cameroon. They are possibly not the nearest living relatives (NLR) of our fossil pollen, as they have African and Central American distributions. However, we cannot exclude the possibility that our fossil pollen may have an affinity with African taxa facilitated by the Africa-India floristic interchange (e.g., Basal et al., 2022; Shi et al., 2022).

HCA on our fossil pollen and the 33 parasyncolporate genera in Sapindaceae (Fig. 2A) shows that *Grimmipollis* does not share similarity with any of these genera in terms of ornamentation of exine. This further supports the establishment of the genus *Grimmipollis*. Besides, HCA also suggests that the ornamentation pattern of the exine cannot be used to differentiate tribes in the subfamily Sapindoideae.

#### 4.2. Comparisons of *Grimmipollis burmanica* with parasyncolporate fossil pollen genera in Jansonius and Hills (1976)

We compared our fossil pollen with all 10 syncolporate and parasyncolporate fossil pollen genera from Jansonius and Hills (1976) (Table 2). We included syncolporate fossil pollen genera because these genera may share similar sculptural patterns with our fossil pollen and may have developed from syncolporate to parasyncolporate aperture over geological time.

Considering the ornamentation of the exine along the colpi, it shows that the nearest form-genus is *Phaseolidites*, as it has sexinous thickening which pass over the poles from aperture to aperture, while our fossil pollen grains have distinct psilate and thickened margins. However, the ornamentation of the exine of *Phaseolidites* pollen is psilate, scabrate to granulate, weakly verrucate or vermiculate. Moreover, *Phaseolidites* pollen is bigger than our fossil pollen.

The exine of *Syncolporites* pollen is scabrate to micro-verrucate, psilate, or rugulate, with annulus psilate (Table 2). In the Americas, it mostly resembles *Syncolporites rugucostatus* Sarmiento and *Syncolporites planiverrucosus* Jan du Chêne (pers. comm., Carlos Jaramillo, Smithsonian Tropical Research Institute). Nonetheless, the ornamentations of their exine (psilate, Sarmiento, 1992; and psilate to verrucate, Jan du Chêne, 1977) are different from that of our fossil pollen.

*Meyeripollis*, a genus described from the Eocene–Miocene sediments of Assam (India) (Baksi and Venkatachala, 1970), which has syncolporate pollen with thickened margins and has received little attention, but closely matches our fossil pollen from a broad perspective. It is thought to be derived from trees of swamp forests, and probably from Myrtaceae (Huang et al., 2021). However, the exine of its pollen is gemmate and scabrate without apocolpia and tuberculate ridges, which is different from our fossil pollen. The aforementioned genus *Periomphale* with an East Gondwanan distribution shows some close similarities to *Meyeripollis* and may be a contender for the parent plant of *Meyeripollis*, although the specimen of *Eucalyptus spathulata* (Myrtaceae) illustrated by Thornhill and MacPhail (2012, Fig. 2c), may be a closer match, suggesting a Myrtaceous affinity.

The exine of *Cupanieidites* is distinctly to faintly reticulate (Cookson and Pike, 1954), smooth, punctate, granulate, striate or reticulate (Krutzsch, 1969), punctate to reticulate (Chmura, 1973). Therefore, the exine of our fossil pollen (with tuberculate ridges) is outside the variation of any previous emendations of *Cupanieidites*, namely, the circumscription for *Cupanieidites* does not include the exine morphology seen in our fossil pollen. *Cupanieidites* has been reported from the Late Cretaceous onwards (Muller, 1981). It was later found in many areas and from different time periods, including the Senonian of India, Maastrichtian of Brazil and USA, Paleocene of Pakistan, Eocene of Australia, middle Eocene of Indonesia, and the late Eocene of Myanmar, and is thought to be derived from a riant group that dispersed from Africa, into India, and then Southeast Asia (Huang et al., 2021).

The other 12 genera have different sculptures compared with our fossil pollen without tuberculate exine (Table 2): *Cranwellia* has a striate appearance; *Duplopollis* is minutely reticulate; *Myrtaceidites* is not tuberculate; granules of *Nymphoideipites* are often joined in striae running parallel to the side, forming finely reticulate contour; *Retisyncolporites* and *Retitrisyncolpites* are reticulate; although *Rhamneaepites* has no

description, it is not tuberculate from the micrograph; *Rhoiptepollis* is only faintly granulate; *Sapindaceapites* is echinate or otherwise ornamented and not tuberculate; *Striatellipollis* is striate with reticulate apocolpia; *Symplocacites* is indistinctly reticulate with sinuous muri; *Xinjiangpollis* can also be punctate, scabrate, reticulate or striate.

