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SYNTHESIS

Climate and geological change as drivers of Mauritiinae palm biogeography

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ABSTRACT

Aim: Forest composition and distribution are determined by a myriad of factors, including climate. As models of tropical rain forest, palms are often used as indicator taxa, particularly the Mauritiinae. We question, what characterizes the Mauritiinae pollen in the global fossil record? And when did the Mauritiinae become endemic to South America?

Location: Global tropics.

Taxon: Mauritiinae palms (Arecaceae: Lepidocaryeae).

Giovanni Bogotá-Ángel and Huasheng Huang contributed equally to this work.

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Methods: Pollen trait data from extinct and extant Mauritiinae pollen were generated from light-, scanning-, and transmission electron microscopy. Statistical morphometric analysis was used to define species and their relationships to other Mauritiinae. We also compiled a comprehensive pollen database for extinct and extant Mauritiinae and mapped their global geographical distribution from Late Cretaceous to present, using GBIF and fossil data.

Results: Our morphometric analysis identified 18 species (11 extinct and seven extant), all exhibiting exine indentations, a synapomorphy of the subtribe. The fossil taxa and early divergent extant *Lepidocaryum* are all monosulcate, whereas the extant *Mauritia* and *Mauritiella* species are all monoulcerate. Paleobiogeographical maps of fossil Mauritiinae pollen occurrences suggest the taxon originated in equatorial Africa during the Cretaceous, and expanded their range to South America, and to India in the Paleocene. Range retraction started in the early Eocene with extirpation from India, and reduction in diversity in Africa culminating at the Eocene–Oligocene Transition (EOT). In contrast, in South America, the distribution is maintained, and since the Neogene Mauritiinae palms are mostly restricted to swampy, lowland habitats.

Main conclusions: Morphometric analysis shows that since their origin Mauritiinae pollen are relatively species poor, and *Mauritiidites* resembles *Lepidocaryum*. We also conclude that the biogeographical history of the Mauritiinae and, by extension, tropical forests was strongly affected by global climatic cooling events. In particular, the climate change at the EOT was a fundamental determinant of current tropical forest distribution.

KEYWORDS

Arecaceae, Eocene–Oligocene Transition (EOT), fossil record, global cooling, interplate dispersal, *Lepidocaryum*, *Mauritia*, *Mauritiella*, Neotropics, palynology

1 | INTRODUCTION

Palms (Arecaceae or Palmae) are among the most common and characteristic elements of the tropical forests across the equatorial region (Baker & Couvreur, 2013a,b; Dransfield et al., 2008; Reichgelt et al., 2018; Svenning et al., 2008). Climate plays a crucial role in global palm distribution, but it is not the only driver. Soil quality, topography, hydrology (e.g. Eiserhardt et al., 2011; Muscarella et al., 2020), and geological processes such as mountain building and plate tectonic movement also play a role in their speciation, extinction, and dispersal (e.g. Bacon et al., 2013; Morley, 2000, 2003; Rull, 1998).

Dating back to the mid-Cretaceous, the pollen fossil record of palms is exceptionally rich (Herngreen & Chlonova, 1981; Salard-Cheboldaeff, 1978), as palms are particularly good pollen producers (Harley & Baker, 2001). Palms are therefore excellent bioindicators that monitor temporal and spatial changes in the tropical forest biome (Bacon et al., 2018; Huang et al., 2020; Reichgelt et al., 2018). Moreover, the response of palms to past climate change can help forecast how tropical forests might react to future scenarios of climate change.

Divergence time estimation, using molecular phylogenies and palm macrofossils, suggests that the history of the family started in Laurasia at *c*. 100 Ma (Baker & Couvreur, 2013a,b; Couvreur et al., 2011). At the time, the mega-continents Gondwana and Laurasia were separated, with Gondwana just beginning to breakup and India positioned in southern high latitudes (*c*. 120 Ma; Aitchison et al., 2007). Transoceanic biological dispersal among Africa, South America and India, however, was still possible (Morley, 2003; Poux et al., 2006; Renner, 2004). Global temperatures were warm, and palms formed an important component of the flora in Gondwana (e.g., *Spinizonocolpites* pollen with affinity to *Nypa* in the Barremian (~130–125 Ma) of Argentina; Guler et al., 2015; Martínez et al., 2016). By the Late Cretaceous, palms were extremely abundant, and dominated the pantropical 'Palmae Province' (Herngreen & Chlonova, 1981; Herngreen et al., 1996; Morley, 2000; Pan et al., 2006; Vajda & Bercovici, 2014).

Climate models suggest that in the Paleogene, global temperatures were much higher than at present (Zachos et al., 2003, 2008). During the Paleocene–Eocene Thermal Maximum (*c*. 56 Ma, lasting *c*. 200,000 years), global mean surface temperatures were estimated to be *c*. 18.7°C higher than pre-industrial levels (Inglis et al., 2020), and in the Early Eocene Climatic Optimum (*c*. 53–49 Ma), *c*. 13–15°C higher than pre-industrial levels (Caballero & Huber, 2013; Inglis et al., 2020; Intergovernmental Panel on Climate Change (IPCC), 2014; Zhu et al. 2019). In the Neotropics, these periods coincided with extremely high pollen diversity (Jaramillo et al., 2006, 2010). In contrast, cooler climates, such as those during the late Eocene (*c*. 40–34 Ma; Hutchinson et al., 2020; Liu et al., 2009; Zachos et al., 2008), are associated with periods of significantly lower pollen diversity (Jaramillo et al., 2006). Such changes in pollen diversity are interpreted to indicate matching species diversity changes in tropical forests.

In this study, we use the palm subtribe Mauritiinae (Arecaceae: Calamoideae: Lepidocaryeae) as a model group to trace tropical forest history. Extant Mauritiinae are endemic to South America and include the genera *Mauritia* L.f. (two species; Figure 1), *Mauritiella* Burret (four species) and *Lepidocaryum* Mart. (one species)(Dransfield et al., 2008). While relatively species poor, the Mauritiinae are widely distributed, extending from *c*. 20°S to 10°N (Figure 2), and are highly abundant. An example of this is *Mauritia flexuosa* which is one of the most common species in Amazonia, with an estimated 1.5 billion individuals (ter Steege et al., 2013).

Mauritia and *Mauritiella* are found across a wide range of environments, including swamps and river margins across Amazonia and Orinoquia, the Llanos grasslands and gallery forests, Venezuelan highlands, the back-swamps along the Atlantic coast and in the Caribbean (Lasso et al., 2013; Lindeman, 1953; Melo et al., 2018; Sander et al., 2018). *Mauritia flexuosa* is wind pollinated and a prolific pollen producer (Khorsand Rosa & Koptur, 2013). It occurs along black- and white-water rivers where its pollen accumulates on floodplains and in swamps. *Mauritiella aculeata* and *M. armata* occur along clear- and black-water rivers, whereas *Lepidocaryum* is mainly found in the understory of the *terra firme* lowland forest (Dransfield et al., 2008; Mejia & Kahn, 1996; Navarro et al., 2011). *Mauritiella macroclada* is restricted to the Pacific coast of Colombia and northern Ecuador, occurring on fluvial floodplains, in the mangrove back-swamps, and below 100-m elevation (Galeano & Bernal, 2010). Unfortunately, nothing is known about the pollination syndrome of *Mauritiella* or *Lepidocaryum* (Khorsand Rosa & Koptur, 2013).

The Calamoideae have an extensive macrofossil record, but Mauritiinae macrofossils are rare (Berry, 1929; Dransfield et al., 2008). To our knowledge, the only macrofossil tentatively assigned to *Mauritia* is *Lepidocaryopsis rolloti*, a seed found by Berry (1929) in the Guaduas Formation (earliest Paleocene, Bogotá, Colombia; Sarmiento, 1991). This identification is questionable though, as in recent years many taxa classified by Berry (1929) have been re-evaluated and the botanical affinity has been adapted (see Herrera et al., 2010). Nevertheless, Mauritiinae pollen is very abundant in the fossil record of fluvial and coastal environments (e.g. Behling et al., 1999; Berrio et al., 2002; D'Apolito et al., 2013; Dueñas, 1980; González-Guzmán, 1967; Hoorn, 1993; Lorente, 1986; Rull, 1998).

Climate is thought to be a limiting factor for the Mauritiinae, like in all palms, but it does not entirely explain their geographical distribution (Rull, 1998). In South America, the taxon is absent from areas where environmental conditions are apparently suitable, and where the taxon grew in the past. Rull (1998; following Delcourt et al., 1982) therefore suggested that different mechanisms, other than climate, determined its distribution and that the biogeography of the Mauritiinae should be viewed at "*megascale* (*plate tectonics and*

FIGURE 1 Morphological characteristics of an exemplar species of the Mauritiinae, *Mauritia flexuosa* (Tena, Ecuador), one of the most abundant and widely distributed species in Amazonia. (a) Arborescent habit; (b) inflorescence and infructescence; (c), fruit. Photos credits: C. Hoorn [Colour figure can be viewed at wileyonlinelibrary.com]

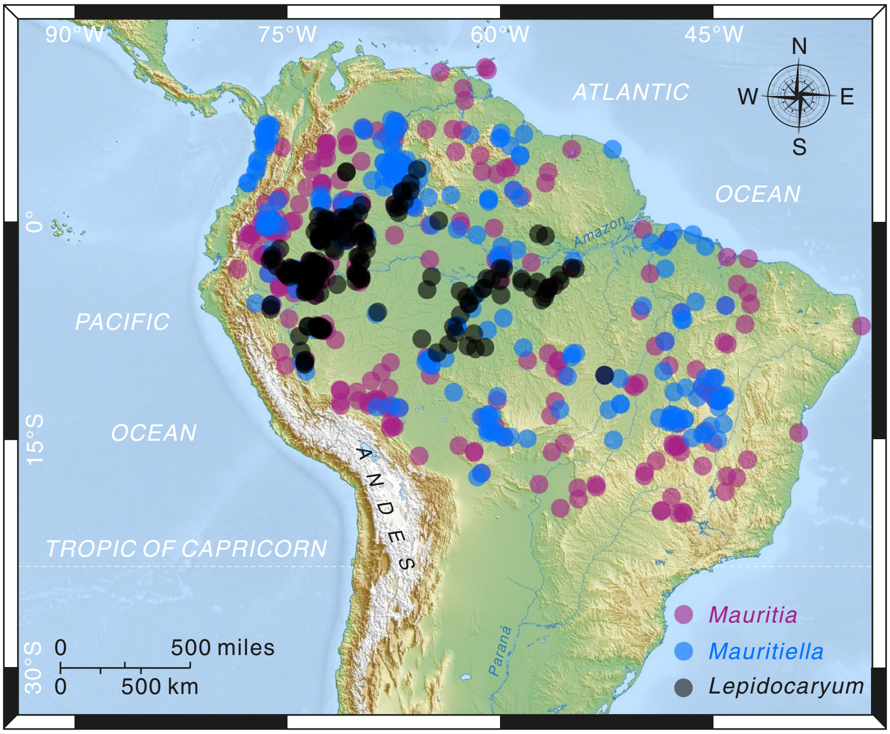

FIGURE 2 Geographical distribution of *Mauritia*, *Mauritiella*, and *Lepidocaryum* (occurrence data from GBIF), using a Miller's projection, with base map from https://mapswire.com/ [Colour figure can be viewed at wileyonlinelibrary.com]

evolution), macroscale (Pleistocene glaciations) and microscale (minor climate shifts and human disturbance)".

