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Going north and south: The biogeographic history of two Malvaceae in the wake of Neogene Andean uplift and connectivity between the Americas

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ABSTRACT

The evolution of the tropical lowland forests in northern South America is poorly understood, yet new insights into past composition and changes through time can be obtained from the rich and diverse fossil pollen record. Here we present a revision of two diagnostic Malvaceae taxa from the Cenozoic record of northern South America and we relate their evolutionary history to recently updated geological models. In our study we review the pollen morphology and botanical affinity of *Rhoipites guianensis* and *Malvacipolloides maristellae*, and integrate these data into a phylogenetic framework. We also produce distribution maps for both fossil and extant taxa, infer the phylogeny and historical biogeography of the lineages to which they belong, and identify their ecological associates and environmental settings. The closest extant relatives of *Rhoipites guianensis* (Grewioideae) are *Vasivaea* and *Trichospermum*, which are taxa of South American origin. During the late Eocene to early Miocene *Rhoipites guianensis* was widely distributed in the lowland floodplain environments of northern South America. The closest living relatives of *Malvacipolloides maristellae* (Malvoideae) are members of Abutilinae (e.g., *Abutilon*, *Bakeridesia*, *Callianthe* and *Herissantia*), which have their origin in the northern hemisphere. This taxon makes its first appearance in the fossil record of northern South America during the early Miocene, and is typically found in fresh water floodplain and lacustrine environments. Our study suggests that both taxa migrated across the Central American Seaway in the early Miocene (around 18 Ma), and virtually disappeared from the fossil record in northern South America during the middle Miocene, coinciding with Andean uplift. However, their descendants expanded and -in the case of the Abutilinae—diversified in the Andes. We conclude that the biogeographic history of these Malvaceae is influenced by Andean uplift and the incipient bridging of the Americas. Thereafter, climate change and diversification of the Andean landscape enabled their descendants to move upslope and into the Andes.

1. Introduction

The history of tropical plant biodiversity in northern South America is difficult to reconstruct due to the discontinuity and limited accessibility of the fossil record. In recent years, however, integration of molecular phylogenetic, paleobotanical and geological studies have greatly advanced our knowledge of the evolution of plant life in the American

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tropics (e.g. Antonelli et al., 2009; Hoorn et al., 2010; Carvalho et al., 2011; Martínez et al., 2013; Meseguer et al., 2015; Lagomarsino et al., 2016). Until now, most attention focused on elucidating the effects of three major events on species diversification: Andean uplift, Quaternary climatic changes, and the bridging of the Isthmus of Panama (e.g. Antonelli et al., 2009; Hughes and Eastwood, 2006; Luebert and Weigend, 2014; Bacon et al., 2015; Luebert and Muller, 2015; Lagomarsino et al., 2016). While these studies have greatly improved our understanding of the interplay between geology and biodiversity, they are necessarily incomplete: extinction or decline is difficult or impossible to estimate from phylogenetic trees (Rabosky, 2010). This is compounded by the fact that some biodiversity patterns, including species richness and distribution through time, cannot be inferred from molecular phylogenies alone.

To improve our knowledge of plant evolutionary history, it is necessary to combine molecular and geological data—including the fossil record. Fortunately, the palynological fossil record of northern South America has been extensively studied. It provides an in-depth record of plant composition across space and time, marking putative regional speciation and extinction events of fossil pollen taxa, as inferred via morphological changes in fossil assemblages (e.g. Van der Hammen and Wijmstra, 1964; Germeraad et al., 1968; Van der Hammen et al., 1973; Gonzalez-Guzman, 1967; Dueñas, 1980; Lorente, 1986; Muller et al., 1987; Hoorn, 1993, 1994a,b; Rull, 2001; Jaramillo and Dilcher, 2001; Jaramillo et al., 2010, 2011). However, a major hurdle in linking the paleobotanical record to molecular phylogenetics lies in the difficulty of establishing the modern botanical affinity of fossils. This can be addressed by careful comparison of fossil pollen to extant species to assign nearest living relatives (NLRs). A few examples have already illustrated the promise of assessing NLRs to better understand past floristic composition, particularly when combined with molecular phylogenetic data (Zetter et al., 2002; Thornhill et al., 2012; Martínez et al., 2013; Jaramillo et al., 2013). In this paper, we follow this approach, targeting key representatives of the pre-Quaternary South American lowland flora while considering the role of geological and climatological factors.

Rhopities guianensis (Malvaceae: Grewioideae) and *Malvacipolloides maristellae* (Malvaceae: Malvoideae) are two key components of the Cenozoic palynological record, and form an appropriate study system to address the effect of the changing South American landscape on plant biodiversity. These species had broad geographic extents, including Amazonia, the Llanos, the Caribbean, and the Guyanas (Fig. 1), and the environmental conditions under which they thrived are well-documented. Importantly, they also are well-known biostratigraphic markers with *Rhopities guianensis* first occurring in the Paleogene, around 55.5 Ma (Jaramillo et al., 2010), and *Malvacipolloides maristellae* first appearing around 17.7 Ma (Muller et al., 1987; Jaramillo et al., 2011). These taxa both declined in the course of the Neogene (Van der Hammen and Wijmstra, 1964; Germeraad et al., 1968; Dueñas, 1980; Lorente, 1986; Muller et al., 1987; Hoorn, 1993, 1994a,b; Rull, 2001; Jaramillo et al., 2011). What the cause of this course of events was is yet unknown, and in this study we aim to find out. Ultimatedly, the history of these two taxa can help us to better understand the evolution of the tropical rain forest as a whole.

The northern Neotropics experienced a major transformation from primarily lowland tropical rainforest to a more heterogeneous landscape following the rise of the Eastern Cordillera (Hoorn et al., 2010; Ochoa et al., 2012). The uplift process promoted changes in the regional climate (Poulsen et al., 2010; Sepulchre et al., 2010) and was contemporaneous with other important paleogeographic events, including the closure of the Central American Seaway (Montes et al., 2015; Bacon et al., 2015; O'dea et al., 2016; Jaramillo et al., 2017a; Molnar, 2017) and Miocene marine incursions into northern South America (Hoorn, 1993; Boonstra et al., 2015; Salamanca et al., 2016; Jaramillo et al.,

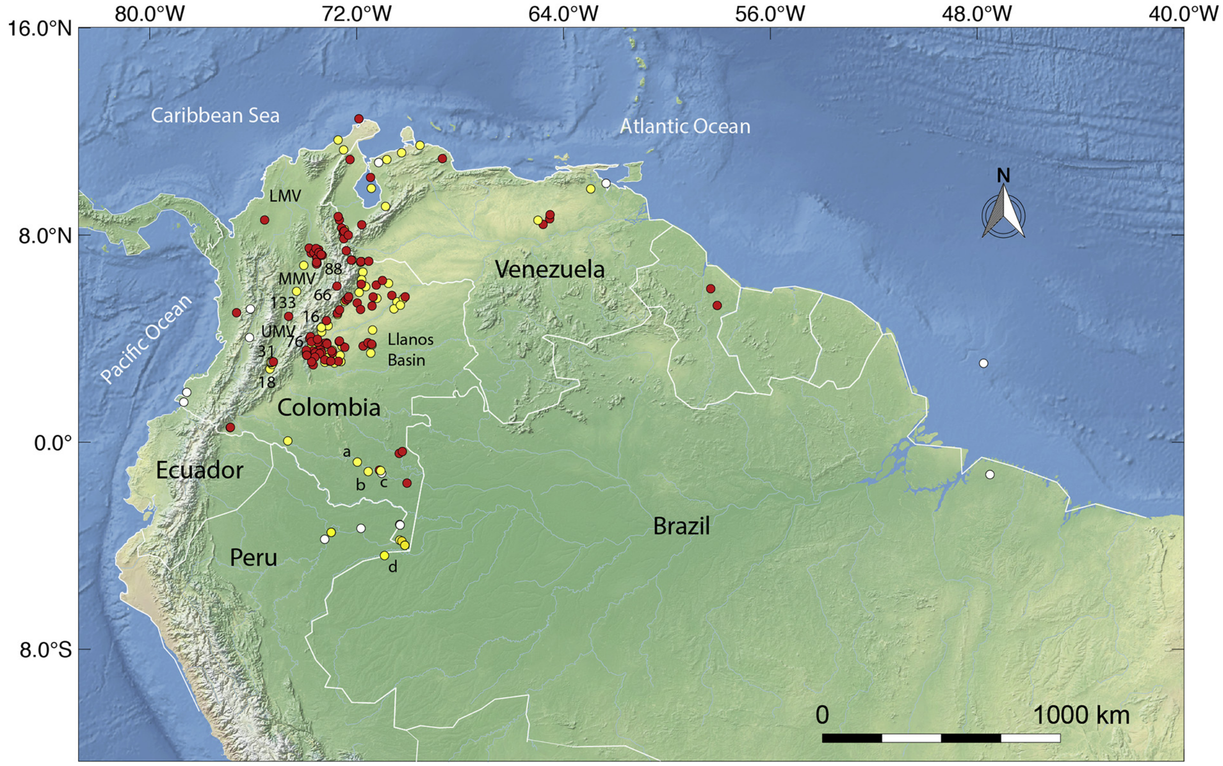


Fig. 1. Map of northern South America with the localities where *Rhoipites guianensis* and *Malvacipolloides maristellae* occur. Red dots indicate the exclusive occurrence of *Rhoipites guianensis*, white dots the exclusive occurrence of *Malvacipolloides maristellae*, and yellow dots the co-occurrence of *R. guianensis* and *M. maristellae*. UMV = Upper Magdalena Valley; MMV = Middle Magdalena Valley; LMV = Lower Magdalena Valley. Key locations of paleopalynological material from Amazonia: a = Mariñame, b = Tres Islas, c = Santa Isabel, d = CPRM well 1AS-4a-AM. Numbers 16, 18, 31, 66, 76, 88 and 136 represent Ecopetrol S.A. wells that are reported in the text.

2017b). Additionally, global climate cooling and aridification during the Neogene (Herbert et al., 2016) also may have affected the diversification of the Andean landscape, and the rainforest composition and its dynamics.

In this study our aim was to understand the impact of these geological processes on past biota of the region by using two key fossil Malvaceae. We first examined fossil and selected extant pollen types by using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM), to determine the botanical affinity of *R. guianensis* and *M. maristellae.* We also applied statistical models to characterize the paleoecology, historical biogeography, and phylogeny of these taxa. Combining our inferences from morphological and statistical analyses, we compared the appearances and disappearances of our focal taxa in the fossil record with the timing of geological and climatic processes. This integrative approach allowed us to assess the evolution of these important stratigraphic markers into an explicit spatial and temporal context, revealing two very different responses to landscape change following mountain uplift.