HCA on our fossil pollen and the 15 (*Rhamnaepites* not included as without description on its sculpture) syncolporate/parasyncolporate genera (Fig. 2B) suggests that *Meyeripollis* and *Grimmipollis* are most similar in terms of ornamentation of exine, although the latter has syncolporate pollen. This similarity can be explained by their common appearance – tubercles on the exine.

#### 4.3. Botanical affinity of *Grimmipollis burmanica* and its source paleoecology

As parasyncolporate pollen mostly exists in Cupanieae, which are trees of rain forests (Yap, 1989), the parent plant of *Grimmipollis burmanica* may be derived from this tribe. However, considering the unique ornamentation of the exine of *G. burmanica*, it may have been derived from an extinct genus, and thus does not exist today.

Palynological analysis of compositional changes of *G. burmanica* and other selected taxa which have known environmental preferences, was performed to understand the source paleoecology of *G. burmanica*. From the bottom to the top of the Kalaung section, the paleoenvironments change from a brackish, tidally influenced setting to a fully freshwater setting (Huang et al., 2020), more specifically, from a barrier-bound estuary to a fluvial setting (Licht et al., 2019). This is suggested by palynological evidence (the up-section increase in percentages of freshwater taxa, i.e., *Dicolpopollis*, *Longapertites* and *Palmaepollenites kutchensis*, and the decrease of coastal taxa, i.e., *Spinizonocolpites*, *Proxapertites operculatus*, *Acrosctichum*, *florschuetzia* and *Avicennia*; Fig. 3; Huang et al., 2020) and sedimentological data (change of lithofacies associations; Licht et al., 2019). The reconstructed pollen diagram (Fig. 3, with pollen count data in Supplementary Material 1, Table S5) indicates that *Grimmipollis burmanica* is common in the basal part of the succession and missing from the uppermost samples. Otherwise, towards to the top of the section the compositional percentages of *Grimmipollis*

*burmanica* keep steady generally. The predominance of occurrences in the basal part, coinciding with the PaBart-1 lowstand, and the upper part, coinciding with the PaPr-1 lowstand and early transgressive systems tracts, suggest that the source taxon may have occurred during periods of more seasonal climate, and most likely was an element of seasonal swamp forests.

## 5. Conclusions

We report a new fossil genus and species, *Grimmipollis burmanica*, from the upper Eocene Yaw Formation in Central Myanmar Basins, examined using light microscopy (LM) and scanning electron microscopy (SEM). Pollen of *G. burmanica* is triparasyncolporate with verrucate or fossulate apocolpial fields, and granulate, rugulate and tuberculate mesocolpia, and is characterized by distinct plicate and rugulate margins bordering the colpi. Based on its unique pollen morphology and its close similarity to the tribe Cupanieae, *G. burmanica* is likely to have been derived from an extinct member of the tribe Cupanieae within the soapberry family (Sapindaceae). HCA indicates that *Grimmipollis* is morphologically closest to *Meyeripollis*, whereas palynological analysis suggests that *G. burmanica* was most likely a member of seasonal swamp forests.

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## Appendix A. Supplementary data

Supplementary material 1

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**Fig. 1.** Topographic map (A) and sedimentary log (B), showing the locality, lithology, and pollen-productive sampling layers of the upper Eocene Yaw Formation in Central Myanmar Basins. (A) was made with base map from Natural Earth (<https://www.natureearthdata.com/>), with ranges referring to Licht et al. (2014, 2019) and Morley et al. (2020) and red square indicating the locality of the Kalewa section, while (B) was modified after Licht et al. (2019), with geomagnetic polarity timescale (GTS16) from Ogg et al. (2016), and magnetostratigraphy from Westerweel et al. (2020). In the Paleosol column of (B), black lines indicate histosols. Abbreviations: in (A), HB = Hukawng Basin, CB = Chindwin Basin, SB = Shwebo Basin, MB = Minbu Basin, PB = Pegu Basin, WPA = Wuntho-Popa Arc; in (B), vfs = very fine sand, fs = fine sand, ms = medium sand, cs = coarse sand, B = Boulder.