The central questions in this study are focused on taxonomy and biogeography. We ask, when did the first Mauritiinae appear, and are all fossil species assigned to this group truly Mauritiinae? How did their geographical distribution change over time? To address these questions, we analyze and characterize the pollen morphology of the fossil and extant Mauritiinae taxa. We compile a database of occurrences and morphological data from the pollen of extinct and extant taxa from the Late Cretaceous onwards. Based on this dataset, we objectively identify Mauritiinae species and determine how the distribution changed through time. Ultimately, these results are important for understanding how past tropical forests responded to climate change, and what can be expected in the future in the face of climate change.

2 | MATERIALS AND METHODS

2.1 | Palynological samples and sample processing

Extant material was compiled from the pollen collection at the Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, and the Royal Botanical Gardens, Kew (RBGK), UK. Pollen extraction involved acetolysis (Erdtman, 1952), residues were preserved in glycerine, and permanent slides were mounted in glycerine jelly and sealed with paraffin.

The fossil pollen samples from outcrops in Amazonia (Hoorn, 1993, 1994a,b, 2006) and Nigeria (this study) were processed at the pollen laboratory of IBED. One cm^3 of organic-rich clay was soaked in sodium pyrophosphate ($Na_4P_2O_7{\cdot}10H_2O$) in a 10% solution with H_2O; lignites were oxidized with Schulze mixture ($2HNO_3$, 60%: $KClO_3$, 7%). The samples were sieved over a 250-µm sieve mesh. Density separation, to separate the inorganic fraction, was performed with bromoform (2.0 g/cm^3). The resulting organic residue was mounted in glycerine and sealed with paraffin. Sediment samples from India (S.P.) and Colombia (A.P.T. & A.P.) were processed according to standard maceration methods (Vidal, 1988). Since the recovered macerals were dark in color, they were treated with dilute HNO_3 for 8 hr to oxidize them mildly. They were then washed and sieved with a 7-µm sieve. The Indian sample residues containing pollen material was divided into two fractions. One fraction was applied to stubs and viewed under scanning electron microscopy (SEM), and another was used to prepare slides for light microscopy (LM). The Colombian samples were photographed with LM.

The palynological slides with materials from Amazonia and Nigeria are stored at the pollen laboratory of IBED. Other palynological slides are stored at Birbal Sahni Institute of Palaeosciences (India), Universidad de Caldas (Colombia), Colombian Geological Service (Colombia), and Al Neelain University (Sudan). Information on sample source, location, sampling number, laboratory number, England Finder locations, age, and geological formations is listed in Table S1, Supporting Information.

2.2 | Morphology, measurements, and data processing

LM: For both extant and fossil taxa, when possible, 10–20 grains were measured for each species covering polar and equatorial views.

For *Grimsdalea minor*, only three grains were available. If no material was available, literature information was adapted and used to describe the pollen morphology.

SEM: Single grains were separated from the organic residue following Zetter and Ferguson (2001), Ferguson et al. (2007), and Halbritter et al. (2018). The pollen grains were mounted on stubs and sputter coated with gold. SEM micrographs were taken at the Jodrell Laboratory (RBGK) using a Hitachi S-4700 field-emission SEM. Materials from India were studied entirely from the routine scanning strew mounts from many studied localities with a Jeol-JSM-7800F SEM.

Transmission electron microscopy (TEM): Pollen grains were rehydrated and fixed in 0.1% glutaraldehyde (3 weeks), fixed with 1% OsO_4 (2 hr), pre-stained with 1% uranyl acetate during dehydration, embedded in 3/7 Epon (Luft; here: 47,5% Epon 812, 21,1% DDSA, 29% MNA, and 1% BDMA), and post-stained with 3% uranyl acetate (20 min) and Reynolds' lead citrate (10 min). Ultrathin sections (80–90 nm) were cut with a Diatome diamond knife on a LKB 8800 Ultrotome III. The TEM micrographs were taken with a Jeol JEM 1010.

In addition, we photographed specimens with Nomarski Differential Interference Contrast (DIC) microscopy (Bercovici et al., 2009). We varied the *z*-axes and images were later combined through manual *z*-stacking. This stacking technique combines different layers to provide depth to the images comparable to 3D photography (Figures S1 and S2 except for 26–31 in Figure S1). All the pollen morphological data are summarized in Appendix S1, Tables S2 and S3.

2.3 | Morphometric analyses

We used morphometric analyses to compare extant and fossil pollen types. Pollen morphology was characterized using nine continuous and three discrete morphological characters (Appendix S1; Tables S2 and S3). We used the Gower distance (Gower, 1971) to measure pairwise morphological dissimilarity because this metric can accommodate both continuous and discrete data. The Gower distance matrix was then ordinated to produce a morphospace, using principal coordinates analysis (PCO) with a Cailliez correction to ensure that only non-negative eigenvalues were produced (Cailliez, 1983). Missing data were coded as 'NA', and were ignored in the pairwise distance calculations.

We ordinated the data for both the entire dataset and for the extant taxa. To differentiate both within- and among-taxon morphological variability, we first analyzed the data at the specimen level. To confirm the results at the inter-specific level and bring out any other among-taxon morphological patterns, we also analyzed the data at the taxon level, by calculating the mean within-taxon values for the continuous characters and combining these with the character states for the discrete characters. The discrete characters are mostly uniform at the taxon level, that is, they each occupy a single character state within each taxon. Where character states varied within a taxon, we avoided polymorphisms by coding that character as the most frequently observed state within the taxon. All *Mauritia* and *Mauritiella* species were therefore coded as being ulcerate despite some rare grains having sulci, and all *Mauritiidites* van Hoeken-Klinkenberg species were coded as being sulcate despite some rare ulcerate grains. Similarly, *Mauritiella pumila* produces two morphotypes, with small psilate grains and large scabrate ones. We therefore coded *M. pumila* as scabrate since this is the character state present in the rest of the *Mauritiella* species.

In addition to using PCO, the Gower distances of the taxon-level morphometric data were analyzed via hierarchical cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) clustering algorithm. Morphometric analyses were carried out in R v. 3.6.2 (R Core Team, 2019) using the packages 'FD' v. 1.0-12 (Laliberté et al., 2014), 'ape' v. 5.3 (Paradis et al., 2004) and 'phytools' v. 0.6-99 (Revell, 2012). R code for carrying out these analyses is provided in Appendix S2.

2.4 | Present and past distribution of the Mauritiinae

Global occurrence data of the extant members of the subtribe Mauritiinae were obtained from GBIF (Global Biodiversity Information Facility, https://www.gbif.org) on 29 February 2020. The data were cleaned following Palazzesi et al. (2014) and Zizka et al. (2019). The cleaned GBIF data were plotted on a physical map of South America (Figure 2) with a Miller's projection (from https://mapswire.com/).

We created a database of records of pollen fossil taxa assigned to *Mauritiidites*, *Grimsdalea* Germeraad et al., and *Echidiporites* Muller from Palynodata (Palynodata Inc. & White, 2008), which we extended with a revision of literature (Table S4). We only included records of the modern genera *Mauritia* and *Mauritiella*, as to our knowledge *Lepidocaryum* has no fossil pollen record. The records with uncertain ages spanning three or more epochs (such as the age using Paleogene, comprising Paleocene, Eocene, and Oligocene) were excluded.

We divided our records into six time intervals: Cretaceous, Paleocene, Eocene, Oligocene, Miocene, and Pliocene–Quaternary. The distribution data were plotted in GPlates 2.1.0 (EarthByte; https://www.gplates.org) with plate models from Matthews et al. (2016) for the Cretaceous (80 Ma) and Paleocene (60 Ma) and from Westerweel et al. (2019) for the Eocene (40 Ma), Oligocene (30 Ma), Miocene (20 Ma), and Pliocene–Quaternary (5 Ma).

Global distribution maps were generated using a Mollweide's projection, which is a pseudocylindrical equal-area projection best for geographical distribution mapping (Environment Systems Research Institute (ESRI), 2019; Kraak & Ormeling, 2003). We added the southern and northern lines of the tropical boundaries through Late Cretaceous–Quaternary referring to Morley (2007), Hay and Floegel (2012), and Beck et al. (2018). Following the approach from

Huang et al. (2020), the certainty in the identification of the records was divided into three levels from high to low certainty: level 3 comprised references with pollen micrographs corroborating the identification; level 2 included references without pollen micrographs; and level 1 were referenced in Palynodata (Palynodata Inc. & White, 2008), but without accessible literature from the public libraries or internet. Where pollen micrographs were provided in the references and could be evaluated, taxonomic assignments were checked, and misidentifications were removed. Geographical coordinates for each fossil species and locality were georeferenced either using locality information or extracted directly from the literature (Table S4; Figures S4 and S5). The age ranges of all taxa were summarized in a comparative biostratigraphic chart (Table S5), and made in CorelDRAW 2019 (Corel Corporation), using the GSA Geologic Time Scale version 5.0 (Walker et al., 2018). All data points were crosschecked with Table S4 and collated in Table S5 (age ranges and sources).