2. Materials and methods

2.1. Palynological material and sites

The fossil pollen was retrieved from samples of early Miocene fluvial deposits that outcrop along the Caquetá River in Colombian Amazonia (Hoorn, 1994a; Salamanca et al., 2016), and from a core drilled in Brazilian Amazonia by the Companhia de Pesquisa de Recursos Minerais (CPRM) (Hoorn, 1993) (Fig. 1; Appendix 1 Tables 1.1 and 1.2). This sample material was processed in the nineties (Hoorn, 1993, 1994a-b, Hoorn, 2006). In addition, modern reference material was processed at the University of Amsterdam and at Naturalis Biodiversity Center (The Netherlands). All palynological slides, both of extant and fossil taxa, form part of the reference collection at the University of Amsterdam and the Naturalis Biodiversity Center (Appendix 1 Table 1.3). The authorities of plant taxa are presented in alphabetical order in Appendix 1 (Table 1.4).

2.2. Pollen morphological analysis

Our study focused on making the best possible match between the fossil Malvaceae and their NLRs. Most palynological studies of the fossil record use LM, with SEM and TEM only rarely applied, largely because these are labour and cost intensive methods. Nevertheless, the three techniques combined can form an ideal bridge to accurately determine the botanical affinity of fossil taxa. To achieve this, we extended on the original descriptions of the fossils following the terminology by Punt et al. (2007) and we carried out new LM, SEM, and TEM analysis (Plates I–IV). We applied similar techniques on selected NLRs. By scrutinizing each tribe of Malvaceae using the available pollen morphological literature and reference collections, we selected extant taxa in which the character combination present in the fossil taxa also occurs (see the “nearest living relative” subsections in Section 3). For a complete photographic overview of the revised taxa we refer to Appendix 2 Plate I (Grewioideae) and Plate II (Malvoideae).

Microphotography from LM was carried out using Nikon D7000 and/or Fujifilm X-E2 and a Zeiss Universal microscope with 63 × Plan Neofluar NA1,25 oil applying Nomarski Differential Interference Contrast (DIC) following (Bercovici et al., 2009). While making the photos, the varying z-axis was recorded and images were later combined through manual z-stacking in Helicon Focus and Photoshop CC. This stacking technique combines different layers to provide a more detailed image. The plates (Plates I–IV and Appendix 2) were made with InDesign CC.

Scanning electron microscopy was performed at the Jodrell Laboratory (Royal Botanical Gardens, Kew) using a Hitachi S-4700 field-emission SEM (Plate II, IV). Preparation for TEM included rehydration and fixing in 0.1% glutaraldehyde (3 weeks) followed by fixation with 1% OsO4 (1 h), pre-staining with 1% uranyl acetate during dehydration, embedding in 3/7 Epon 218 (Luft), post-staining with 3% uranyl acetate (10 min) and Reynolds' lead citrate (10 min). Pollen was observed with a JEOL JEM 1010 (Plate II, IV). Plant vouchers and palynological slides that were used for the morphological analysis are found in Appendix 1 (Table 1.3).

2.3. Past and present distribution

We evaluated the historical records in northern South America and visualized the changes in abundance and distribution through time of the selected Malvaceae in a series of maps (Figs. 2–3). The results were used to determine the relationship between past distribution and paleogeography. The temporal and spatial variation of *Rhoipites guianensis* and *Malvacipolloides maristellae* were estimated based on a compilation of published and unpublished records from northern South America (Fig. 1; Appendix 1 Tables 1.1 and 1.2). The compilation was made based on presence–absence data and on counts of the number of palynomorphs per sample. Additional presence–absence data were obtained from publications and previously unpublished records that lacked quantitative information or information that was not suitable for statistical analysis.

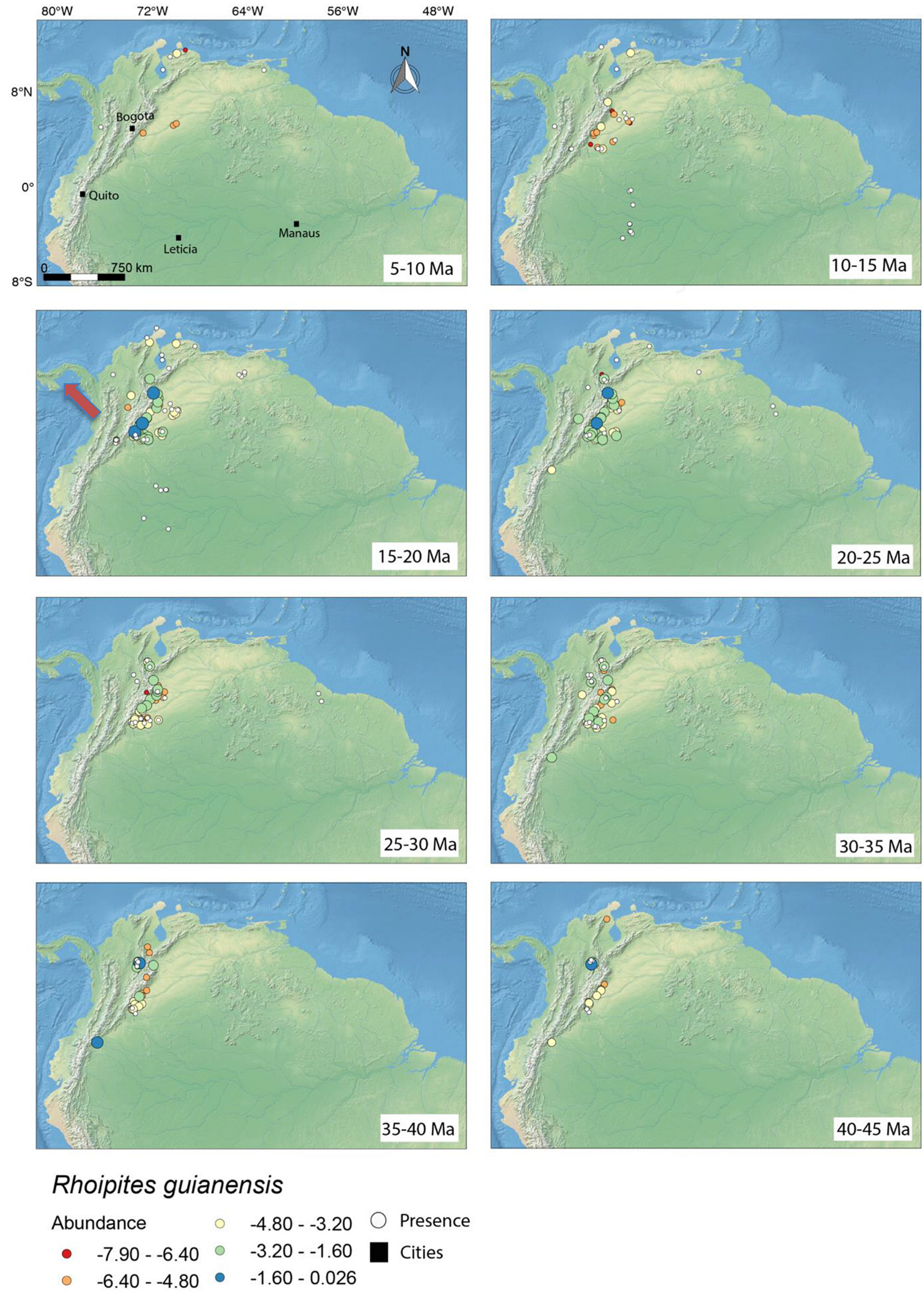
The quantitative data were produced by the Biostratigraphy Team of the Instituto Colombiano del Petroleo-Ecopetrol S.A (Colombia), and are based on studies of 96 and 48 sites for *Rhoipites guianensis* and *Malvacipolloides maristellae* respectively. Samples with counts fewer than 50 grains were eliminated from the analysis to avoid underrepresentation of the abundance distribution of the population (Hayek and Buzas, 2010). We standardized the data using a Wisconsin double standardization (Bray and Curtis, 1957) to compensate for differences in the counts between the samples, following the procedure of Jaramillo et al. (2013). The double standardized abundance matrix was used to construct abundance maps for the Cenozoic in 5 million year (Myr) time intervals (bins), encompassing the complete age range of each species. To produce the abundance maps (Figs. 2–3), each sample was assigned to a given bin and all the samples from the same locality for a given bin were summed to produce a single sample per bin per locality (Appendix 1 Table 1.2). Then, we used the logarithm of the standardized data as an estimation of the abundance of the species, which is represented by coloured circles in the maps. For the qualitative data (i.e., presence–absence), we assigned the presence of the species to each bin according to the age of the sample in which the species was recorded (Figs. 2–3).

The statistical analysis of pollen distribution was performed in R (R Development Core Team, 2016) using modifications of the code described in Jaramillo et al. (2013) and the maps were produced in QGIS (QGIS Development Team, 2016). Because *Rhoipites guianensis* is first abundant and widely reported from the middle Eocene, maps of *R. guianensis* were produced between 5 and 45 Ma. The oldest record of *R. guianensis* in northern South America is ~55.5 Ma (Jaramillo et al., 2011), though this corresponds to a single specimen from one locality, making it impossible to construct a map for this interval. Maps of *M. maristellae* were produced for a time period between 5 and 20 Ma; the oldest record is ~18 Ma (Jaramillo et al., 2011).

The distribution of the NLRs of *Rhoipites guianensis* (*Vasivaea* and *Trichospermum*) and *Malvacipolloides maristellae* (Abutilinae) was inferred from data downloaded from the Global Biodiversity Information Facility (GBIF) using R. There are relatively few (i.e., 96) known collections of *Vasivaea* (*R. guianensis*, type 1), suggesting that this taxon is either very rare or not well collected. Both *Trichospermum* (690 locality points) and Abutilinae (3889 locality points: *Abutilon*, 1630; *Bakeridesia*, 95; *Callianthe*, 915; *Herissantia*, 1249) had more information available.

2.4. Multivariate analysis of the palynological record

We carried out a multivariate analysis of four selected palynological records from Amazonia to document the relationship between the fossil


80°W
72°W
64°W
56°W
48°W
8°N
0°
8°S
N
Bogota
Quito
Leticia
Manaus
0
750 km
5-10 Ma
10-15 Ma
15-20 Ma
20-25 Ma
25-30 Ma
30-35 Ma
35-40 Ma
40-45 Ma
Rhoipites guianensis
Abundance
-7.90 - -6.40
-6.40 - -4.80
-4.80 - -3.20
-3.20 - -1.60
-1.60 - 0.026
Presence
Cities

Malvaceae and their contemporaries in the tropical lowland forest. To achieve this, we analyzed the palynological counts from the sedimentary record of four different sites situated in Amazonia. Three sites (Mariñame, Santa Isabel and Tres Islas) are situated along the Caquetá River in Colombian Amazonia, and one site (CPRM core) is situated along the Amazon River and near the meeting point of the Colombian, Brazilian and Peruvian border (Fig. 1). The data were analyzed in R using the libraries *vegan* (Oksanen et al., 2015), *stats* (R Core Team, 2016), and *corrplot* (Wei, 2013). We applied Wisconsin standardization (Bray and Curtis, 1957) to the counted palynomorphs of each of the site-specific datasets after filtering out singletons and doubletons. This standardization method was chosen because it performs well when the count data involves different scales (Bray and Curtis, 1957), such as in our datasets where different palynomorphs (pollen, spores, dinoflagellate cysts and foraminifer linings) occur together. The analysis is based on 137 palynomorphs from Mariñame, 85 of Santa Isabel, 75 of Tres Islas, and 139 of the CPRM core. The standardized data sets were used as input to obtain distance matrixes (Appendix 3 Table 1–4) applying the Horn-Morisita similarity index (Horn, 1966; Chao et al., 2006) and in non-metric multidimensional scaling (nMDS) plots (Fig. 4).