**Fig. 2.** Dendrograms (constructed with data from Supplementary Material 1, Tables S3 and S4) based on hierarchical cluster analysis (HCA) with Ward's method of pollen morphological characters from selected extant and fossil genera. Extant genera are those with parasyncolporate pollen in Sapindaceae, and fossil general are those with syncolporate/parasyncolporate pollen in Jansonium and Hills (1976). The dendrograms support our establishment of the new genus *Grimmipollis*, and its similarity with *Meyeripollis*. Abbreviations of tribes: C = Cupanieae, N = Nephelieae, S = Schleichereae, I = Inbertae sedis.

**Fig. 3. A,** Details of Sedimentary log referring to Fig. 1B. **B and D–F,** Sequence biostratigraphic contents from Huang et al. (2023): B shows depositional sequences and systems tracts; D is pollen zones; E indicates Geomagnetic polarity timescale (GTS16) (Ogg et al., 2016) and corresponding epoch and age; F is succession of late Eocene depositional sequences according to Hardenbol et al. (1998) and the coastal onlap curve of International Commission on Stratigraphy (ICS) (2020); Abbreviations: TST = transgressive systems tract, LST = lowstand systems tract, HST = highstand systems tract, PF = planktonic foraminifer, N = calcareous nannofossil. **C,** Pollen diagram showing the compositional change of *Grimmipollis burmanica* and freshwater palms (*Dicolpopollis*, *Longapertites* and *Palmaepollenites kutchensis*), coastal palm(-like) taxa

(*Spinizonocolpites* and *Proxapertites operculatus*) and (back-)mangroves (*Acrostichum*, *Florschuetzia* and *Avicennia*) throughout the upper Eocene Yaw Formation in Central Myanmar Basins.

**Plate I.** LM micrographs of *Grimmipollis burmanica* from the upper Eocene Yaw Formation in Central Myanmar Basins. A is holotype and B is one of the paratypes. Scale bar = 5  $\mu\text{m}$ .

**Plate II.** LM (A–D) and SEM (E–J) micrographs of *Grimmipollis burmanica* from the upper Eocene Yaw Formation in Central Myanmar Basins. A–B, E, G–I are the same grain, and C–D, F, J are the same grain. Both are paratypes. Scale bars: A–D = 10  $\mu\text{m}$ ; E–F = 5  $\mu\text{m}$ ; G–J = 1  $\mu\text{m}$ .

**Plate III.** LM (A–D) and SEM (E–J) micrographs of *Grimmipollis burmanica* from the upper Eocene Yaw Formation in Central Myanmar Basins. A–B, E, G, I are the same grain, and C–D, F, H, J are the same grain. Both are paratypes. Scale bars: A–D = 10  $\mu\text{m}$ ; E–F = 5  $\mu\text{m}$ ; G–J = 1  $\mu\text{m}$ .

**Plate IV.** LM (A–D) and SEM (E–J) micrographs of *Grimmipollis burmanica* from the upper Eocene Yaw Formation in Central Myanmar Basins. A–B, E, G, I are the same grain, and C–D, F, H, J are the same grain. Both are paratypes. Scale bars: A–D = 10  $\mu\text{m}$ ; E–F = 5  $\mu\text{m}$ ; G–J = 1  $\mu\text{m}$ .

**Table 1** Sapindaceae genera with para-syncolporate pollen types (occurring only in the subfamily Sapindoideae, and mostly in the tribe Cupanieae) and their features of aperture and sculpture, based on Acevedo-Rodríguez et al. (2011). Abbreviations: C = Cupanieae, N = Nephelieae, S = Schleichereae, I = Incertae sedis.

Genus and tribe	Aperture	Sculpture
<i>Arytera</i> (C)	Colporate to parasyncolporate, rarely syncolporate	Rugulate to striate-rugulate
<i>Cnesmocarpon</i> (C)	Syncolporate or parasyncolporate	Psilate or indistinctly rugulate
<i>Cupania</i> (C)	Syncolporate or parasyncolporate	Rugulate
<i>Cupaniopsis</i> (C)	Syncolporate or parasyncolporate,	Rugulate, striate-reticulate, reticulate or