3 | RESULTS

3.1 | Diagnostic pollen characters of the Mauritiinae

The synapomorphy (diagnostic feature) of Mauritiinae pollen is the presence of 'inserted' ektexinal sculptural elements (baculae, clavae, or echinae), which exhibit inward bulging (Figures 3 and 4; Figure S1). This feature was previously used by Harley (2006) and Pocknall and Jarzen (2012) to relate fossil taxa *Mauritiidites* and *Grimsdalea* to the Mauritiinae and is here also used to include the form-genus *Echidiporites*. Based on the presence of inward-bulging sculptural elements and other pollen morphological features, we recognize 11 fossil Mauritiinae morphotypes that occurred across the former Gondwanan tropics from the Late Cretaceous to Pleistocene, namely: *Mauritiidites crassiexinus*, *M. lehmanii*, *M. crassibaculatus*, *M. franciscoi* (var. *franciscoi*, *minutus*, and *pachyexinatus*), *Mauritiidites* sp. (to be described), *Grimsdalea magnaclavata*, *G. polygonalis*, and *Echidiporites barbeitoensis*.

In LM analysis, the exine in Mauritiinae pollen appears to be intectate with two sorts of supraexinic elements: microelements such as scabrae, microspines, or/and micropila, and distinctively inserted macroelements such as bacula, spines, or clavae. Many extant and fossil pollen taxa have an exine that seems to consist of two layers. TEM and SEM analysis confirms the LM observations, but also shows that inserted supraexinic macroelements are attached to the exine by columellae, while microsculptural elements are just projections from this. These analyses also reinforce the distinction of two layers in the exine. In contrast to the dense and thick upper layer, the inner layer looks lamellate, a feature found by Dransfield et al. (2008) and here probably present in *Grimsdalea* (Figure 4).

Our palynological revision of *Mauritiidites crassiexinus*, *M. lehmanii*, *M. crassibaculatus*, and *M. franciscoi* from South America, Nigeria, Sudan, and India, and the revision of the original description or micrographs by the authors, suggest that echinate and monosulcate pollen are diagnostic for *Mauritiidites*. These features have been used to relate *Mauritiidites franciscoi* (var. *franciscoi*, *minutus*, and *pachyexinatus*) to the extant Neotropical Mauritiinae: *Mauritia* (van der Hammen & Garcia, 1966; see Rull, 1998, 2001 for overview), *Lepidocaryum*, and *Mauritiella* (Rull, 1998, 2001). Nevertheless, exceptions are found within *Mauritiidites franciscoi* and particularly *M. franciscoi* var. *pachyexinatus* with some monoulcerate grains (Figure S1, 28–29 and 31), and in *M. crassibaculatus* that has pollen with baculae.

In spite of the diagnostic Mauritiinae feature of inward-bulging sculptural elements, *Grimsdalea* is morphologically different from the other Mauritiinae taxa due to its characteristic inserted large clavae with conspicuous supraexinic scabrate, micropilate, or microspinulose sculptural elements seen in SEM and TEM (Figures 3 and 4). In contrast, the confirmed absence of inward bulges beneath clavae in *G. minor* prompts us to exclude this taxon from the Mauritiinae (Figure S1). *Grimsdalea* pollen was originally described as inaperturate (Germeraad et al., 1968); however, the monosulcate or monoulcerate condition has been, respectively, proposed for *G. polygonalis* (Jan Du Chêne et al., 1978) and *G. magnaclavata* (Pocknall & Jarzen, 2012). Our LM results for the Amazonian sample material of *G. magnaclavata* confirm its monosulcate character. This and our TEM analyses of the clavae implants and exine structure confirm that *Grimsdalea* fits within the Mauritiinae subtribe (Figure 4).

Inward bulging under the spines in palm-like pollen is, however, not exclusive to monoaperturate or indistinct to inaperturate pollen. Diporate pollen grains of *E. barbeitoensis* also show this feature. Previously, this taxon was thought to be related to *Korthalsia ferox* (Lorente, 1986), a species that has diporate pollen, which does not show inward bulging spines (Figure S2). Based on the absence of this diagnostic feature in *Korthalsia* Blume, we suggest that *E. barbeitoensis* is not related to *Korthalsia*, but rather is a member of Mauritiinae.

All pollen of the seven extant Mauritiinae are monoaperturate (either monsulcate-monocolpate or monoulcerate-monoporate; Figure S2) or rarely trichotomosulcate (Rull, 2003), but there is a gradation of the aperture and supraexinal elemental characters (Figure 4; Figure S1). The gradation goes from ulcus to either brevisulcus or sulcus, and from stylized to robust bottle-shaped spines or even capitate spines as in *Mauritiella carana*. Pollen of the extant genera *Mauritia* and *Mauritiella* are mostly ulcerate, rarely distal diporate (Figure 5; Ferguson & Harley, 1993), while *Lepidocaryum* is sulcate. However, the circular character of the ulcus in *Mauritia* and *Mauritiella* is not always perfect and can vary from slightly elliptic to brevisulcate (L/W: 1.04 to 2.5–3.6). This differentiation between *Mauritia*/*Mauritiella* and *Lepidocaryum* (Figure 6a) is consistent with the genus-level phylogeny (i.e. *Lepidocaryum* as sister to *Mauritia* and *Mauritiella*; Baker et al., 2009). It should also be noted that there is a general relationship among grain outline, shape, and aperture type, with sulcate grains being more elongate/oval and ulcerate grains being more spherical (Figures S1 and S2).

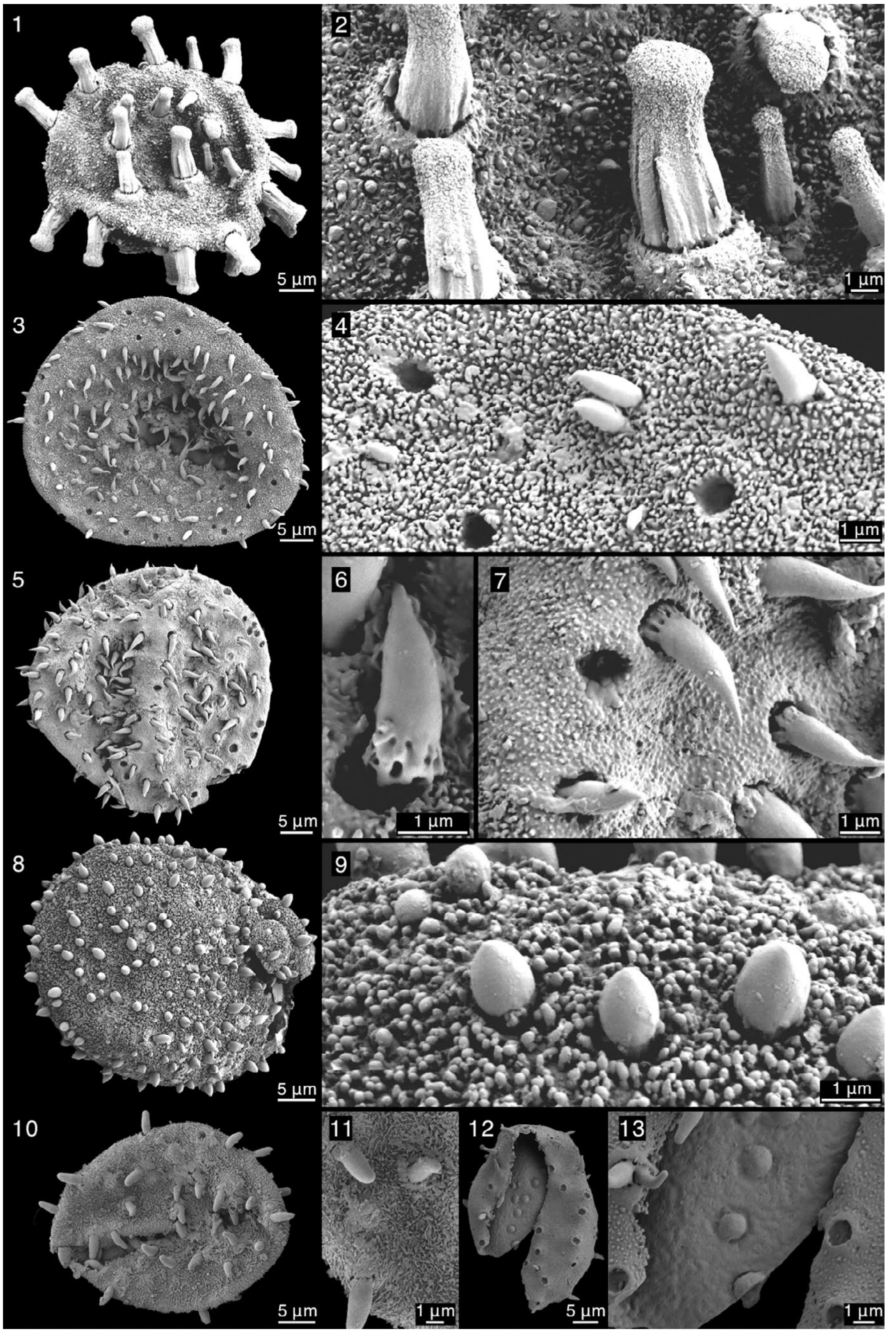

FIGURE 3 SEM micrographs of fossil Mauritiinae pollen. 1. *Grimsdalea magnaclavata* overview, with clavae of different size, and heads not well developed in some clavae (Santa Sofia 46, Colombia; 18190); 2. *G. magnaclavata*, of the exine surface showing clavae and a diverse size scabrae, with the area around clavae insertion slightly protruded and columellae holding and attaching the clava to the exine structure; 3. *Mauritiidites franciscoi* polar view showing the brevisulcus (Apaporis 181, Colombia; 17410); 4. *M. franciscoi* detail of the exine surface showing spines and a fine and dense scabrae surface; 5. *M. franciscoi* equatorial view (Apaporis 181, Colombia; 17410); 6. *M. franciscoi* detail of characteristic 'bottles-shape' spines, with a complex structure holding and attaching the spines to the exine structure; 7. *M. franciscoi* detail of characteristic 'bottles-shape' spines, with columellae holding and attaching the spines to the exine structure; 8. *Echidiporites barbeitoensis* general overview of a grain, an ulcus area is located to the right of the grain (Cotuhe 77, Colombia; 16882); 9. *E. barbeitoensis*, detail of the exine surface showing short conic spines and a coarse scabrate surface, some spines are attached by a columellae-like structure (Cotuhe 77, Colombia; 16882); 10. *M. crassibaculatus* polar view, with baculae and scabrae exine surface (Paleocene, India); 11. *M. crassibaculatus* detail of exine surface, notice scabrae to micropila and a psilate area around baculae insertion and columellae holding and attaching the baculae to the exine structure (Paleocene, India); 12. *Mauritiidites* sp. polar view from Indian Paleocene showing a broken sulcus and holes left after bottle-shape spines are lost; 13. *Mauritiidites* sp. from Indian Paleocene, detail of scabrate exine surface, with the psilate areas around spine insertion and evidence of the inward bulging observed from interior of the grain