The Horn-Morisita index ranges from zero to one and satisfactorily handles heterogeneity in sample size and diversity (Wolda, 1981; Magurran, 2004). An index near to zero means high similarity in the distribution pattern of two taxa, whereas an index of one means no similarity.

2.5. Phylogenetic framework

Phylogenies were inferred for the extant relatives of each of our focal taxa to understand the origins of the fossil Malvaceae and their NLRs. To infer these phylogenies, DNA sequences from previous phylogenetic analyses of the subfamilies Grewioideae and Malvoideae, with an emphasis on Abutilineae, were downloaded from GenBank, prioritizing sequences with voucher information (Appendix 4, Table 4.1). These data represent four markers for Grewioideae (*mat*K, *ndh*F, *psb*A-*trn*H, and *rbc*L), and six markers for Malvoideae (ITS, *nad*H, *mat*K, *psb*A-*trn*H, *rbc*L, and *rpl*16). New sequence data from the *psb*A-*trn*H and *rbc*L loci was generated for *Vasivaea*, which was not previously represented in GenBank. DNA was extracted from leaf material from a herbarium specimen of *V. alchorneoides* Baill. (P. Mutchrick 717; MO, barcode MO-1890228) using a modified Qiagen DNeasy Plant Mini kit (Qiagen, Valencia, California, USA). Polymerase chain reaction (PCR) amplification and subsequent Sanger sequencing of two loci used previously in phylogenetics of Grewioideae (i.e., *psbA-trnH* and *rbc*L) followed standard protocols and utilized standard, angiosperm-wide primers (Li et al., 2011). For each subfamily, individual markers were aligned using MUSCLE (Edgar, 2004) and concatenated in Geneious v. 6.1.8 (http://www.geneious.com). PartitionFinder (Lanfear et al., 2012) was used to determine the best-fitting model of molecular evolution and partitioning scheme for phylogenetic inference.

Phylogenies for both subfamilies were inferred separately using the best partitioning scheme with Bayesian inference as implemented in BEAST 2.1.3 (Bouckaert et al., 2014). These analyses were each performed with 10 separate runs, each conducted for 100 million generations of Markov chain Monte Carlo (MCMC). Convergence was assessed using effective sample size (ESS) values of the runs with a cutoff value of 200, and the maximum clade credibility tree, including credibility intervals (CI) for ages and posterior probabilities (PP) for node support, was assembled. The non-Eumalvoideae members of Malvoideae (i.e., the clade including *Uladendron*, *Radyera*, *Lagunaria*, and *Howittia*) were used to root the tree based on their placement in previous studies (Baum et al., 2004; Koopman and Baum, 2008). Members of the Byttnerioideae (i.e., *Byttneria aculeata*, *Abroma augustum*, *Commersonia bartramia*, *Guazuma ulmifolia*) were used to root the phylogeny of Grewioideae, in accord with relationships from previous studies (e.g., Bayer et al., 1999; Brunken and Muellner, 2012).

For both subfamilies, divergence dates were estimated simultaneously with the tree topology in BEAST using a variety of secondary calibration points from Richardson et al. (2015). All secondary calibration points were assigned normally distributed priors (Ho and Phillips, 2009), with mean and standard deviations chosen to best represent the 95% highest posterior density values for the corresponding nodes in Richardson et al. (2015). For Malvoideae, a normal prior with a mean of 61.2 Ma and a standard deviation of 1 Ma was applied to the root node in BEAST. For Grewioideae, three secondary calibration points were applied: one at the base of Grewioideae, a second at the base of Byttnerioideae, and a final at the split between these two subfamilies. In BEAST, these corresponded to three normal priors, with means and standard deviations of 42.2 ± 10.5, 53.4 ± 10, and 59.72 ± 10 Ma, respectively. For Grewioideae, an additional calibration point corresponding to the origination date of *R. guianensis* (Jaramillo et al., 2010), was placed at 55.3 Ma, on the clade containing its nearest living relatives (see Section 3), *Trichospermum*, *Tetralix*, *Mollia*, *Hydrogaster*, and *Vasivaea.* This calibration point was assigned a lognormal prior with a mean of 1.0 and standard deviation of 1.25, offset by 55.3 Ma.

2.6. Biogeographic inference

The biogeographic history of each of the focal Malvoideae subfamilies was inferred to better understand the timing and place of the origin of our focal taxa. Each species in both phylogenies was coded for presence/absence in the following six broad biogeographic regions: (1) North and Central America (including the Choco region of Colombia); (2) South America; (3) Europe; (4) Asia; (5) Africa; and (6) Australasia. Occurrence information was accessed from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) and the Tropicos database maintained by the Missouri Botanical Garden (http://www.tropicos.org/). The likelihood of ancestral ranges along the BEAST maximum clade credibility (MCC) tree was inferred in the R package *BioGeoBears* (Matzke, 2013) using a standard dispersal-extinction-cladogenesis (DEC) model (Ree and Smith, 2008). Biogeographic inference was performed in a time-stratified manner by applying a dispersal probability matrix derived from Mao et al. (2012) that models the connectivity of the biogeographic regions through time. Following recent recommendations on best practices in biogeographic inference (Ree and Sanmartin, 2018), we did not apply models of biogeographic models that allow for founder event speciation.

3. Results

3.1. Systematic palynology of Rhoipites guianensis

Introduction: This taxon was first described by Van der Hammen and Wijmstra (1964) as *Retitricolporites guianensis*, a species with an affinity to Malvaceae from a drilled section offshore Guyana. *Rhoipites guianensis* is a biostratigraphic marker with a wide age range (Jaramillo et al., 2010, 2011; 55.3–1.79 Ma). However, it predominated during the middle Eocene to early Miocene and declined afterwards (Jaramillo et al., 2011) (Fig. 2). It is reported from the Colombian Llanos Basin (Dueñas, 1980; Jaramillo et al., 2011), the Middle Magdalena Valley (MMV) Basin (Rodriguez-Forero et al., 2012), the Venezuelan coastal basins (Lorente, 1986; Rull, 2001), Brazilian Amazonia (Hoorn,

Fig. 2. Geographical abundance distribution of *Rhoipites guianensis* from 45 to 5 Ma in time windows of 5 Myr. The red arrow indicates migration into a northern direction based on fossil findings in Central America dated 18.5 Ma (Jaramillo et al., 2014). The color and size of the circles represents the variation in the logarithm of the double standardized *R. guianensis* abundance. White circles correspond to localities where the presence of the species was reported but no quantitative information was available.

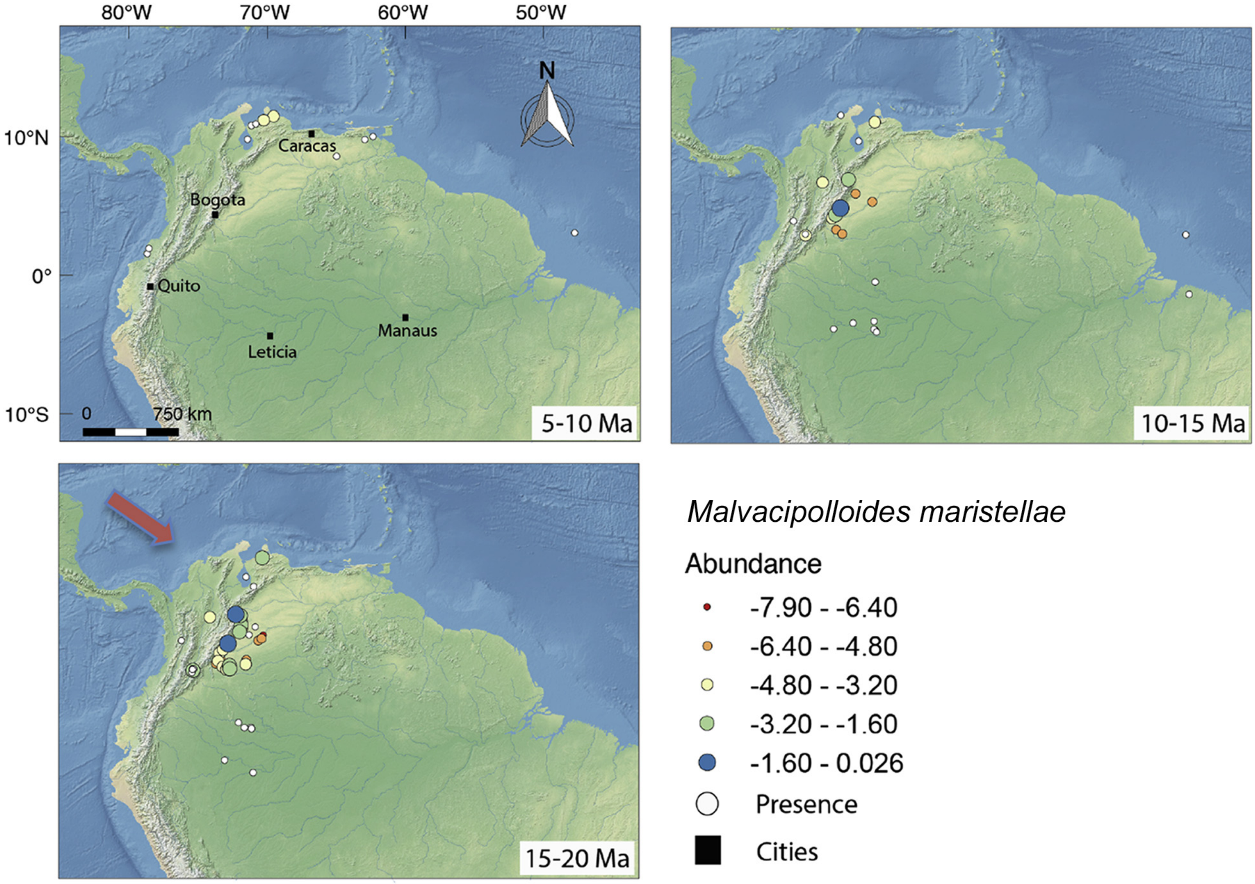


Fig. 3. Geographical abundance distribution *Malvacipolloides maristellae* from 20 to 5 Ma in time windows of 5 Myr. The red arrow indicates migration into a southern direction based on fossil findings dated 17.7 Ma (Jaramillo et al., 2011). The color and size of the circles represents the variation in the logarithm of the double standardized *M. maristellae* abundance. White circles correspond to localities where the presence of the species was reported but not quantitative information was available.

1993; Da Silva-Caminha et al., 2010), and in Panama (Jaramillo et al., 2014). Here we revisit this species and use Miocene Amazonian specimens for an improved description, including higher resolution imaging.