	sometimes colporate	perforate, sometimes verrucate
<i>Diploglottis</i> (C)	Parasyncolporate	Rugulate or psilate
<i>Elattostachys</i> (C)	Colporate or parasyncolporate	Striate to rugulate
<i>Euphorianthus</i> (C)	Parasyncolporate	Rugulate
<i>Gloeocarpus</i> (C)	Syncolporate or parasyncolporate	Rugulate
<i>Gongrodiscus</i> (C)	Parasyncolporate	Rugulate
<i>Guioa</i> (C)	Syncolporate or parasyncolporate	Rarely colporate, rugulate to perforate or psilate
<i>Jagera</i> (C)	Syncolporate or parasyncolporate	Perforate or reticulate with often finely tapering scabrae
<i>Lepiderema</i> (C)	Syncolporate, parasyncolporate or colporate	Rugulate–reticulate
<i>Matayba</i> (C)	Syncolporate or parasyncolporate, sometimes colporate	Rugulate
<i>Mischarytera</i> (C)	Parasyncolporate, sometimes colporate	Rugulate
<i>Mischocarpus</i> (C)	Syncolporate or parasyncolporate, sometimes colporate	Rugulate to rugulate–reticulate
<i>Molinaea</i> (C)	Parasyncolporate, rarely syncolporate or colporate	Rugulate
<i>Neotina</i> (C)	Parasyncolporate or colporate	Rugulate to rugulate–reticulate
<i>Paranephelium</i> (C)	Syncolporate or parasyncolporate	Rugulate
<i>Pentascyphus</i> (C)	Syncolporate or parasyncolporate	Rugulate
<i>Phyllotrichum</i> (C)	Syncolporate or parasyncolporate	Striate
<i>Rhysotoechia</i> (C)	Syncolporate or parasyncolporate	Rugulate to perforate, sometimes psilate
<i>Sarcopteryx</i> (C)	Syncolporate or parasyncolporate	Rugulate to rugulate–reticulate
<i>Sarcotoechia</i> (C)	Parasyncolporate	Rugulate
<i>Synima</i> (C)	Parasyncolporate	Rugulate–reticulate
<i>Tina</i> (C)	Syncolporate or parasyncolporate	Rugulate
<i>Toechima</i> (C)	Parasyncolporate	Rugulate to rugulate–reticulate
<i>Trigonachras</i> (C)	Syncolporate or parasyncolporate	Perforate to scabrate with often finely tapering scabrae
<i>Vouarana</i> (C)	Parasyncolporate	Rugulate

<i>Alectryon</i> (N)	Colporate to parasyncolporate	Striate to rugulate
<i>Schleichera</i> (S)	Parasyncolporate	Striate
<i>Castanospora</i> (I)	Parasyncolporate	Striate–rugulate
<i>Tristira</i> (I)	Parasyncolporate	Rugulate
<i>Tristiropsis</i> (I)	Parasyncolporate	Rugulate

**Table 2** Fossil genera with syncolporate and parasyncolporate pollen types in Jansonius and Hills (1976).

<b>Genus</b>	<b>Aperture</b>	<b>Sculpture</b>
<i>Cranwellia</i>	Occasionally syncolporate	Granulate with a striate appearance
<i>Cupanieidites</i>	Syncolporate or parasyncolporate	Distinctly or faintly reticulate, smooth, punctate, granulate, striate or reticulate, or scabrate to reticulate
<i>Duplopollis</i>	Syncolporate or parasyncolporate	Minutely reticulate with underlying collumellae layer
<i>Meyeripollis</i>	Syncolporate	Gemmate, tuberculate and verrucate
<i>Myrtaceidites</i>	Syncolporate or parasyncolporate	Smooth, rugulate, delicately granulate or finely infratextured, never distinctly reticulate
<i>Nymphoideipites</i>	Parasyncolporate	Finely granulate, granules often joined in striae running parallel to the side, contour finely reticulate
<i>Phaseoliidites</i>	Syncolporate	Psilate, scabrate to granulate, weakly verrucate or vermiculate
<i>Retisyncolporites</i>	Syncolporate	Reticulate, muri simplibaculate
<i>Retitrisyncolpites</i>	Mostly syncolporate, but also recognized as trichotomoculate	Reticulate
<i>Rhamneaepites</i>	Syncolporate	No description
<i>Rhoipteapollis</i>	Syncolporate	Faint, granulate
<i>Sapindaceaeipites</i>	Syncolporate	Reticulate, or otherwise ornamented, but never echinate or verrucate
<i>Striatellipollis</i>	Syncolporate	Punctate or radially striate, apocolpia reticulate
<i>Symplocacites</i>	Syncolporate	Indistinctly reticulate with sinuous muri
<i>Syncolporites</i>	Syncolporate	Scabrate to micro-verrucate, psilate, or rugulate, annulus psilate
<i>Xinjiangpollis</i>	Occasionally syncolporate	Smooth, punctate, scabrate, granulate, reticulate or striate