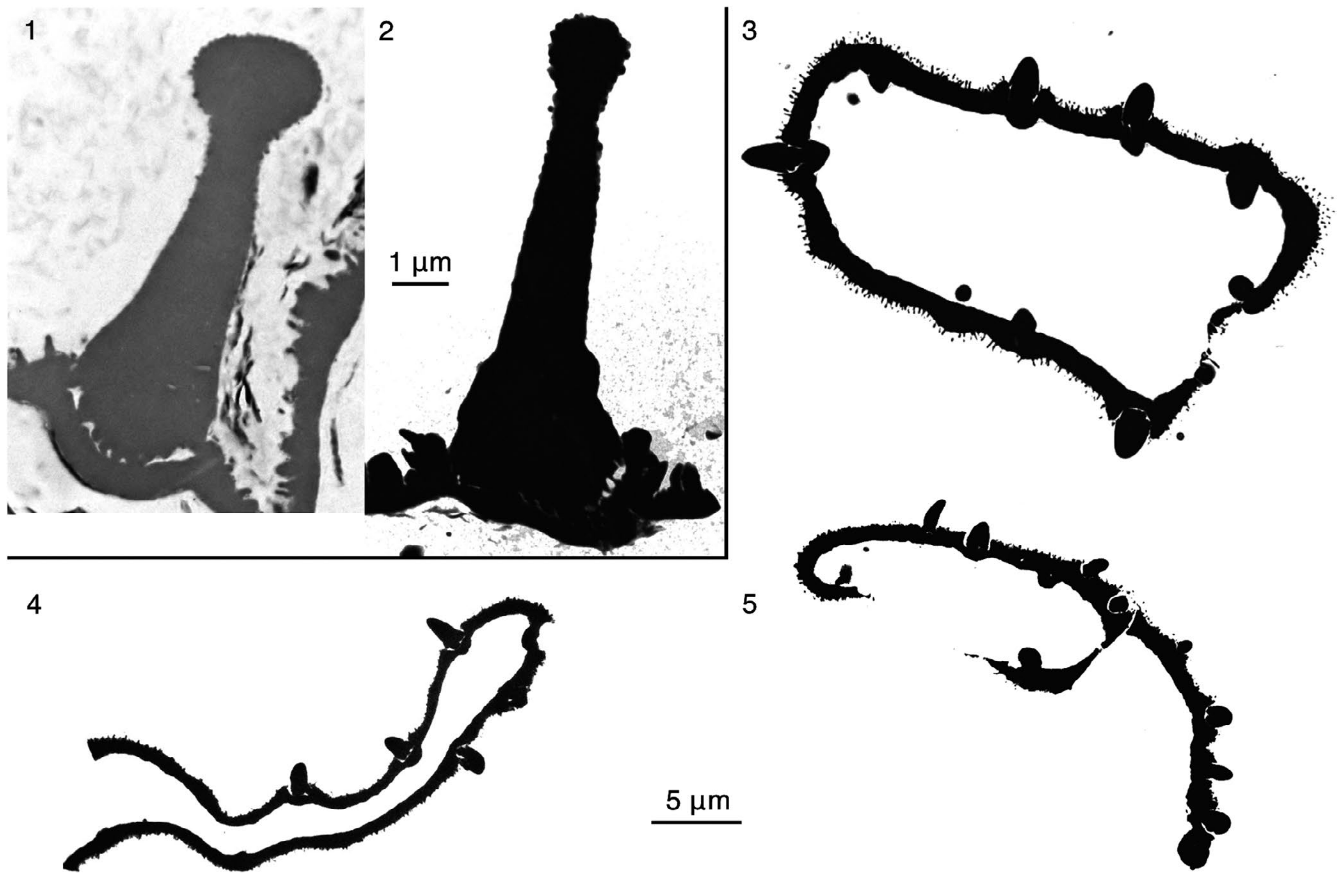

FIGURE 4 TEM micrographs of fossil and extant Mauritiinae pollen. 1. *Grimsdalea magnaclavata* detail of clavae with characteristic concave embedding in the exine, and projections/micropila on the exine (Cotuhe 77; 16882, Colombia/12348-1 T4); 2. Idem from another grain, notice the non-stratified exine, and columellae attaching the clavae to the exine (Cotuhe 77; 16882, Colombia/94640B4, Amazonas Colombia); 3. cross section of *Mauritia flexuosa*, with the aperture to the right, the non-stratified exine covered by very small and stylized processes/scabrae and robust spines embedded in concave exine areas, and attached by a coarse structure (columella) to the exine structure (courtesy of Madeline M. Harley, RBGK; Dransfield et al., 2008); 4. Fossil Mauritiinae pollen, detail of spine with characteristic concave embedding in the exine (Cotuhe 77; 16882, Colombia/12348P5); 5. Fossil Mauritiinae pollen, detail of spine with characteristic concave embedding in the exine (Cotuhe 77; 16682, Colombia/12348L2)

3.2 | Palynological revision of Indian Mauritiinae informs biogeographical models

We revised the fossil record to define the systematics of the Mauritiinae. Until now, the number of fossil species classified as Mauritiinae has varied significantly due to synonymic and identification difficulties. This is illustrated, for instance, in that the African *Mauritiidites minimus* is a synonym of *M. crassiexinus* (Mbesse, 2013) and *Monosulcites perspinosus* of *M. lehmanii* (Boltenhagen, 1967; Kaska, 1989).

In India, Rawat et al. (1977) transferred three species of *Spinainaperturites* (*S. conatus*, *S. horridus*, and *S. densispinus*) to *Mauritiidites* because they have a sulcus, without considering the requirement of sunken spine bases. There is no suggestion of sunken spine bases in any of the published light microscope images by Venkatachala and Rawat (1972) or Rawat et al. (1977), and therefore these three species must be excluded from the Mauritiinae.

Our study of spine-bearing monosulcate pollen from India shows that *Mauritiidites* is present there, despite former misidentifications. Moreover, the pollen could easily be identified from the feature of sunken spine bases (Figures S1 and S2). Based on our SEM photography of pollen from the Indian Paleocene, two *Mauritiidites* species have been recorded from Indian sediments (Figure 3; Figure S1). Some specimens are clearly baculate and therefore belong to *Mauritiidites crassibaculatus*, others have scattered, short bottle-shape spines, and might represent an undescribed *Mauritiidites* sp., which shows some similarities to *M. franciscoi*. Most monosulcate echinate pollen observed from the Paleogene of India, however, do not show the diagnostic sunken spine bases of *Mauritiiidites* or the deep holes remaining after a spine is lost (Figure 3; Figure S1), but a superficial scar on the ektexine when spines are lost. Thus, these specimens should be retained in *Spinainaperturites* or transferred to a more appropriate form genus. This group has caused confusion with respect to the presence of the genus *Mauritiidites* in the Cenozoic of India. No records of *Mauritiidites* are known from Southeast Asia.

3.3 | Morphometric analyses

Summary statistics of the measured nine continuous and three discrete morphological characters are presented in box and jitter plots