Genus: **Rhoipites**Wodehouse, 1933.

Species: **Rhoipites guianensis** (van der Hammen et Wijmstra, 1964) Jaramillo et Dilcher, 2001

Description: LM (Plate I, 11–16). Pollen grains isopolar monads; medium-sized, polar axis (P) = 31.8–39.4 μm, equatorial diameter (E) = 21.8–32.1 μm; prolate spheroidal to prolate, P/E = 1.08–1.58 (n = 6). Aperture system colporate; number of apertures three (5x) or four (1x). Colpi long, 27–31 μm, with distinct margos; pori lalongate, 2.3–3.6 μm "high", with distinct costae along the polar sides (= parallel to equatorial plane). Exine up to c. 2.5 μm thick (in mesocolpium centers), distinctly stratified; nexine ¼–½ of exine; infratectum distinct, undulate, c. ¼ of exine; tectum ¼–½ of exine. Ornamentation reticulate in upper focus, with distinct LO/OL-patterns in slightly lower focus (esp. in lumina); muri c. 0.5 μm wide; lumina up to c. 3 μm diameter, ± angular.

Remark: The relatively large range of E (and P/E) is due to folding of the colpi. Additionally, the width of the colpi and the shape of the pori depend of the folding state of the colpi.

Description: SEM (Plate II, 1, 2, 4, 5, III) (n = 16). Ornamentation reticulate; muri 0.4–0.6 μm wide; lumina up to c. 5 μm diameter, distinctly smaller (up to 0.7 μm) and less angular along colpi (margos); small ± circular lumina occur sparsely throughout mesocolpia; larger lumina (>c. 0.5 μm) irregularly cup- to funnel-shaped, with perforations from the bottom until just below outer edge of muri; perforations from minute up to c. 0.6 μm.

Remarks: (I) Two of the 11 visible pollen grains in the cluster in Plate III are relatively small: 17–18 μm diameter, though their ornamentation is similar to that of the larger grains; they might represent aborted pollen grains. (II) The exine in the lumina is considered here as tectum. (III) Reticulate pollen with a perforate tectum in the lumina is sometimes described as bireticulate. (IV) Some variation is present in the distribution and size of the perforations in the lumina. We distinguish two types: type 1 (Plate II, 1, 2) and type 2 (Plate II, 4, 5, and Plate III). In type 1 pollen grains, perforation size decreases towards the edge of the muri, while in type 2 grains relatively large perforations are adjacent to the muri.

Description: TEM (Plate II, 3, 10). Exine 1.7–2.0 μm thick (in mesocolpium centers), distinctly stratified; nexine 0.4–0.5 μm thick; endexine (innermost sublayer of nexine) < 0.1 μm in mesocolpium centers, slightly thickening (up to 0.2–0.3 μm) and ± granular towards colpi; infratectum 0.3–0.9 μm thick, columellate; tectum ± undulate, 0.3–0.7 μm thick, finely perforate in depressions; muri ± triangular in cross-section.

Comparison: The pollen grains described above more or less match the descriptions and images of *Rhoipites guianensis* given by Van der Hammen and Wijmstra (1964), Germeraad et al. (1968), Lorente (1986), Jaramillo and Dilcher (2001) and Jaramillo et al. (2011). However, there is no mention in these descriptions of the LO/OL-patterns within the lumina (due to perforate tectum and underlying columellae), unless this feature is indicated by "*columellae distributed regularly*". There is a discrepancy between Van der Hammen and Wijmstra (1964) on the one side, and Germeraad et al. (1968) and Jaramillo and Dilcher (2001) on the other. According to van der Hammen and

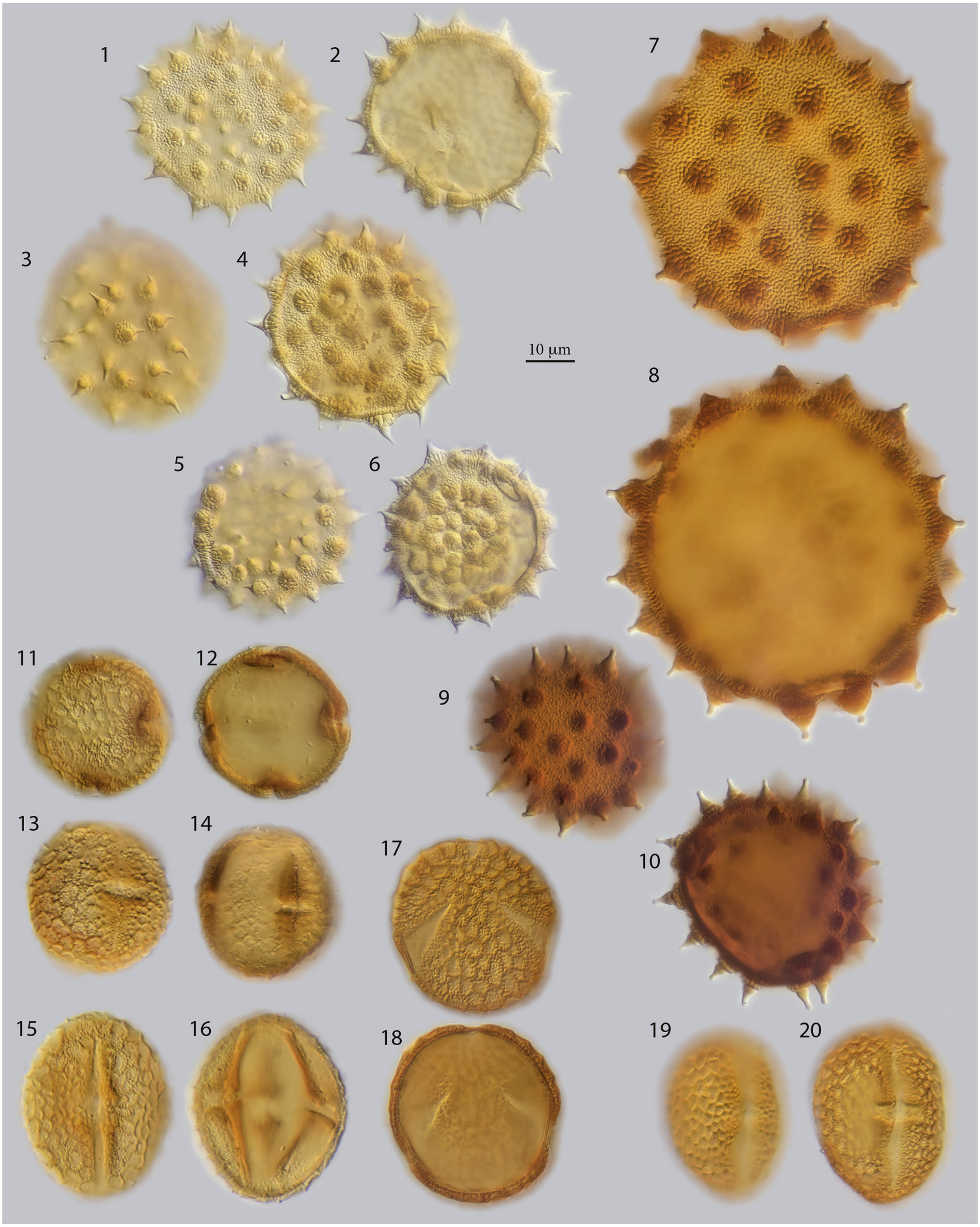


Plate I. LM micrographs of fossil and recent Malvaceae pollen. (1–6) Fossil *Malvacipolloides maristellae* (Hoorn, 1994a). (1, 2) Polar view; note three equatorial apertures in 2 (Mar 40-2; EF: P48-3). (3, 4) Oblique view; note costate pore in 4 (Mar 34-2.1, EF: T-U 46). (5, 6) Near polar view; note two costate pores in 6 (Mar 40-2; EF: H-J60). (7–10) Recent *Callianthe*. (7, 8) *C. monteiroi* (8125 IBED, EF: P46-47). Oblique view; apertures out of focus. (9, 10) *C. striata* (8126 IBED, F-G 46-47). Near polar view; note two costate pores in 10. (11–16) Fossil *Rhoipites guianensis* (Hoorn, 1994a). (11, 12) Polar view of 4-aperturate pollen grain (Mar14-91, EF J51-3). (13, 14) Equatorial view; note colporate aperture (Mar14-91; EF: M49-4). (15, 16) Equatorial view; note three colporate apertures (Mar14-91; EF: K46-4). (17–20) Recent *Vasivaea alchorneoides* (8122 & 5094 IBED). (17, 18) Near polar view; note three colpi (8122 IBED, EF: J44-3). (19, 20) Equatorial view; note colporate aperture (5094 IBED, EF, M34). Each pair (1 and 2, 3 and 4, etc.) of micrographs presents an upper focus view (1, 3, etc.) and a lower focus view (2, 4, etc.). Scale bars = 10 μm (1–20).

Wijmstra, the muri are simplibaculate, whereas Germeraad et al. and Jaramillo and Dilcher describe them as multi/pluricolumellate. The arrangement of the columellae, however, is hard to observe (only possible in LM in surface views). In our material, both simplibaculate and multi/pluricolumellate seem to occur, but a row of columellae may be confused with the wall (sloping edge) of a lumen. These walls (edges) are interpreted as tectum (see Remark II under SEM).