**Declaration of interests**

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

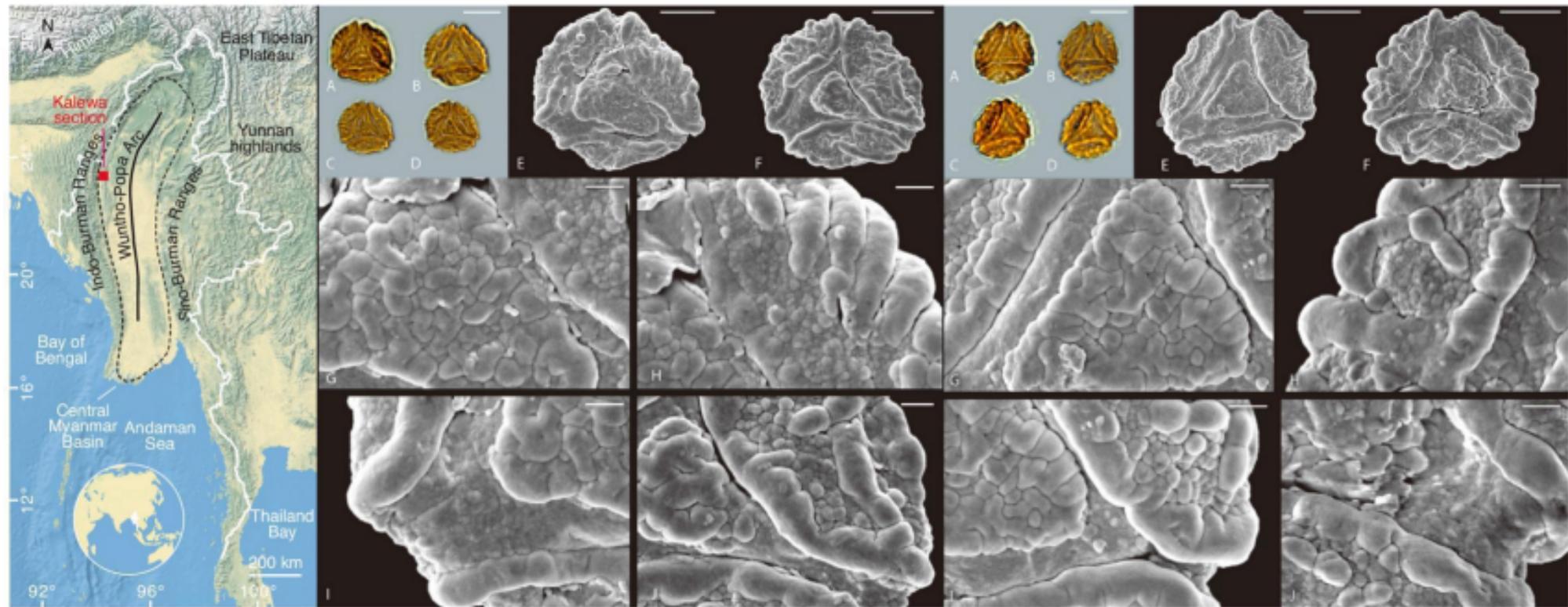
The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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### Highlights

- *Grimmipollis burmanica*, a new genus and species was reported from the late Eocene central Myanmar.
- *Grimmipollis* pollen grains are parasyncolporate with specific sculpture.
- Hierarchical cluster analysis suggests *Grimmipollis* has closest similarity with *Meyeripollis*.
- *G. burmanica* is likely derived from an extinct Cupanieae and thus a rainforest tree species.
- *G. burmanica* could be a member of seasonal swamp forests.