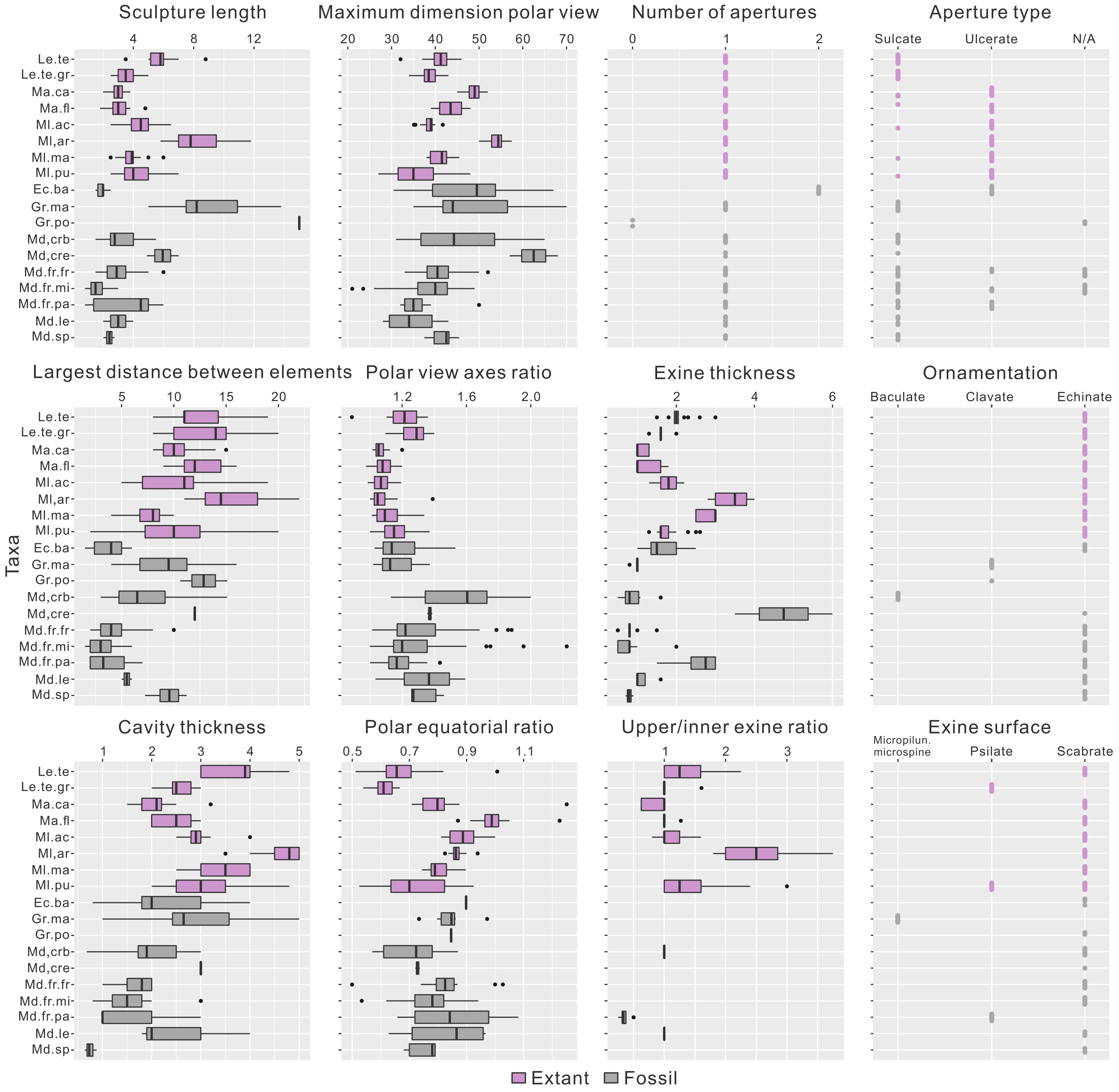

FIGURE 5 Discrete (aperture, ornamentation, and exine surface) and continuous (sculpture and exine) pollen morphological character data showing variation among taxa and between specimens. Sizes of all measurements are in µm; for taxa names and corresponding abbreviations, see Table S3. The order of the taxa is the same as the key in Figure 6 [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 5; see Appendix S2 for the statistical procedure) and based on the data in Table S2. The first two axes of a PCO of the extant taxa (Figure 6a) account for ~23% of the variance in the data. There is a clear separation between *Lepidocaryum* and *Mauritia*/*Mauritiella*. *Mauritiella pumila* occurs as two separate groups, representing the small and large morphotypes, with the small morphotype occurring higher on PCO 1 and closer to *Lepidocaryum*. The few sulcate *Mauritia* and *Mauritiella* grains plot separately from their main clusters and closer to *Lepidocaryum*. PCO 1 is determined by pollen size, shape, exine thickness, aperture type, and surface texture, and shows a gradient from *Lepidocaryum* and the *M. pumila* small morphotype (generally smaller, more elongate, thinner walled, sulcate, and psilate/scabrate pollen) at the upper end of the axis to *Mauritia* and the other *Mauritiella* species (larger, more spherical, thicker walled, ulcerate, and scabrate pollen) at the lower end of the axis (Figures 5 and 6a). PCO 2 shows a gradient based around sculpture length, cavity thickness, and aperture type, which extends from *Mauritia* and the *M. pumila* small morphotype at the upper end of the axis (shorter elements, thinner cavity, and ulcerate) to *Lepidocaryum* and *M. armata* at the lower end of the axis (generally longer sculptural elements, thicker cavity, and sulcate or ulcerate; Figures 5 and 6a).

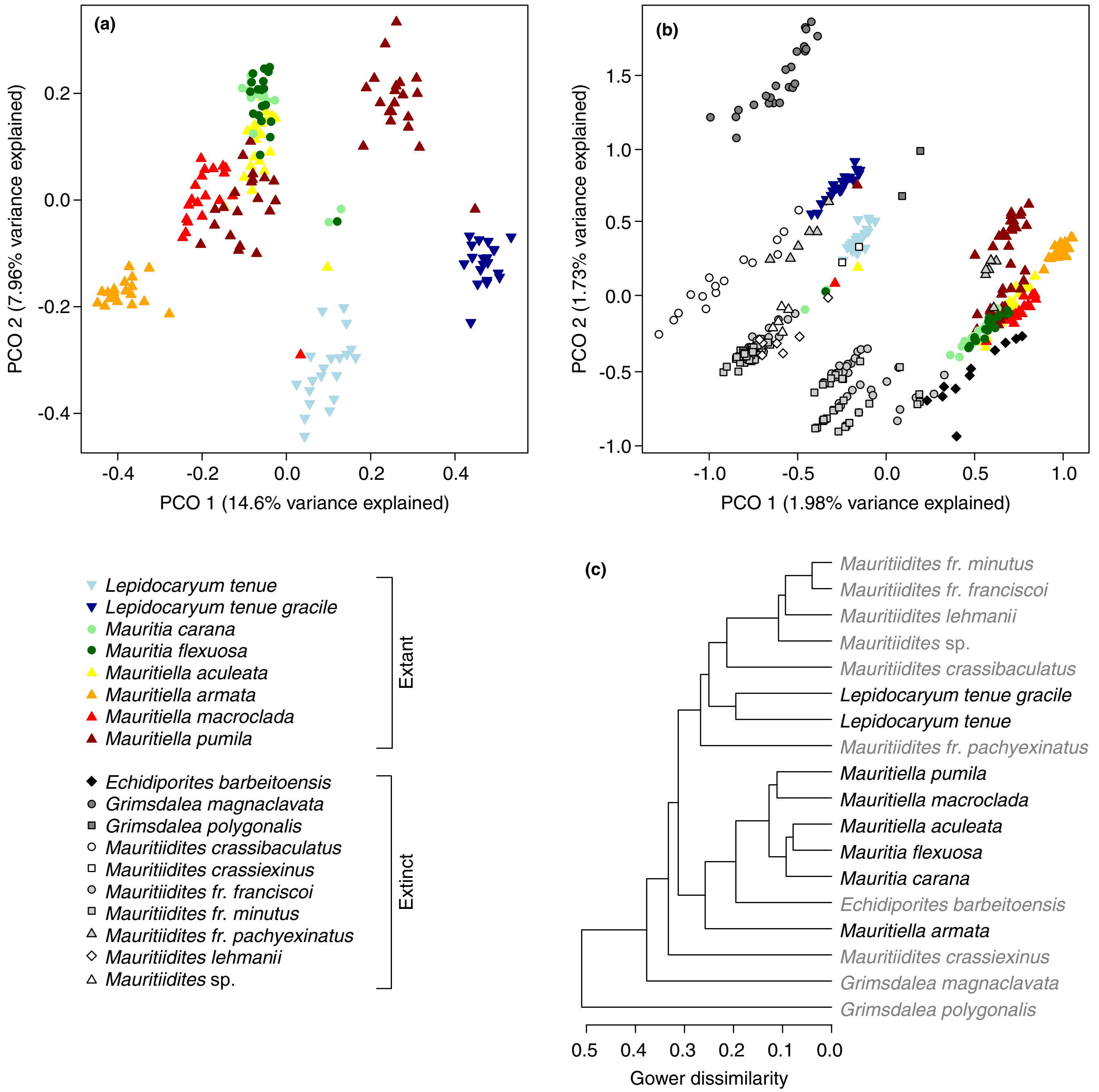

FIGURE 6 Principal coordinates analysis (a and b) and hierarchical cluster analysis (c) of Mauritiinae pollen morphology. (a) Extant taxa only; (b and c), full dataset analyses. Plots of higher PCO axes can be found in Figure S6, while Figure S8 shows the taxon-level analyses [Colour figure can be viewed at wileyonlinelibrary.com]

The first two axes of the full dataset PCO (i.e., with both extant and fossil taxa; Figure 6b) account for ~4% of the variance in the data. The morphological relationships among the extant taxa are broadly similar to those recovered by the extant taxon PCO, with a separation between *Mauritia*/*Mauritiella* and *Lepidocaryum*. *E. barbeitoensis* is clustered with extant *Mauritia*/*Mauritiella* at the upper end of PCO 1, while *Mauritiidites* form-species mostly occur closer to *Lepidocaryum* (Figure 6b,c). The *Grimsdalea* form-species occur at the upper end of PCO 2. Higher principal coordinates show further within-taxon groupings, but with progressively more overlap among the taxa (Figure S6).

The variance in these ordinations is spread over many principal coordinates rather than being concentrated on the first few; this is particularly the case for the full dataset PCO (Figure 6b; Figure S6). This low variance accounting on the uppermost axes is likely because of substantial within-taxon variability in the continuous characters (Figure 5), the among-taxon morphological variability demonstrated by the separation of taxa in the ordinations (Figure 6a), and a high proportion of missing data for some of the fossil specimens (Table S2). Excluding specimens with ≥4 missing characters and re-running the PCO produce a highly similar ordination result to the full dataset (Figure S7), suggesting that missing data are not driving the ordination result shown in Figure 6b. Similar inter-taxon relationships are also shown by the taxon-level PCOs and cluster analyses (Figure 6c; Figure S8), which suggests that the main inter-taxon patterns are being recovered in the specimen-level analyses despite the low percentage of variance accounted for.

3.4 | Paleobiogeography and age ranges of the Mauritiinae

In this section we present a summary of Mauritiinae pollen distribution across the world (Figures 7 and 8). The level of certainty in literature reports varies (see Section 2) and further study is needed to fully comprehend the biogeographical history of the Mauritiinae.