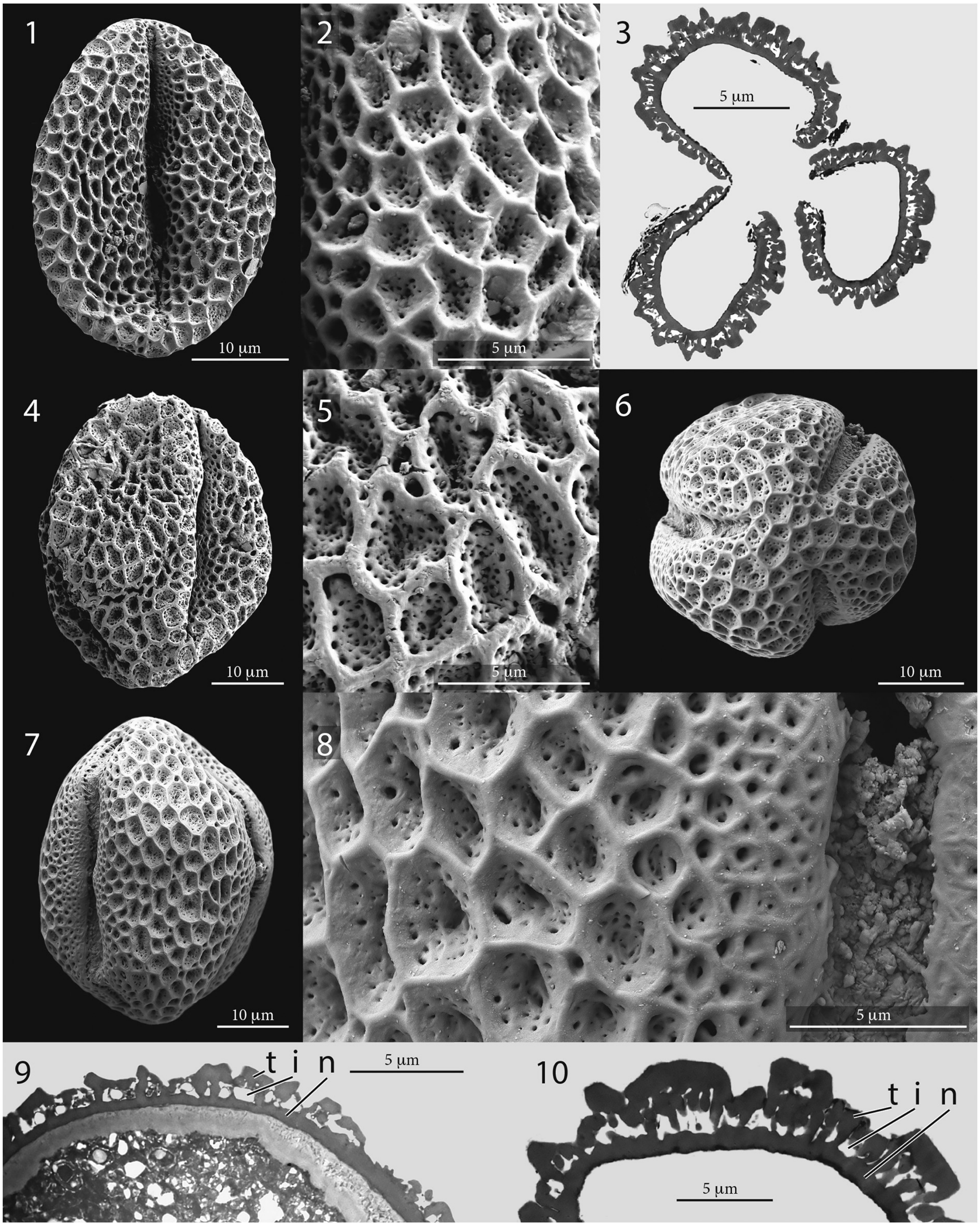


Plate II. SEM and TEM micrographs of fossil and recent Grewioideae pollen. (1–5, 10) Fossil *Rhoipites guianensis* (Hoorn, 1994a). (1) SEM type 1: equatorial view (Mar 40; CH20_q04). (2) SEM type 1: detail of ornamentation (Mar 40; CH20_q05). (3) TEM: near polar view, showing three apertures (Mar14-91; 014057.194652 J5). (4) SEM type 2: equatorial view (3 Islas 35; 4CH_q05). (5) SEM type 2: detail of ornamentation (3 Islas 35; 4CH_q06). (10) TEM: detail, showing nexine (n), infratectum (i) and tectum (t). (6–9) Recent *Vasivaea alchorneoides* (Naturalis 1889; Kuhlmann 2968, Brazil). (6) SEM: polar view. (7) SEM: equatorial view. (8) SEM: detail of ornamentation. (9) TEM: detail, showing nexine (n), infratectum (i) and tectum (t). (10) See above. Scale bars = 10 μm (1, 4, 6, 7), 5 μm (2, 3, 5, 8–10).

Rhoipites guianensis has some resemblance to *R. cienaguensis* (Dueñas, 1980) Barreda, 1997 (age 41.15–17.33 Ma), but the latter is oblate, has a finer reticulum and a thinner exine; *R. planipolaris* (Jaramillo and Rueda, 2008) (age 31.5–13.04 Ma) has a flat polar area, whereas *R. gigantiporus* Da Silva-Caminha et al., 2010 (age 14.94–4.77 Ma) has distinctly larger pores. Another closely resembling species is *Rhoipites? perprolatus*, with angular reticula towards the poles and decreasing to the aperture. However, this taxon is perprolate, slightly hetrobrochate,

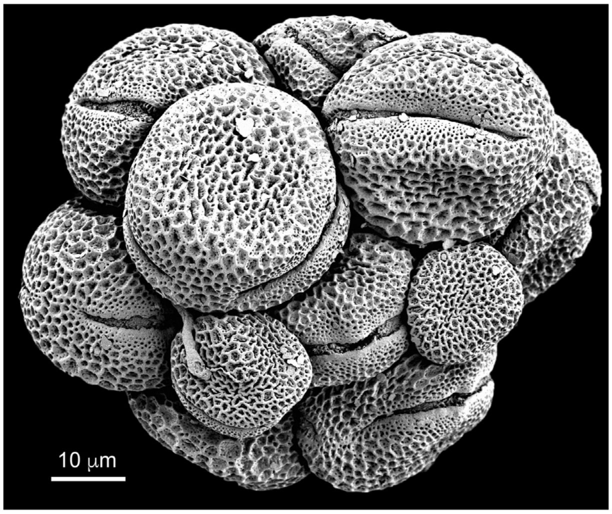


Plate III. Pollen cluster of *Rhoipites guianensis* type 2 (sample Mar14-91), SEM; botanical affinity *Trichospermum*.

and sometimes tricolpate and other times tricolporate. (vs. prolate, strongly heterobrochate and always tricolporate in *R. guianensis*) (Rodriguez-Forero et al., 2012).

Nearest living relative: Wodehouse (1933) proposed *Rhus typhina* (Anacardiaceae) as NLR for *Rhoipites*, but this was rejected (Pocknall and Crosbie, 1982) and the affinity for the genus remained uncertain. The character combination used here to determine the NLR of *Rhoipites guianensis* is bireticulate ornamentation plus long colpi with distinct margos. Bireticulate ornamentation is very similar to the ornamentation in the pollen of some Malvaceae *s.l.* genera. Germeraad et al. (1968) noticed resemblance with *Firmiana colorata*, *Glossostemon bruguieri*, *Hildegardia barteri*, *Pterocymbium beccarii*, *Sterculia mexicana*, and *Trichospermum*,. Though a specific affinity was not provided, Byttnerioideae and Tilioideae were the only clades (now considered as part of the Malvaceae *s.l.*) in which this pollen type was found so far (Germeraad et al., 1968; see also D'Apolito, 2016). In the meantime, several detailed Malvaceae pollen studies have been conducted, including Bombacoideae, Malvoideae, Byttnerioideae, and Tilioideae of Madagascar and the Mascarene Islands (Presting et al., 1983), Brownlowioideae, Grewioideae, and Tilioideae globally (Perveen et al., 2004), Byttnerioideae and Helicterioideae from Bahia, Brazil (Saba et al., 2004), and Grewioideae from southern South America (Mambrín et al., 2010).

Perveen et al. (2004) described the *Corchorus* pollen type on the basis of pollen grain shape: prolate–subprolate, rarely prolate–spheroidal (i.e. P/E 1.14–2.00, rarely 1.00–1.14), as opposed to the oblate–suboblate, rarely oblate-spheroidal (i.e. P/E 0.50–0.88, rarely 0.88–1.00) pollen types of *Berrya* and *Mortoniodendron*. Associated with the prolate shape is the presence of long colpi. The *Corchorus* type comprises nearly all 25 genera of Grewioideae (though not *Apeiba*, and the pollen of *Hydrogaster* remains uncharacterized) (Appendix 2 Plate I). Most Grewioideae also show bireticulate ornamentation, with the exceptions of *Duboscia*, *Erinocarpus*, *Luehea*, and *Pseudocorchorus* (though own data demonstrated bireticulate pollen in *Luehea candida*). In *Clappertonia*, the lumina become much smaller towards the poles. The presence of distinct margos along the colpi narrows down the likely NLRs of *R. guianensis* to *Corchorus*, *Eleutherostylis, Heliocarpus*, *Trichospermum*, *Triumfetta*, and *Vasivaea* (Appendix 2 Plate I). Similar pollen, though with less distinct margos, is found in *Goethalsia*, *Sparrmannia*, and *Tetralix*. Within the Malvaceae *s.l.* the occurrence of prolate–subprolate bireticulate pollen with long colpi and distinct margos is restricted to Grewioideae. The pollen of sister group Byttnerioideae is clearly different (Saba et al., 2004). Except for *Trichospermum* (Grewioideae), this morphological pattern is unknown in the genera mentioned by Germeraad et al. (1968): *Firmiana*, *Glossostemon*, *Hildegardia*, *Pterocymbium*, and *Sterculia*.

Only few TEM images of Grewioideae pollen are available for comparison with *R. guinanensis*: *Ancistrocarpus* (Perveen et al., 2004), *Luehea* (Lattar et al., 2012), *Lueheopsis* (own data), and *Vasivaea* (own data). Clear, unambiguous differences between *R. guianensis* and the pollen of the recent species could not be determined (compare with Plate II, 6–9).

The variation in the distribution and size of the perforations in the lumina of *Rhoipites guianensis* (SEM), as indicated above, might be due to intraspecific diversity or heterogeneity of the material, with more than one taxon being represented. This hampers matching *R. guianensis* with a single recent species, or even genus. Furthermore, the nine genera mentioned above do not form a monophyletic group (Alverson et al., 1999; Brunken and Muellner, 2012; Richardson et al., 2015), including lineages that are younger than the Miocene. This means that *R. guianensis* might represent one or more ancestral species of one or more recent genera, which makes comparison to extant taxa a particular challenge. That said, the greatest resemblance of *R. guinanensis* (type 1: perforation size decreasing towards edge muri Plate II, 1, 2) is with *Vasivaea alchorneoides* (Plate II, 6–9), while *R. guinanensis* (type 2: large perforations adjacent to muri; Plates II, 4, 5, III) is most similar to the pollen of *Eleutherostylis renistipulata* and *Trichospermum* (Perveen et al., 2004). *Eleutherostylis* is a monotypic genus from New Guinea, while *Trichospermum* (incl. *Belotia*) is a genus of ca. 36 species from tropical America, Malesia and the western Pacific. We confidently place *R. guinanensis* in a specific subclade of Grewioideae including *Vasivaea* and *Trichospermum* (Appendix 2, Plate I), from which it does not morphologically deviate.

Paleoenvironment: An evaluation of fossil data from outcrops and oil wells in northern South America indicates that during the middle to late Eocene *Rhoipites guianensis* was abundant in fluvial environments in the MMV (Fig. 1) (Rodriguez-Forero et al., 2012), where it was also found associated with lacustrine environments (Pilsbry and Olsson, 1935; Nuttall, 1990). Well records (wells 88 and 136) also document the occurrence of *R. guianensis* in the Oligocene meandering fluvial Mugrosa Formation. In the Llanos Basin, *R. guianensis* is present in both fluvial to transitional environments from middle Eocene up to the middle Miocene, and in Amazonia *Rhoipites guianensis* occurs in early Miocene sediments, both in Andes- and Amazonia-derived fluvial floodplain deposits and in environments of raised salinity (Salamanca et al., 2016).