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Graphics Abstract

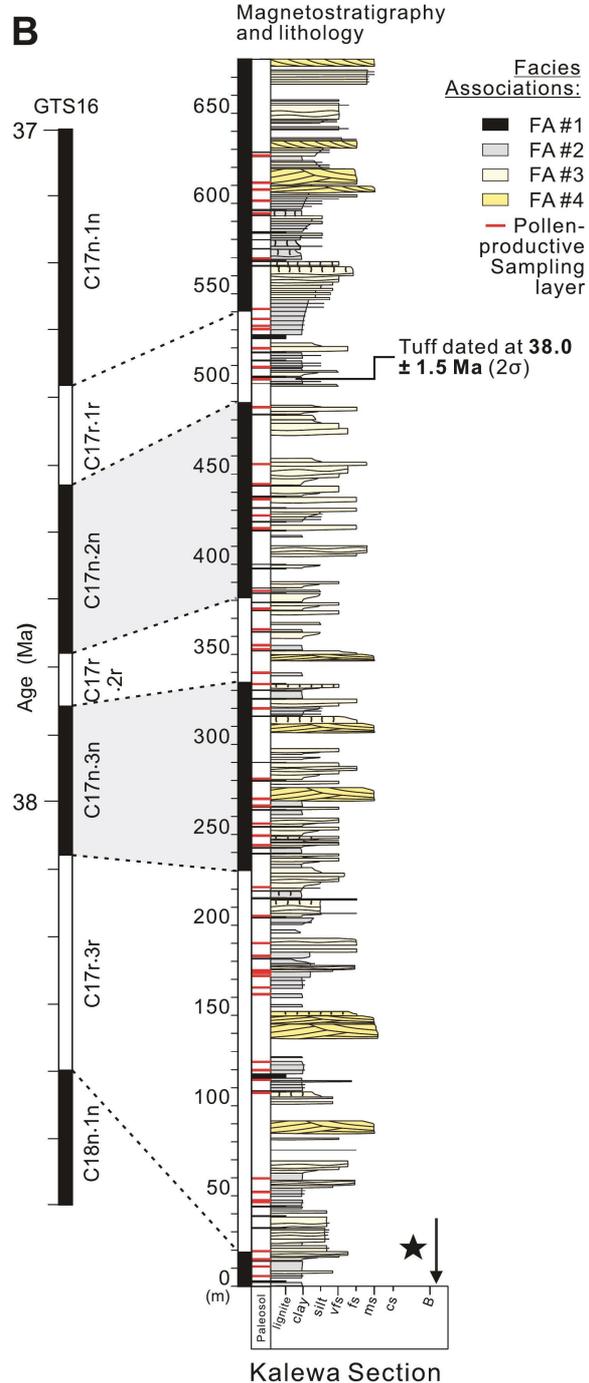