3.4.1 | Cretaceous

The first occurrence of Mauritiinae pollen in the stratigraphic record is *Mauritiidites crassiexinus* from Africa (<93.9 Ma; Fo & Fa, 2018), a species that was first described by Jan du Chêne, Onyke, et al. (1978) in Eocene sediments (Figure S3). Nevertheless, Jan du Chêne, Adegoke, et al. (1978) did not report this species in a subsequent study on the Cretaceous, suggesting that the early origins of *M. crassiexinus* need

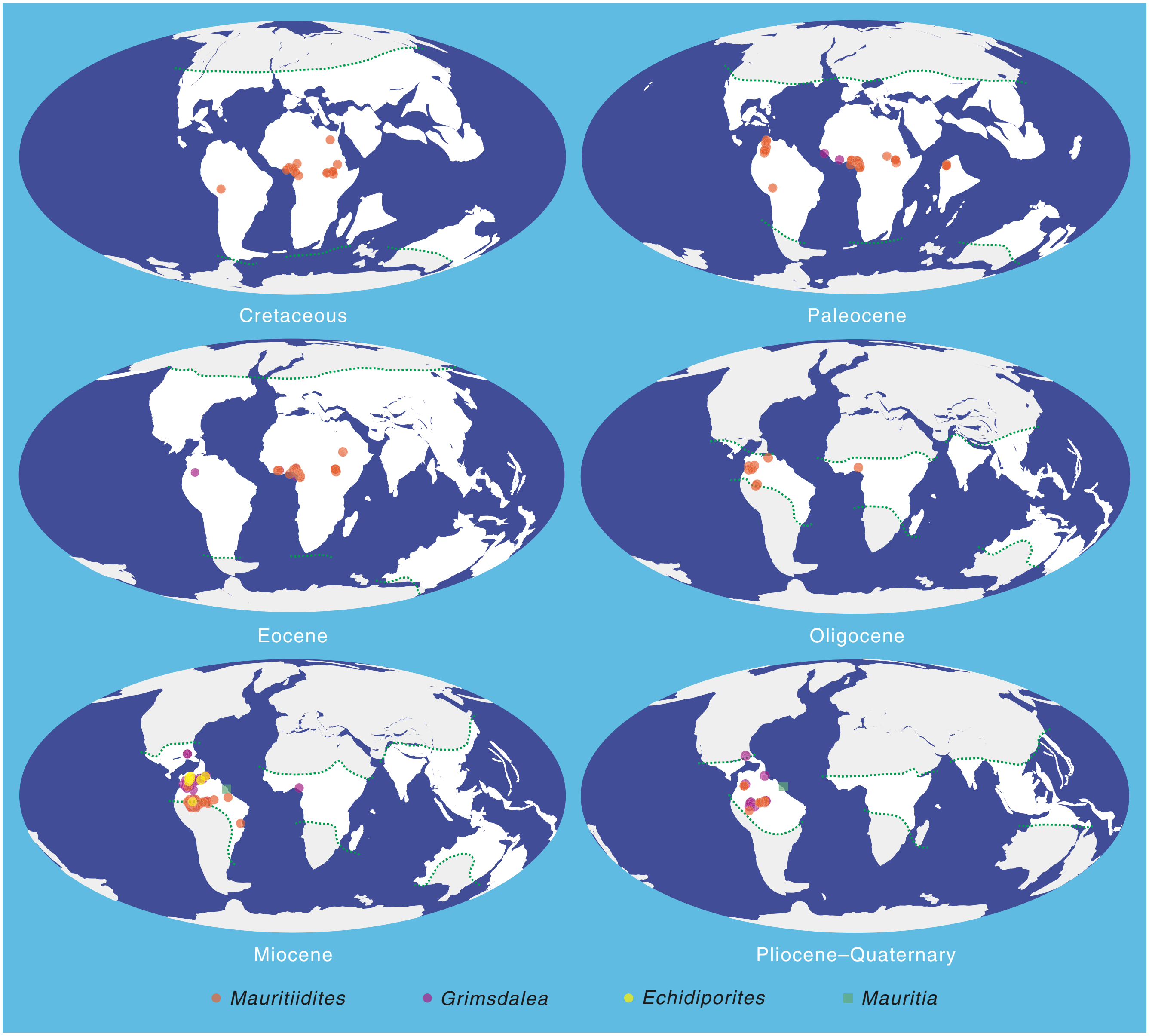

FIGURE 7 Global distribution of *Mauritiidites*, *Grimsdalea*, and *Echidiporites*, and pollen fossil *Mauritia* and *Mauritiella* from the Cretaceous to Quaternary (maps show the former position of the continents after GPlates), using a Mollweide's projection, with only level 3 data, namely the literature with pollen micrographs. *Lepidocaryum* is not included because it does not have a fossil record. Green dash lines indicate the southern and northern tropical boundaries [Colour figure can be viewed at wileyonlinelibrary.com]

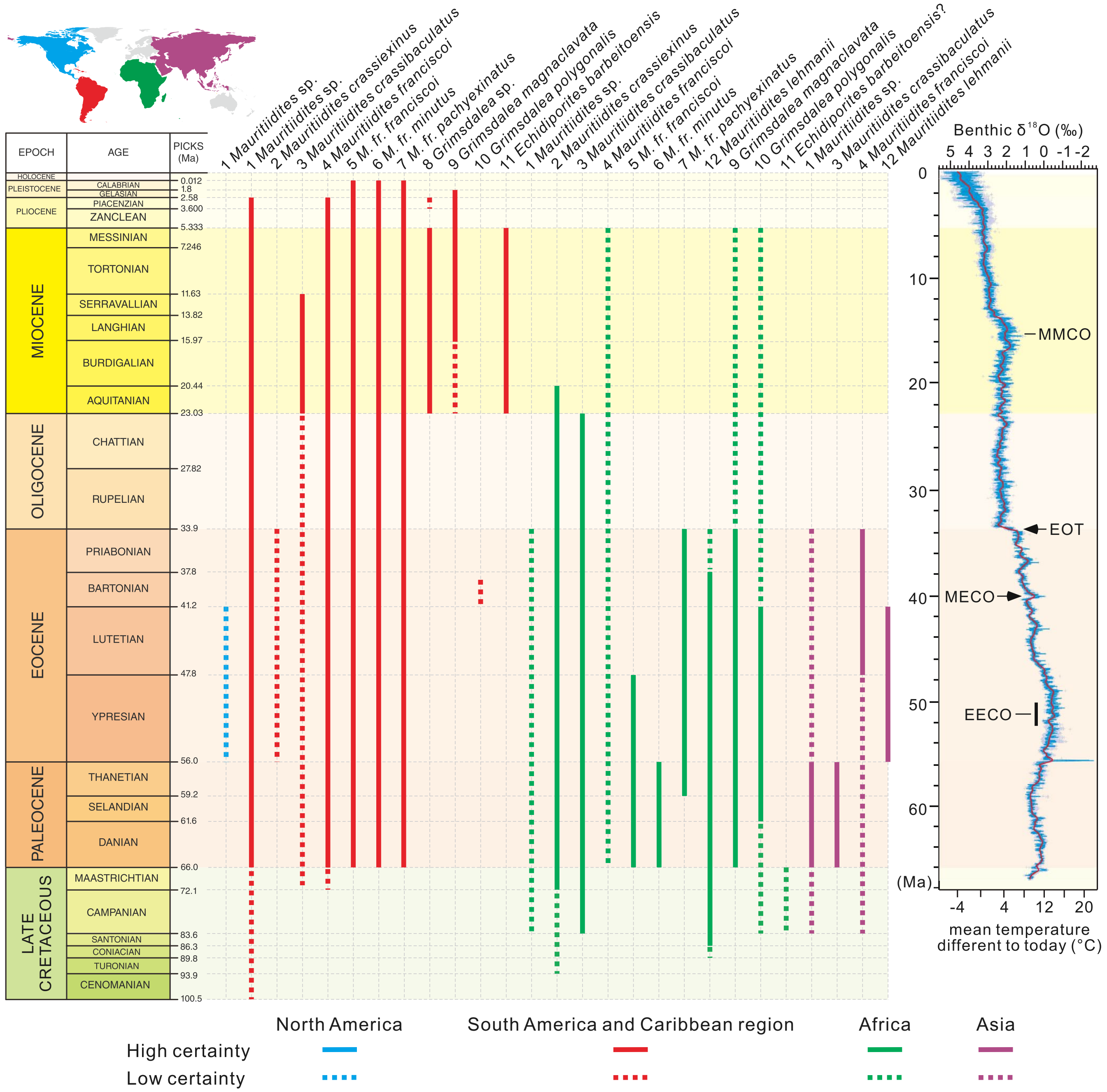

FIGURE 8 Range chart of Mauritiinae (pollen) morphotypes through the Late Cretaceous and Cenozoic. Records with high certainty (solid line) are level 3 data, while those with low certainty (dash line) are levels 2 and 1 data. Geological time scale was modified from Walker et al. (2018); global sea surface temperature curve is from Westerhold et al. (2020): MMCO = Miocene Climate Optimum; EOT = Eocene–Oligocene Transition; MECO = Middle Eocene Climate Optimum; EECO = Early Eocene Climate Optimum [Colour figure can be viewed at wileyonlinelibrary.com]

some further investigation. Subsequent appearances of Mauritiinae are *M. lehmanii* (<89.8 Ma; Boltenhagen, 1967) and *M. crassibaculatus* (<83.6 Ma; Atta-Peters & Salami, 2006). In South America, the earliest Mauritiinae fossil pollen (*M. crassibaculatus*) is reported in Venezuela, at *c.* 72 Ma (Pocknall et al., 2001) and later (~66.0 Ma) the taxon also appears in Colombia (Doubinger, 1973).

Some reports of Mauritiinae occurrences cannot be confirmed, or pollen were mistakenly classified as Mauritiinae. Macphail and Jordan (2015) report an occurrence of *Mauritiidites* for the earliest Late Cretaceous of Tasmania; however, the morphology does not correspond to Mauritiinae, and we here exclude it. Similarly, *Echidiporites* is reported in the Senonian (83.6–66 Ma), representing the only Mauritiinae taxon recorded from Sudan and Egypt (Cheng et al., 2019; Mahmoud & Schrank, 2007), but these occurrences could not be confirmed. Neither could occurrences of *M. franciscoi*, reported in Saudi Arabia (Filatoff & Hughes, 1996), and *Grimsdalea* *polygonalis*, in the Campanian of Nigeria (Chiadikobi et al., 2018; Figures 7 and 8) be confirmed. In South America, *Echimonocolpites protofranciscoi* was recorded (Correa et al., 2010; Garzon et al., 2012; Muller et al., 1987); however, this taxon lacks the typical embedding of the spines that is a diagnostic feature of the Mauritiinae (Sarmiento, 1991). The lack of pollen micrographs from *M. franciscoi* in Vergara and Rodríguez (1997) prevents us from accepting their report on first occurrences of *M. franciscoi* in Colombia during the late Maastrichtian. On similar grounds, reports on the Caribbean Cretaceous occurrences of *Mauritidiites* in Cuba are also rejected (Bóna & Nagy, 1981). Finally, there are no records of *Mauritiidites* from the Cretaceous in India. Venkatachala and Sharma (1984) report *Mauritiidites densispinus* from the Late Cretaceous of Narasapur 1 well from the Krishna Godvari Basin, but the identity of this taxon as *Mauritiidites* is disputed. Moreover, these records are from cuttings (i.e., chipping samples from drill cores), and could be contaminated with material from the overlying Paleocene, where this taxon is common.