3.2. Systematic palynology of Malvacipolloides maristellae

Introduction: Muller et al. (1987) originally described this species as *Echitricolporites maristellae* and first reported it from the Venezuelan coastal basins (see also Lorente, 1986). *Malvacipolloides maristellae* is a biostratigraphic marker indicative of the lower Miocene (Muller et al., 1985). It has had a complicated taxonomic past with a documented need for an in-depth study to determine the nearest living relative, which we address in this study. This taxon is commonly associated with floodplain or lacustrine deposits of the early Miocene age (17.7–16.1 Ma, T13 Zone of Jaramillo et al., 2011) (Hoorn, 1994a; Salamanca et al., 2016; Instituto Colombiano del Petroleo, internal report) and declines in the late Miocene. *Malvacipolloides maristellae* is reported in the Colombian Llanos Basin (Jaramillo et al., 2011), the MMV (Instituto Colombiano del Petroleo, internal report), and in Brazilian and Colombian Amazonia (Hoorn, 1993, 1994a; Da Silva-Caminha et al., 2010; Leite et al., 2017). Here we revisit this species and use Miocene Amazonian specimens for an improved description, including higher resolution imaging.

Genus: **Malvacipolloides** Anzótegui et Garralla 1985.

Species: ***Malvacipolloides maristellae*** (Muller, Di Giacomo et van Erve Muller et al., 1987) n. comb. da Silva-Caminha, Jaramillo et Absy 2010.

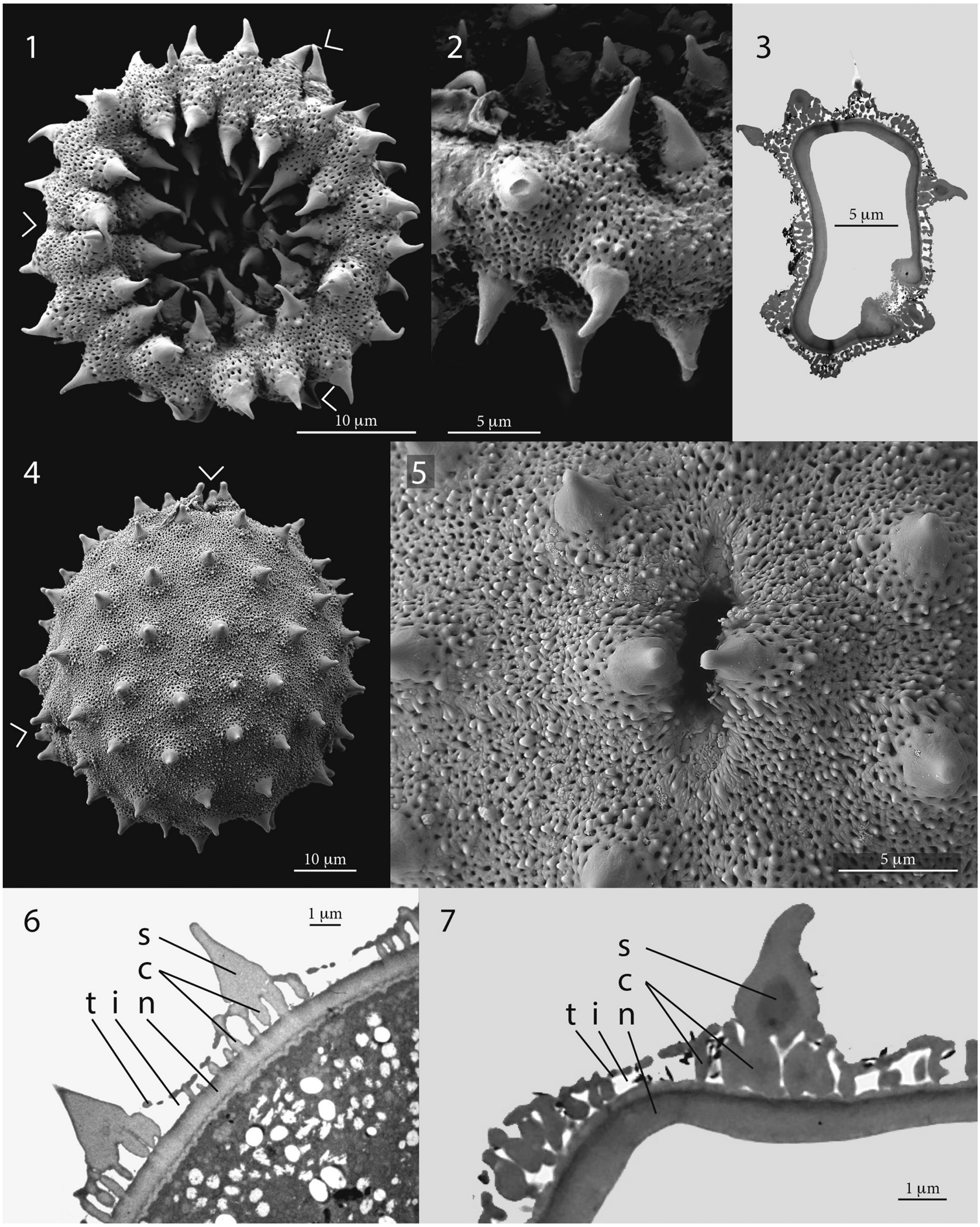


Plate IV. SEM and TEM micrographs of fossil and recent Malvoideae pollen. (1–3, 7) Fossil *Malvacipolloides maristellae* (Hoorn, 1994a). (1) SEM: near polar view of collapsed pollen grain; probably, the apertures are situated where two spines lean to each other (arrows) (Mar40; 13CH_q04). (2) SEM: detail of ornamentation (Mar40; 13CH_q04). (3) TEM: oblique section, showing one costate pore (Mar39; 14996 13661h1). (7) TEM: detail, showing nexine (n), infratectum (i) with columellae (c) and tectum (t) with spine (s). (4, 5) SEM recent *Callianthe rufinerva* (Naturalis 1890; Lindeman & de Haas 2359, Brazil). (4) Near polar view, showing two apertures (arrows). (5) Equatorial view, showing a colporate aperture. (6) TEM recent *Callianthe striata* (8126 IBED, F-G 46-47). Detail, showing nexine (n), infratectum (i) with columellae (c) and tectum (t) with spine (s). (7) See above. Scale bars = 10 μm (1, 4), 5 μm (2, 3, 5), 1 μm (6, 7).

Description: LM (Plate I, 1–6). Pollen grains isopolar monads; medium-sized, largest diameter 34.9–43.3 μm, smallest diameter 32.0–38.8 μm; largest/smallest diameter 1.09–1.15 (n = 3). Aperture system 3-colporate; colpi short, narrow; pores costate. Exine c. 1.5 μm thick between spines, distinctly stratified; nexine c. 0.7 μm thick throughout pollen grain (except near apertures: costae); infratectum distinct, columellate, undulate, c. 0.6 μm thick between spines, up to c. 1.8 μm thick under spines; tectum c. 0.2 μm thick between spines.

Ornamentation echinate, with distinct LO/OL-patterns due to perforate tectum and columellate infratectum; spines smooth, solid, 3–4 μm long.

Remark: The small colpi are difficult to see. Usually, a colpus is bordered and hidden by two spines that more or less lean towards each other over the colpus. Such a spine pair indicates a colpus. Another way to find the colpi is looking for the costate pores.

Description: SEM (Plate IV, 1, 2). Ornamentation echinate; spines smooth, 3–4 μm long, on perforate base; perforations between spines from minute up to 0.4 μm diameter; scabrae up to 0.5 μm occur sparsely, especially around spines.

Description: TEM (Plate IV, 3, 7). Exine c. 1.5 μm thick between spines, distinctly stratified; nexine c. 0.9 μm thick throughout pollen grain, up to c. 2.5 μm near apertures (costae); infratectum distinct, columellate, undulate, c. 0.4 μm thick between spines, up to c. 1.5 μm thick under spines; columellae under and near spines larger than below tectum between spines; tectum c. 0.2 μm thick between spines; spines solid.

Comparison: The pollen grains described above match the descriptions and images of *Echitricolporites*/*Malvacipolloides maristellae* given by Lorente (1986), Muller et al. (1987), Rull (2001) and Da Silva-Caminha et al. (2010). On the SEM photos in Lorente (1986), even the scabrae on and between the spine bases are visible. *Malvacipolloides maristellae* somewhat resembles pollen of *M. comodorensis*, found in Oligocene–Miocene sediments (Barreda, 1993), and *M. tucumanensis*, found in middle Miocene sediments (Mautino et al., 2004). The latter two taxa were both described from Argentina, where they commonly occur together with Asteraceae and Polygonaceae.

Nearest living relative: According to Lorente (1986), *Echitricolporites maristellae* has some resemblance with pollen from Malvoideae, and a similar pollen type would also be produced by some genera of Bombacoideae (e.g., *Camptostemon*). Muller et al. (1987) did not mention a botanical affinity. Da Silva-Caminha et al. (2010) transferred *E. maristellae* to the genus *Malvacipolloides,* which was erected by Anzótegui and Garralla (1986) to replace the invalidly published name *Echitricolporites*, and to accommodate fossil pollen with an affinity to the Malvaceae sensu stricto (subfamily Malvoideae in the present circumscription of Malvaceae *s.l.*) (see also Barreda, 1993). Jaramillo and Rueda (2008) suggested that *Malvacipolloides maristellae* has affinity to Asteraceae, and D'Apolito (2016) mentioned Bombacoideae.

Using light and scanning electron microscopy, *Malvacipolloides maristellae* indeed looks like Asteraceae pollen, although the colporate apertures are usually larger, and therefore more distinct in the pollen of this family. Using transmission electron microscopy, however, it is obvious that *M. maristellae* (Plate IV, 3, 7) does not represent Asteraceae (see also Skvarla and Turner, 1966). In *Malvacipolloides maristellae* there is/are no internal tectum(s), nor more than one columellate layer. Neither are there caveae, nor internal foramina, and the columellae are not branched. Furthermore, the spines in this taxon are solid instead of being provided with cavities. TEM demonstrates the exine stratification similar to that found in a number of Malvaceae *s.l.* genera: a tripartite exine consisting of a nexine, a single columellate layer, and a tectum with conical solid spines, each on a basal cushion and supported by relatively large columellae, while smaller columellae are present in between the spines (compare Plate IV, 6 and 7).

Spines on pollen grains are widespread in Malvaceae *s.l*, and are found in at least four of the nine subfamilies: Bombacoideae (*Adansonia*, *Pachira*, *Scleronema*), Byttnerioideae (*Ayenia*, *Melochia*, *Waltheria*), Dombeyoideae (at least 14 of the ca. 20 genera), Helicteroideae (*Helicteres*), and Malvoideae (see below) (references via Thanikaimoni and van der Ham, 1999; especially: Erdtman, 1952; Coetzee and van der Schijff, 1979; Presting et al., 1983; Christensen, 1986). Unlike those of *Malvacipolloides maristellae*, the spines in the Bombacoideae, Byttnerioideae, and Helicteroideae are small and lack a basal cushion. Moreover, there is further evidence that *M. maristellae* does not have an affinity to these subfamilies. Within Byttnerioideae, pollen with spines occurs only in a few species of *Ayenia*, the pollen of which always also deviates by distinctly aspidate apertures, while in *Melochia* and *Waltheria*, the spines are found only in brevistylous flowers. In *Helicteres* (Helicteroideae), pollen differs from *M. maristellae* by its oblate shape (P/E = 0.51–0.77).