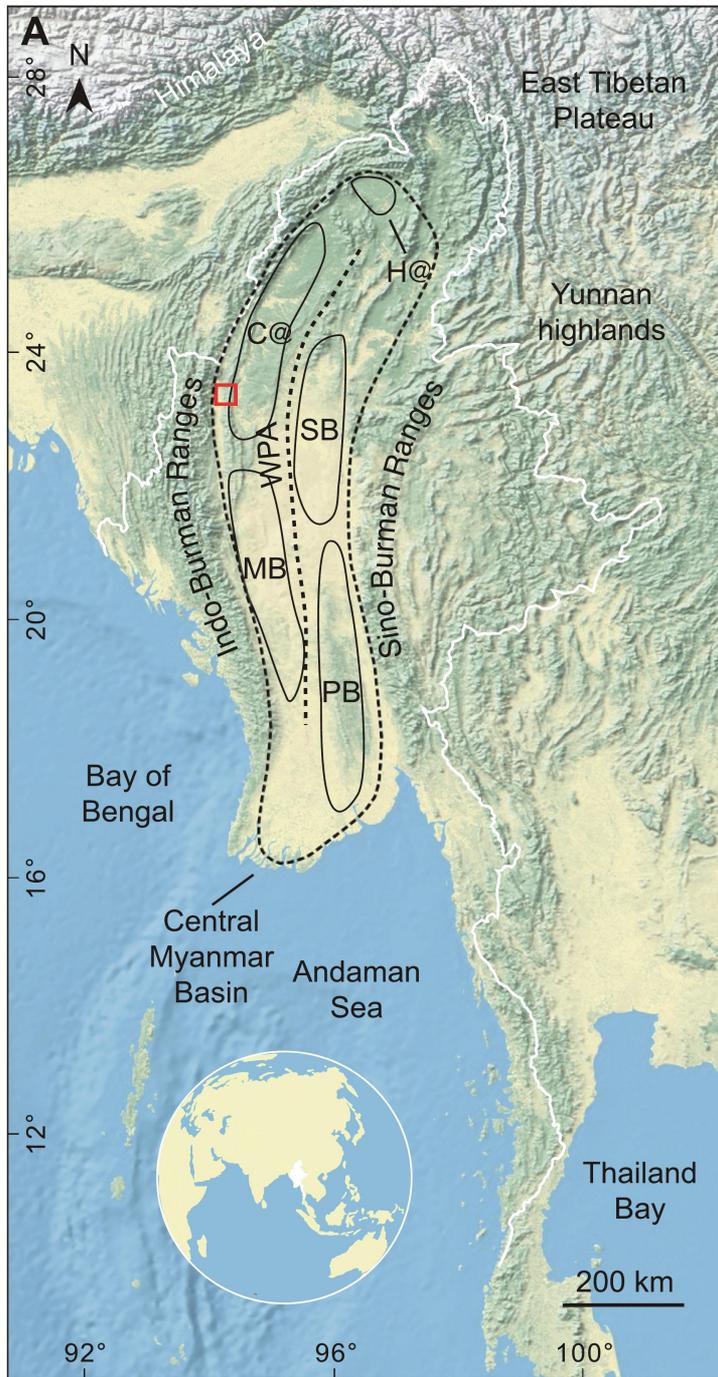
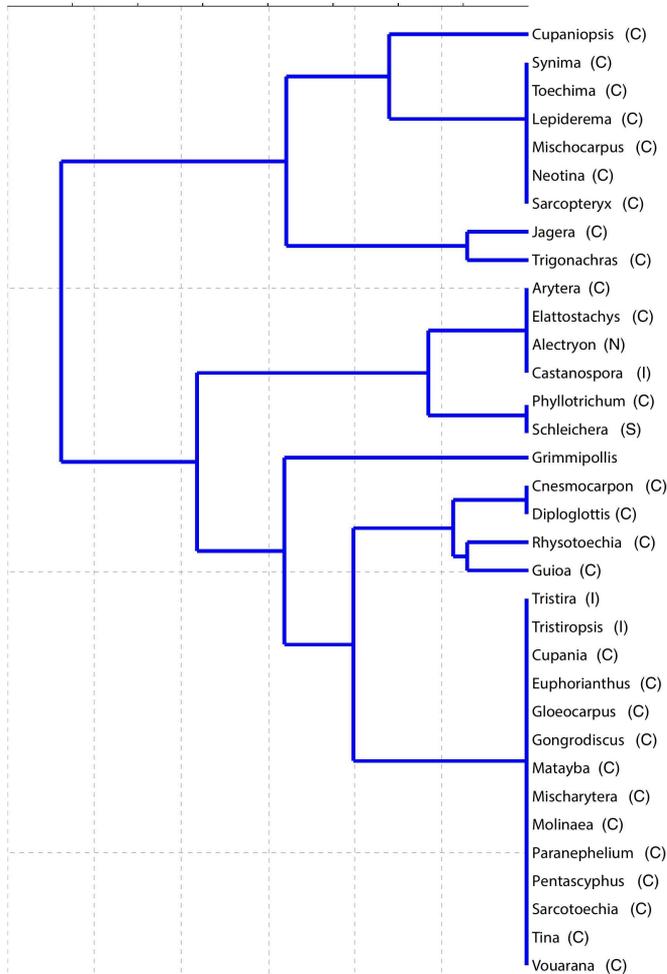