3.4.2 | Paleogene

Mauritiidites reached its widest geographical distribution during the Paleocene, when it extended from South America across Africa (Eisawi & Schrank, 2008; van Hoeken-Klinkenberg, 1964) and to India (this study). The first occurrences of *Grimsdalea magnaclavata* (Salard-Cheboldaeff, 1990) and *G. polygonalis* (Bolaji et al., 2020) were reported from tropical Africa. There are no Paleocene records of *Echidiporites* (Figures 7 and 8). African and South American records include *M. crassiexinus*, *M. crassibaculatus*, *M. franciscoi*, and particularly *M. franciscoi* var. *pachyexinatus*, *franciscoi*, *minutus* (i.e., Africa: Bolaji et al., 2020; Mbesse, 2013; Ngon Ngon et al., 2016: Oloto, 1990; Raymer, 2010; South America: de la Parra, 2009; Jaramillo & Dilcher, 2001; Jaramillo et al., 2007; Muller et al., 1987; Pardo-Trujillo & Roche, 2009; Sarmiento, 1991; Vajda-Santivanez, 1999; van der Hammen & Garcia, 1966). Records from India include *M. crassibaculatus* and *M.* sp. (this study). Records of *M. densispinus*, *M. conatus*, and *M. horridus* (Rawat et al., 1977; Venkatachala & Sharma, 1984) are not thought to be Mauritiinae (see section above). *M. franciscoi* in Saudi Arabia (Filatoff & Hughes, 1996) also remains to be confirmed.

In the Eocene, *Mauritidiites* extends from South America, Africa, and to the Middle East, whereas *Grimsdalea* exclusively occurred in Africa and South America. In tropical Africa, there was a continuous presence of *M. crassiexinus* (Eisawi & Schrank, 2008; Mbesse, 2013; Okeke & Umeji, 2016; Oloto & Promise, 2014) and *M. crassibaculatus* (Atta-Peters & Salami, 2004; Bié et al., 2012). *M. franciscoi* var. *franciscoi* disappeared from the record by the end of the early Eocene (47.8 Ma; Mbesse, 2013), while *M. lehmanii* and *M. franciscoi* var. *pachyexinatus* disappeared at the end of the late Eocene (33.9 Ma; Digbehi et al. 2011; Mbesse, 2013; Ngon Ngon et al., 2016).

In South America, *M. franciscoi* was widely distributed and occurred in French Guiana (Leidelmeyer, 1966), Surinam (Escobar, 1982; Wijmstra, 1969), Venezuela (Colmenares & Teran, 1993), and Colombia (Pardo-Trujillo et al., 2003; Pardo-Trujillo & Roche, 2009), while *M. crassibaculatus* and *M. franciscoi* var. *minutus* and *pachyexinatus* have only been recorded in Colombia (Escobar, 1982; Jaramillo & Dilcher, 2001; Jaramillo et al., 2011; Ochoa et al., 2012; Osorio-Granada et al., 2020; Pardo-Trujillo & Jaramillo, 2014; Pardo-Trujillo & Roche, 2009; Rodríguez-Forero et al., 2012). There are also records of *M. franciscoi* in the Middle East (Turkey, Akkiraz et al., 2006, 2008; and probably Saudi Arabia, Filatoff & Hughes, 1996) and of *M. lehmanni* (Arabia Saudi, Moltzer & Binda, 1981, 1984; Srivastava & Binda, 1991). There is also a possible record of *Mauritiidites* from North America (rare and debatable; Jones, 1961).

Grimsdalea, mostly occurred in Africa and was represented by *G. polygonalis* and *G. magnaclavata* (Bié et al., 2012; Jan du Chêne, Onyke, et al., 1978; Lang et al., 1990; Salard-Cheboldaeff, 1979, 1990), whereas in South America *G. polygonalis* first occurred in, and was limited to, the early late Eocene (Jaramillo et al., 2011).

Despite extensive searches, no proper occurrences of *Mauritiidites* have been recorded in the Eocene of India (this study), and we reject records of *M. conatus*, *M. horridus*, and M *densispinus* (see section above). The suggestion of *M. franciscoi* in India by Rawat et al. (1977) cannot be considered as they did not include an illustration. However, *Neocouperipollis ankeleshwarensis*, *N. rarispinus*, and *Arengapollenites ovatus* from India (Kar & Bhattacharya, 1992) deserve a pollen revision, as they strongly resemble *Mauritiidites*.

At the EOT, the distribution of Mauritiinae taxa in Africa was reduced, with just limited occurrences in Nigeria of *M. crassibaculatus* until the late Oligocene (Ikegwuonu et al., 2020) and *M. crassiexinus* until the earliest Miocene (Okeke & Umeji, 2016). *G. magnaclavata*, and possibly *G. polygonalis* became restricted to Nigeria and Niger (e.g. Okeke & Umeji, 2016; Oloto & Promise, 2014; Umeji, 2003; Figure 7). A wide-ranging study of Nigerian wells suggested the extinction of *G. polygonalis* is in the late Eocene (R. J. Morley, pers. commu.). In the Neotropics, Mauritiinae such as *M. crassibaculatus* and *M. franciscoi* (plus three varieties) remained present.

3.4.3 | **Neogene–Quaternary**

From the Neogene onwards, the Mauritiinae were among the most common pollen types of the Neotropical fossil record. During this period, *G. magnaclavata* and *E. barbeitoensis* first occurred in South America. *G. magnaclavata* is an important biostratigraphic marker for the Miocene (Germeraad et al., 1968; Lorente, 1986) and very common in the sediments left behind by the Pebas wetland (Hoorn, 1994a). This environment was influenced by marine incursions, and there is a distinct possibility that this species was favored by brackish water. Subsequently, *G. magnaclavata* disappeared from the fossil record at the end of the Pliocene (D'Apolito et al., 2019; Germeraad et al., 1968; Jaramillo et al., 2011; Lorente, 1986; Pocknall et al., 2001; Soares et al., 2017). Records of *E. barbeitoensis* were found only in the Miocene (Hoorn, 1994a; Jaramillo et al., 2011; Lorente, 1986; Muller et al., 1987; Rull, 1998). In Africa, *G. magnaclavata* and *G. polygonalis* are recorded until the late Miocene (Asadu & Ofuyah, 2017; Umeji, 2003).

Except for *M. crassibaculatus*, whose last appearance is dated as middle Miocene (Jaramillo et al., 2011), most of the remaining *Mauritiidites* spp. continued until the end of the Pleistocene in Brazil, Colombia, and Venezuela (i.e. D'Apolito et al., 2019; Guimarães et al., 2015; Jaramillo et al., 2011, 2017; Lorente, 1986; Muller et al., 1987; Nogueira et al., 2013; Soares et al., 2017). *M. franciscoi* var. *franciscoi* is reported for Brazil (Soares et al., 2015), and Silveira and Souza (2015) recorded *M. franciscoi* from the Brazilian Pliocene. The monoulcerate character of the latter specimen (Figure S1, 31) is a feature distinctive of the extant *Mauritia* and *Mauritiella* pollen. Although the monoulcerate condition was also observed in *M. franciscoi* var. *pachyexinatus* (Figure S1, 28–29), the prevalent monosulcate feature of *Mauritiidites* is only observed in the extant *Lepidocaryum*, and to some degree in *Mauritia* and *Mauritiella* with some brevisulcate pollen. However, there are no references of *Lepidocaryum* pollen records. Pollen of the extant taxa *Mauritia* and *Mauritiella* is present in the Holocene in the tropical lowlands of South America, but the transition from fossil to extant taxon has not yet been evaluated.

4 | DISCUSSION

4.1 | Paleoecological implications from the palynological revision

Our multivariate analyses show that *Mauritiidites* is more similar to *Lepidocaryum* than to *Mauritia* (Figure 6b,c), although there are specimens of *M. franciscoi* and *M. franciscoi* var. *pachyexinatus* with a monoulcerate feature (Figure S1, 31), while some specimens of *Mauritia* and *Mauritiella* present a brevisulcus. This similarity is attributed because they are sulcate, thinner walled, and have a more elongate polar outline, contrary to the ulcerate, thicker walled, and more circular outline of *Mauritia* and *Mauritiella*. Because of this, *Mauritia/Mauritiella* should not be considered the nearest living relative of *Mauritiidites*.

The higher morphological similarity between *Lepidocaryum* and some *Mauritiidites* taxa compared to *Mauritia* has important implications for the use of *Mauritiidites* as a paleoenvironmental proxy. Paleopalynologists often assume that *Mauritia* represents the nearest living relative of *Mauritiidites* because their pollen are found in association with floodplain and deltaic deposits (Atta-Peters & Salami, 2004; Lorente, 1986; Rull, 1998, 2001; Salamanca et al., 2016; van der Hammen & Garcia, 1966). These settings include poorly drained soils in swamps and fluvial or coastal floodplains in which the extant *Mauritia* occurs (Lasso et al. 2013; Urrego et al., 2013). In contrast, *Lepidocaryum* mostly grows in the understory of on *terra firme* lowland forests, and is not strongly associated with fluvial or riparian habitats (Dransfield et al., 2008; Mejia & Kahn, 1996; Navarro et al., 2011). The resemblance of *Mauritiidites*-type pollen to *Lepidocaryum* points at the intriguing new possibility that *Mauritiidites* occupied a much greater environmental and ecological range than was previously implied by its assumed affinity with extant *Mauritia*. Paleoecological and paleoenvironmental reconstructions based on *Mauritiidites* records should thus reflect this broader niche.

Our results do not preclude the possibility that at least some *Mauritiidites* taxa represent sister lineages to *Mauritia* and *Mauritiella*. These taxa may have diverged from an extinct lineage represented by *Mauritiidites* or *Echidiporites* pollen types, while retaining some shared ancestral characters of the subtribe. The taxonomic affinity of *Grimsdalea* is less certain, and morphological variation of both *Grimsdalea* taxa in our analysis does not overlap significantly with extant or other fossil Mauritiinae taxa. We find little support for the supposed affinity between *Grimsdalea* and *Mauritia-Mauritiella* (Pocknall & Jarzen, 2012). *Grimsdalea* may have retained plesiomorphic traits of the subtribe (i.e., features inherited from its ancestors), and subsequent evolution in pollen morphology in other Mauritiinae lineages led to the observed morphological divergence from *Grimsdalea* taxa.