The spines of the pollen of Dombeyoideae and Malvoideae are similar to those of *M. maristellae* (Appendix 2 Plate. II). Dombeyoideae pollen is mostly much larger (35–120 μm) than *M. maristellae* pollen (c. 35–43 μm) and has por(or)ate apertures, although the difference between the latter and the diminutive colporate apertures of *M. maristellae* are small and inconspicuous. Dombeyoideae have an exclusively Old World distribution.

The cosmopolitan Malvoideae is the largest subfamily of Malvaceae *s.l.*, including 78 (Stevens, 2012) to 111–115 genera (Klitgård et al., 2011). Malvoideae pollen is nearly always echinate, although the spines are sometimes minute, and the pollen of the small Brazilian genus *Goethea* seems to lack spines (Erdtman, 1952). The number of apertures (pori or short colpi) varies from three to much more than 100. Pollen with three apertures is found only in the tribe Malveae, in at least 16 of the 60 Neotropical genera (Klitgård et al., 2011). Detailed SEM images are available for only a few of these genera. Pollen of *Abutilon* and their close relatives, including for example the genera *Callianthe* (Donnell et al., 2012; see Plate IV, 4, 5 in present paper) and *Herissantia* (Hanks and Fryxell, 1979), is very similar to *M. maristellae*, even in the details of the perforations and scabrae in/on the tectum (SEM); see also Presting et al. (1983) and Perveen et al. (1994).

Paleoenvironment: Malvacipolloides maristellae is common among fluvial and lacustrine environments. In the Upper Magdalena Valley (UMV, Fig. 1), the taxon is accompanied by high abundances of colonies of the freshwater algae *Pediastrum* spp., and this is replicated in the MMV, where it is found in association with freshwater algae (*Pediastrum* spp. and *Botryococcus* spp.) (Fig. 1; Appendix 1 Table 1.1). Although *M. maristellae* is rare in the palynological record of the MMV, data of the well number 76 (Fig. 1; Appendix 1 Table 1.1) show similar associations of freshwater algae (*Pediastrum* spp. and *Botryococcus* spp.), with some specimens of *M. maristellae* within the La Cira Shale (or La Cira Fossil Horizon) (Instituto Colombiano del Petroleo, internal report). In the central part of the Llanos Basin *M. maristellae* is found in the early Miocene Huesser Fossil Horizon (Uppermost part of the C2 member C2, Carbonera Formation) (Gomez et al., 2009) and associated with fresh water malacofauna and a palynoflora characterized by tropical lowland taxa (*M. maristellae* was scarce, but also included in this group) together with fresh water algae such as *Botryococcus* spp. and *Pediastrum* spp. In Amazonia, *M. maristellae* almost exclusively occurs in Andes-derived sediments that are formed in an open water environment on the floodplain (Hoorn, 1994a; Salamanca et al., 2016), whereas the taxon is absent in the overlying strata formed in brackish water environment.

3.3. Historical biogeography of Rhoipites guianensis and Malvacipolloides maristellae

The past distribution of *Rhoipites guianensis* and *Malvacipolloides maristellae* in northern South America is shown in Figs. 2 and 3, respectively. The calculations that were made to produce the maps suggest that the total count per time slice does not explain the inferred abundance of the two species. This suggests that our results are robust and relate to higher – or lower – frequencies of the taxon in the landscape. There was only very weak correlation between the total number of grains per time slice versus the number of grains of the study species (*R. guianensis*: $r^2 = 0.065$, $P < .001$; *M. maristellae*: $r^2 = 0.07$, $P < .001$).

Rhoipites guianensis was reported in 27 localities (Lorente, 1986; Van der Hammen and Wijmstra, 1964), Hoorn, 1993, 1994a, 1994b, 2006). Unpublished reports included 46 localities, 44 of which correspond to wells analyzed by Ecopetrol S.A. in Colombia. The other two localities correspond to recent studies carried out by researchers from the

Universidad de Caldas in western Colombia. Although *R. guianensis* originates in the earliest Eocene (55.3 Ma), it became prominent in the middle Eocene (40–45 Ma), and was even more abundant from late Eocene to earliest middle Miocene (35–15 Ma) (Fig. 3). However, it begins to decline in abundance in the middle Miocene (15–10 Ma). Notably, the taxon is also recorded around c. 18.5 Ma in Panama (Jaramillo et al., 2014)

Malvacipolloides maristellae has been reported in 22 localities (Lorente, 1986; Van der Hammen and Wijmstra, 1964; Hoorn, 1993, 1994a, 1994b). Unpublished records include 14 localities, 10 of which correspond to wells analyzed by Ecopetrol S.A and 4 correspond to recent studies carried out by researchers from the Universidad de Caldas in western Colombia. The taxon first appeared in the early Miocene (20–15 Ma) and is abundant until the late Miocene (15–10 Ma). Although late Miocene sedimentary records have a poor pollen recovery, both *M maristellae* and *R. guianensis* are relatively common in the Venezuelan Coastal basins (Figs. 2–3).

3.4. Rhoipites guianensis and Malvacipolloides maristellae in Amazonian paleoenvironments

We analyzed pollen records from four key sites in Amazonia to understand the past environments in this region. *Rhoipites guianensis* (NLRs: *Vasivaea* and *Trichospermum*) is abundant at all of the four sites that were analyzed, while *M. maristellae* (NLRs: Abutilinae) occurred in all records except for Tres Islas. At these sites the sedimentary record presents three characteristic ecological assemblages. The first is either dominated by *R. guianensis* or by both *R. guianensis* and *M. maristellae* (Fig. 4 in red). The second assemblage is dominated by *Mauritiidites* (NLR*: Mauritia*), a palm pollen whose modern analog is an indicator of mature lowland tropical forests and floodplain swamps, and accompanied by minor amounts of *R. guianensis* (Fig. 4 in green). The third assemblage represents a mangrove or coastal environment of perimarine conditions (Fig. 4 in blue), as indicated by the presence of mangroves and marine zoo- and phytoplankton. It is characterized by *Zonocostites ramonae*, *Zonocostites* spp., *Psilastephanocolporites schneideri* (NLR: Rhizophoraceae, black mangroves), foraminifera and dinoflagellate cysts with minor amounts of *R. guianensis* and no *M. maristellae.*

The ecological assemblages have the following characteristics: *Rhoipites guianensis* always co-occurs with three taxa, which are *Ranunculacidites operculatus* (NLR: *Alchornea,* Euphorbiaceae), *Retitricolporites caputoi* (NLR: Araliaceae), and *Ranunculacidites* cf. *operculatus* (NLR: *Symmeria*, Polygonaceae) (see Salamanca et al., 2016). In Mariñame and in the CPRM core, *Crassiectoapertites columbianus* (NLR: Fabaceae) is closely associated with *R. guianensis*, but these two taxa are seldom found together in Tres Islas. On the other hand, *Echiperiporites akanthos* (NLR: *Sagittaria*, Alismataceae) is often associated with *R. guianensis* in Tres Islas, Mariñame, Sta. Isabel, and the CPRM core. *Psilabrevitricolpites rotundus* (unknown affinity) is present in three of the four sedimentary records that include *R. guianensis.* The top eight associated taxa with *R. guianensis* (NLR: *Vasivaea* and *Trichospermum*) in each of the four palynological records are listed in (Fig. 4; Table 1).

Based on this analysis we conclude that *R. guianensis* (NLR: *Vasivaea* and *Trichospermum*), *M. maristellae* (NLR: *Abutilinae*), and their

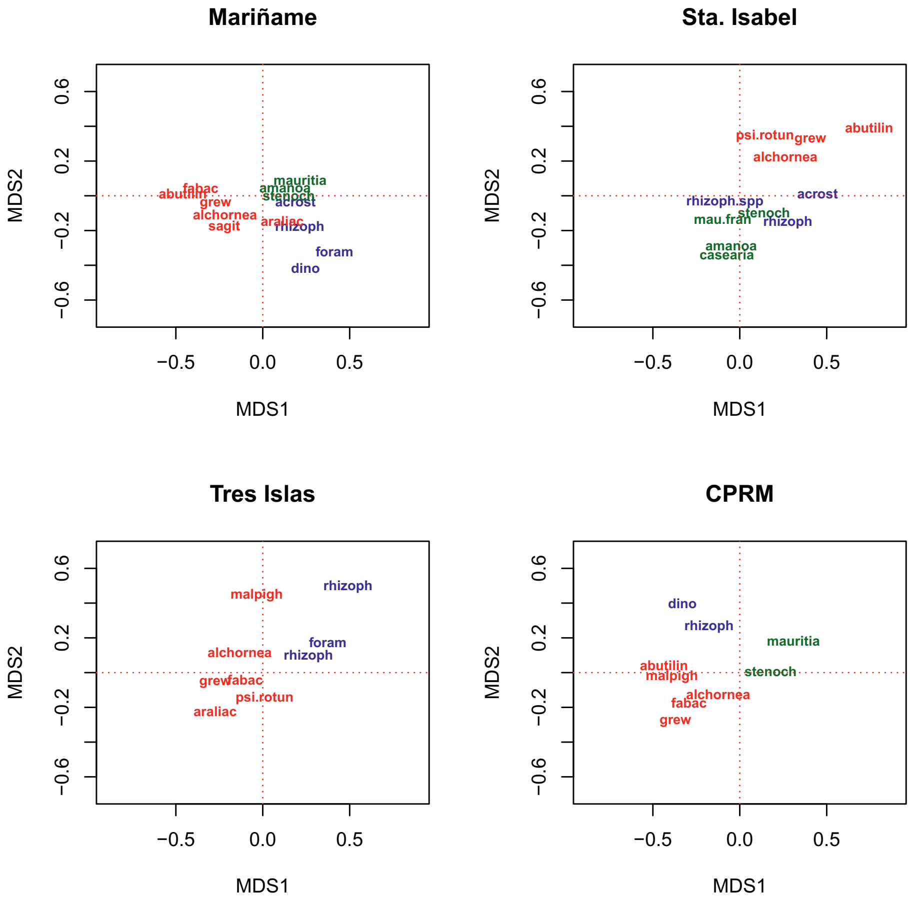


Fig. 4. nMDS plots of four palynological records: Mariñame, Santa Isabel, Tres Islas and the CPRM core (Fig. 1 and Appendix 1 Table 1.1 for locations). Four palynomorph assemblages were recognized. Taxa in red are closely associated with *Rhoipites guianensis* (NLR: *Vasivaea* and *Trichospermum*; Grew = Grewiodeae), and represent the lowland floodplain assemblage; taxa in blue are associated with *Zonocostites* spp. (NLR: *Rhizophora)*, which represent mangrove-like vegetation; taxa in green represent associates of *Mauritiidites* spp. (NLR: *Mauritia* palm).