Figure 1

A - Extant

Euclidean distance

5.25 4.50 3.75 3.00 2.25 1.50 0.75



B - Fossil

Euclidean distance

5.25 4.50 3.75 3.00 2.25 1.50 0.75

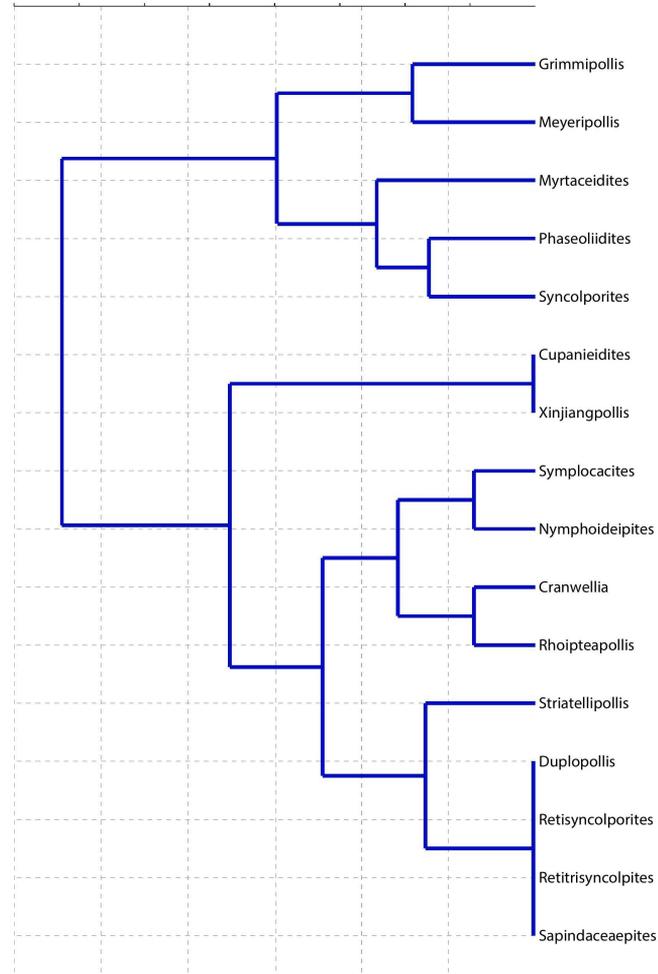


Figure 2

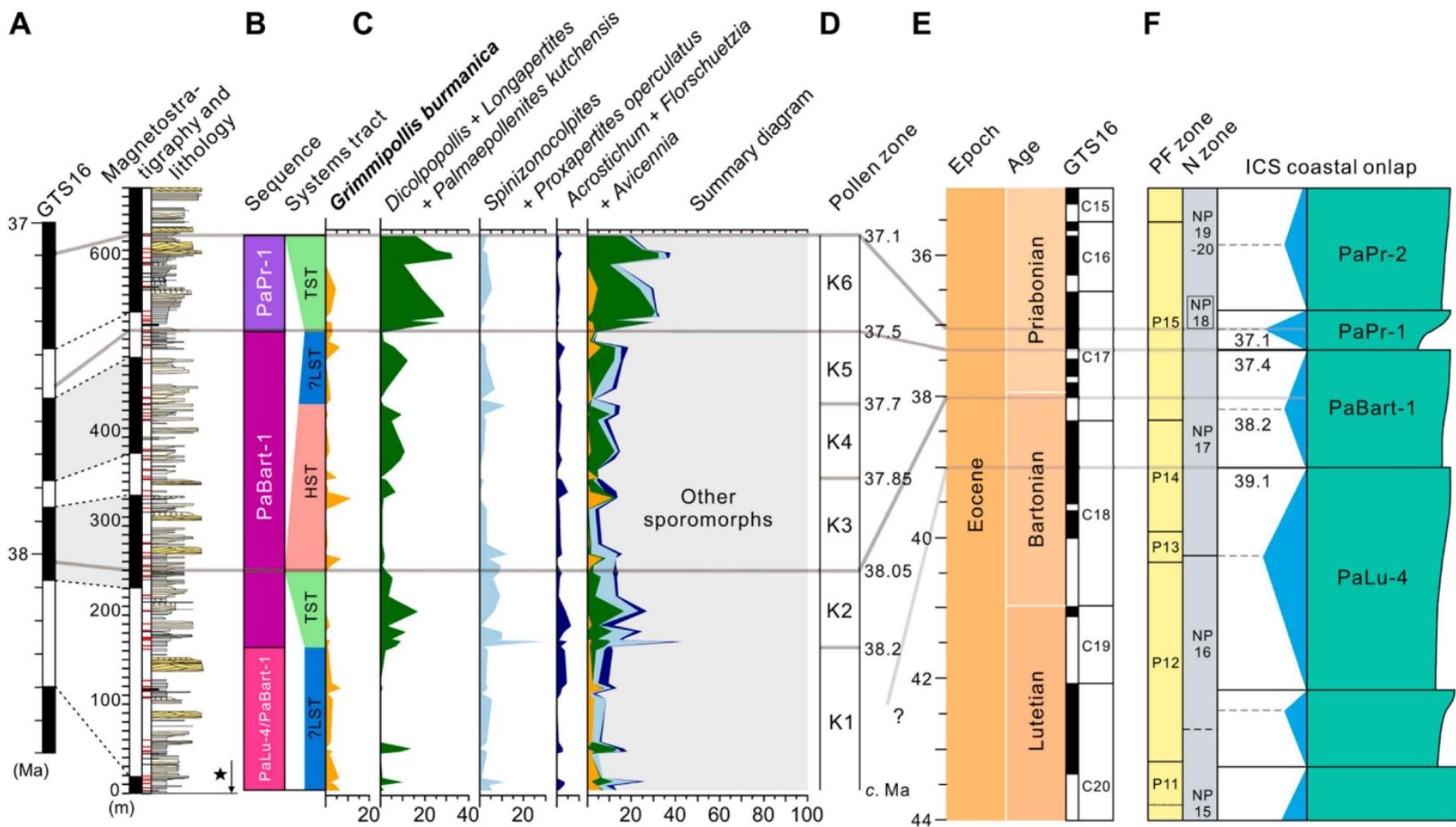


Figure 3