4.2 | Mauritiinae origins: the influence of climate, interplate dispersal pathways, and landscape changes

Phylogenetic and biogeographical studies suggest that calamoid palms diverged from other extant palm lineages between *c*. 100 Ma (stem mean age) and *c*. 80 Ma (crown mean age) in Eurasia, with Lepidocaryeae (including the Mauritiinae) diverging *c*. 75 Ma in Africa, and Mauritiinae *c*. 66 Ma in South America (Baker & Couvreur, 2013a,b; Couvreur et al. 2011). However, previous molecular phylogenies rely on the appearance of *Mauritiidites* in the Maastrichtian fossil record of Africa (72–66 Ma; Schrank, 1994) as a calibration point for the stem node for Mauritiinae (>66 My; Couvreur et al., 2011). Our palynological revision of the Mauritiinae records supports a Gondwanan origin and places their origin in Africa between 94 and 83 Ma (Atta-Peters & Salami, 2006; Boltenhagen, 1967; Fo & Fa, 2018). This suggests that the origin of Mauritiinae and calamoid palms may be much older than previously estimated by Couvreur et al. (2011).

Climate change, and particularly the 'greenhouse conditions' in the Late Cretaceous to Eocene, played an important role in palm biogeography (Kissling et al., 2012; Morley, 2000). In the Cretaceous, and up into the middle Eocene, a reduced latitudinal temperature gradient caused an expansion of the tropical belt which favored the expansion of palms (Herngreen et al., 1996; Huang et al., 2020). African lineages could have diverged following the opening of the Atlantic Ocean in the Cretaceous, with vicariance promoting the formation of sister groups between South America (Mauritiinae) and Africa (Raphiinae; Baker & Dransfield, 2000). More recently, Baker and Couvreur (2013a) estimated ancestral ranges and biogeographical events based on extant lineages to corroborate the hypothesis of long-distance dispersal from Africa to South America in the Late Cretaceous, between 71 and 66 Ma, where the Mauritiinae later became virtually isolated after the late Eocene. Several transatlantic dispersals, especially of palms and palm-like lineages occurred at this time, including *Longapertites*, *Spinizonocolpites echinatus*, *S. baculatus*, and *Proxapertites* spp. Dispersals may have been followed by return dispersals to Africa at the beginning of the Paleocene (Morley, 2000).

In the Paleocene, as India moved from mid to low latitudes and aligned within the same climatic zone as tropical Africa, dispersal from Africa to India became possible (Morley, 2018). Several other tropical taxa dispersed similarly, such as members of Dipterocarpoideae (Ashton & Zhu, 2020; Morley, 2018) and Ctenolophonaceae (Morley, 2003). During the Paleocene, India lay mainly in the seasonal tropics (Prasad et al., 2018), but drifted into the perhumid tropics in the Eocene as the Indian Plate attained an equatorial position. The extinction of *Mauritiidites* in India may relate to its ecological niche favoring a seasonal tropical humid climate in the Paleocene, which subsequently disappeared in the early Eocene (Morley, 2018). The change in India to a perhumid climate would also account for the absence of *Mauritiidites* from Southeast Asia, especially because during the middle Eocene India was the dispersal path for perhumid taxa to Southeast Asia (Morley, 2018). There was a further period of transatlantic dispersal in the middle Eocene, with *Grimsdalea* dispersing to South America from Africa in the Bartonian (<41.2 Ma). Several other taxa dispersed at the same time, including *Amanoa*, *Crudia*, and the parent plant of *Cicatricosisporites dorogensis* (Morley, 2003).

The geographical range contraction of palms at the EOT has previously been linked to global cooling, particularly in relation to the aridification of Africa (Couvreur et al., 2011; Kissling et al., 2012; Pan et al., 2006). For tropical palms, this climatic cooling likely led to a range contraction, where the Mauritiinae distribution became largely limited to South America (Figure 7). The persistence of *Mauritiidites* in South America is further substantiated by data from the Eastern Cordillera and the Middle Magdalena Basin (Colombia) where this taxon is common in pollen zones of early Eocene and Oligocene age (Pardo-Trujillo & Jaramillo, 2014; Rodríguez-Forero et al., 2012).

The Paleocene and Eocene global expansion of the Mauritiinae evidenced by the pollen occurrences coincides with extremely high pollen diversity in the Neotropics (Jaramillo et al., 2006). In contrast, a decline in Neotropical pollen diversity is mirrored by geographical contraction of the Mauritiinae distribution. Together, this suggests that pollen data across time and space provide a helpful estimate of response of tropical forests to climate change.

The Neogene palynological record in western Amazonia indicates that *Mauritiidites*-producing palms were common and abundant in Miocene fluvial deposits (23–16 Ma; Hoorn, 1993, 1994b; Salamanca et al., 2016). However, from c. 16 Ma onwards, it is the parent plant of *Grimsdalea magnaclavata* that prevails. This palm occurred in the large Pebas wetland, an environment that extended almost over the entire western Amazon region and was formed under the influence of Andean uplift and marine influence (Hoorn, 1994a; Hoorn et al., 2010). *Grimsdalea* is also common in the Neogene record of the Venezuelan coastal basins (Lorente, 1986). Pocknall and Jarzen (2012) point out that the western portion of the *G. magnaclavata* distribution is limited by the Eastern Cordillera of Colombia. Other geographical barriers are reflected in its absence from middle Miocene records in eastern Amazonia (Antonioli et al., 2015; Hoorn et al., 2017; Leite, 2004), and the Valle del Magdalena, Cauca, and Choco in westernmost tropical Colombia (A. Pardo-Trujillo, pers. commu.). Jaramillo et al. (2020) found abundant *G. magnaclavata* at 18.81 Ma in the Guajira Peninsula, northern Colombia. However, in Amazonia this taxon occurs at posterior date, suggesting a later distribution into this region (Leandro et al., 2019; Leite et al., 2020).

In the Pleistocene, at *c*. 1.3 Ma, *Grimsdalea* went extinct and Pocknall et al. (2001) relate this extinction to a major cooling event and habitat disappearance. Another factor that may have played a role though is sea level fall, causing a loss of habitat for taxa with coastal distribution such as known for *Nypa* palms (Morley, 2000, p. 140). The transition from *Mauritiidites* to *Mauritia* and *Mauritiella* is less clear, with the latter two being reported in Quaternary palynological records from <150,000 years (Haberle, 1997; Hoorn, 2001).

The distribution and abundance of *Mauritia*, estimated by pollen records (mostly referred as *Mauritia*-*Mauritiella*), suggests these taxa were mainly controlled by climate change, particularly during the Last Glacial Maximum (e.g. Rull, 1998; Salgado-Labouriau, 1997; van der Hammen & Absy, 1994). Most of the pollen records of *Mauritia*-*Mauritiella* are restricted to the Holocene. Their abundance, particularly in swampy areas of western Amazonia and the Cerrado, where wet regional climate together with poorly drained soils likely prompted their evolutionary success (Lima et al., 2014; Melo et al., 2018).

The absence of continuous continental sedimentary records from Pliocene and Pleistocene in the Neotropics suggests that the transition of *Mauritiidites* to *Mauritia*-*Mauritiella* will need further study. Similarly, the remarkable absence of pollen records of *Lepidocaryum* may be an artefact of taxonomic underreporting. Future studies on pre-Quaternary and Quaternary sedimentary records should pay careful attention on pollen morphological details such as the monosulcate versus monoulcerate condition in *Mauritiidites*, when compared with monoulcerate *Mauritia*/*Mauritiella* and monosulcate *Lepidocaryum*. Only in this way we will fully get to understand the ecological position of Mauritiinae in transition to the Quaternary.

5 | CONCLUSIONS

Mauritiinae palm pollen are a good proxy for tropical forest history, as they have an excellent fossil record. In this study, we revised the extant and fossil pollen record of this group, both from a pollen morphological as well as a biogeographical perspective.

The seven extant taxa that belong to *Mauritia*, *Mauritiella*, or *Lepidocaryum* are all echinate and monoaperturate, with diagnostic inserted sculptural elements and inward bulging beneath them, a synapomorphy of this palm subtribe. The 11 fossil taxa belong to *Grimsdalea*, *Echidiporites*, or *Mauritiidites*, and all present the diagnostic inserted sculptural element characteristic of the extant Mauritiinae. Moreover, *Mauritiidites* is monosulcate, making it more similar to *Lepidocaryum*. *Grimsdalea*, and *Echidiporites* differ from *Mauritiidites* because they have clavate sculptural elements and diulcerate pollen, respectively, conditions that are not known in the modern taxa.

Key phases in the Mauritiinae biogeographical history were as follows.

Firstly, Mauritiinae originated in Africa in the Late Cretaceous and became widely distributed across Africa, South America, Middle Asia, and India during the early Paleogene. At that time, tropical terrestrial land coverage was much larger than at present. This expansion coincides with global climatic optima, including hyperthermals such as the Paleocene–Eocene Thermal Maximum (*c*. 56 Ma) and the Early Eocene Climatic Optimum (*c*. 53–49 Ma).

Secondly, a reduction in geographical range occurred in the early Eocene, when India changed in geographical position and there was a shift from a seasonal tropical to a perhumid climate. The disappearance of Mauritiinae from the Indian subcontinent prior to the establishment of dispersal paths between India and Southeast Asia explains its complete absence from Southeast Asian regions.

Thirdly, the Mauritiinae geographical range became severely reduced during the Eocene–Oligocene Transition (*c*. 33.9 Ma), coinciding with a reduction in global temperature and sea level, which impacted the distribution of coastal plants. The Mauritiinae went extinct in Africa and from the Oligocene onwards are largely restricted to the Neotropics.

Finally, Andes uplift and prolonged wetland conditions during the Neogene in western Amazonia facilitated geographical expansion of *Grimsdalea magnaclavata*. Pleistocene climate cooling marked the end of *Grimsdalea*, but the extinction of *Mauritiidites* is uncertain and its exact relation to the Holocene taxa *Mauritia*, *Mauritiella*, and *Lepidocaryum* remains to be resolved.

We conclude that the biogeographical history of the Mauritiinae followed global climatic cooling events, and that Mauritiinae pollen is an important bioindicator of historical tropical forest distribution.

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DATA AVAILABILITY STATEMENT

Data used in the analyses are provided in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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