Table 1
Common associates of *Rhoipites guianensis* and *Malvacipolloides maristellae* in the palynological record at selected sites in Colombian Amazonia with corresponding palynological zones. See also Fig. 4.

Taxa	Affinity	Code Fig. 4	Sites/Occurrence			
Crassiectoapertites columbianus	Fabaceae	crass.col	Mariñame	Tres Islas	x	CPRM
Echiperiporites akanthos	*Sagittaria*	echi.akan	Mariñame (not with *Mauritiidites*)	Tres Islas	Sta. Isabel	CPRM
Malvacipolloides maristellae	*Abutilon*	mal.mari	Mariñame (fresh water deposits)	x	Sta. Isabel	CPRM
Retitricolporites caputoi	Araliaceae	ret.capu	Mariñame (brackish water deposits)	Tres Islas	Sta. Isabel	CPRM
Rhoipites guianensis	*Vasivaea/Trichospermum*	rhoi.gui	Mariñame (fresh and brackish water deposits)	Tres Islas	Sta. Isabel	CPRM
Ranunculacidites operculatus	*Alchornea*	psi.oper	Mariñame	Tres Islas	Sta. Isabel	CPRM
Ranunculacidites cf. operculatus	Polygonaceae	psi.cf.oper	Mariñame (brackish water deposits)	Tres Islas	Sta. Isabel	CPRM
Perisyncolporites pokornyi	Malpighiaceae	peri.pok	Mariñame (rarely with *Mauritiidites*)	Tres Islas	Sta. Isabel	CPRM
Psilabrevitricolpites rotundus	not known	psi.rotu	Mariñame (brackish water deposits)	Tres Islas	Sta. Isabel	x
Pollen zone (as published in Hoorn 1993 & 1994a,b; and following Jaramillo et al., 2011)			Retitricolporites & Psiladiporites-Crototricolpites; T13 (17.7-16.1 Ma)		Retitricolporites & Psiladiporites-Crototricolpites; T13-T14? (17.7-14.2 Ma)	Verrutricolporites to Grimsdalea/T12?-T15 (23?-12.7 Ma)

associated taxa (NLR: *Alchornea*, Araliaceae, Fabaceae, Malpighiaceae, Polygonaceae, and *Sagittaria)* are typical in floodplain forests such as described in modern fluvial settings in the Amazon region (Wittmann et al., 2010; Sá et al., 2016; Salamanca et al., 2016). We also observe that they rarely co-occur with taxa from *Mauritiidites* or *Grimsdalea* palm swamps, nor with taxa from the mangrove vegetation formed by *Zonocostites*-type pollen. This is apparent from the distance matrixes, where the distance is more than 0.7 among these taxa (Appendix 3, Table 3.1–4). Nevertheless, *R. guianensis* seems to have some degree of tolerance to brackish water, whereas *M. maristellae* is incompatible with brackish water. This is consistent with data from palynological records in the Llanos Basin, where *M. maristellae* co-occurs with fresh water algae.

3.5. Ecology and distribution of the modern relatives

Vasivaea, the NLR of a *Rhoipites guianensis* (type 1), is a South American endemic with Amazonian distribution and has been collected most often in seasonally flooded forests and varzeas along rivers (Fig. 5a). It is typically found near wetlands and rocky outcrops of the Precambrian basement, and in savanna and gallery forests (J. Lindeman, pers. observ.). *Trichospermum (Rhoipites guianensis*, type 2) occurs in mixed evergreen forests and has a distribution centered in Central America (Fig. 5b). On average, it occurs around 315 m elevation (1675 sites), although occurrences above 1200 m are also documented. Outside the Neotropics, it occurs in southeast Asia, Papua New Guinea,

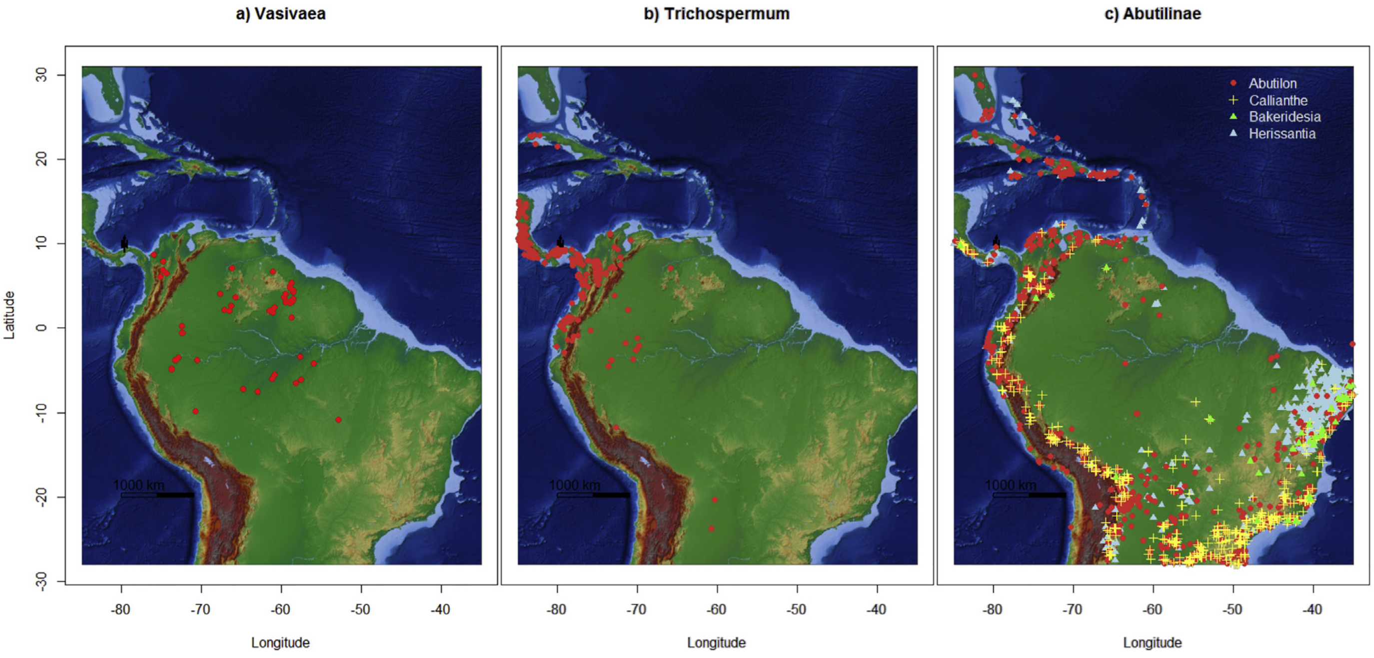


Fig. 5. Modern distribution based on herbarium records of a) *Vasivaea*, b) *Trichospermum* and c) *Abutilon*, *Callianthe*, *Bakeridesia* and *Herrisantia* (data from GBIF, downloaded 29–03-17).

northern Australia and the Pacific islands. This taxon is a late pioneer that prefers humid spots and, together with *Heliocarpus* and *Cecropia*, is known to colonize open forest gaps (Popma et al., 1988; Martínez-Ramos et al., 2016).

The members of the Abutilinae, NLRs of *Malvacipolloides maristellae,* occur in Australia, Asia, East and South Africa (primarily in the west), Europe, North and South America. In the Neotropics, Abutilinae occur in the Andes, Central America, the Caribbean, and in the periphery of Amazonia, including in the Cerrado and the Caatinga (Fig. 5c). It has mainly been collected in seasonally dry forest, with an elevational range from sea level to over 3000 m elevation. In the Latin American Pollen Database, *Abutilon* reportedly forms part of the the lowland rainforest, "*with various species in dry enclaves along river valleys*" (Marchant et al., 2002).

3.6. Phylogeny of Malvoideae

The final alignment for Malvoideae included 65 genera (59% of all Malvoideae genera) and 133 species (including the four taxa used to root the tree) and totaled 9347 base pairs. Within Malvoideae, our topology (Fig. 6; Appendix 4, Fig. 4.1) largely agrees with Donnell et al. (2012). We infer a clade largely corresponding to Donnell et al.'s (2012) *Abutilon s.s.* clade (PP = 0.9694), including *Abutilon s.s.*, *Bastardia bivalvis*, *Bastardiopsis densiflora*, *Briquetia spicata*, and *Wissadula excelsior* (the latter two of which were not included in Donnell et al., 2012's analysis); together, we refer to this clade as the *Abutilon* clade (Fig. 6). This clade is sister to a monophyletic *Bakeridesia* (PP = 1.0) and a grade of members of other genera placed in Donnell et al. (2012)'s "*B*" Clade (including *Anoda*, *Bastardiastrum*, *Horsfordia*, *Periptera*, *Pseudoabutilon, Tetrasida*, and *Wissadula* spp.) (PP = 0.6032); we refer to these taxa together as the *Bakeridesia* clade (Fig. 6). The six species that represent the non-*Callianthe* members of Donnell et al.'s (2012) Clade "C" (*Gaya atiquipana*, *G. calyptrate*, *Briquetia sonorae*, *Hochreutinera amplexifolia*, *Dirhampis Mexicana*, and *Billieturnera helleri*) form a clade sister to the rest of these taxa (PP = 0.8322). This differs from the placement in Donnell et al. (2012), who inferred that these taxa form a grade from which *Callianthe* emerges. Instead, we find that while the genus *Callianthe* and related species form single clade, which also includes *Malacothamnus palmeri* and *Anisodontea triloba* (PP = 1.0; referred to as the *Callianthe* Clade in Fig. 6), this clade is distantly related to the remaining members of Donnell et al.'s (2012) Clade "C" due to the placement of a grade comprised of two subclades: a pair of sister species, *Sida platycalyx* and *S. paniculatum* (PP = 0.9933), and a clade comprising members of *Dendrosida*, *Robinsonella*, *Sida*, and *Tetrasida* (P = .8539). These subclades are successively sister to the *Abutilon* clade, the *Bakeridesia* clade, and non-*Callianthe* members of Donnell et al. (2012)'s Clade "C" (PP = 0.7443 and 0.9015, respectively) (Fig. 6, Appendix 4, Fig. 4.1). We find strong support for monophyletic tribes: Malveae (PP = 1.0), Gossypieae (PP = 1.0), and Hibisceae (PP = 1.0), though the relationships differ from previous analyses (Koopman and Baum, 2008; Baum et al., 2004), perhaps due to the low support for the sister relationship between Gossypieae and Hibisceae (PP = 0.6551). Within Malveae, we find strong support for two subtribes, Malvineae (PP = 1.0) and Abutilinae (PP = 0.9574).

The nearest closest relative of *Malvacipolloides maristellae* is identified as likely *Abutilon*, which we find to be a non-monophyletic genus, consistent with previous studies (e.g., Donnell et al., 2012), or its relatives with similar pollen in Abutilinae, including *Callianthe* (a recently described segregate of *Abutilon*) and *Bakeridesia*. Therefore, we place potential origin of *M. maristellae* at three points, one in each of the *Abutilon*, *Bakeridesia*, and *Callianthe* clades (Fig. 6). We note that representatives of *Herissantia* were not included in our analysis nor in any previous phylogenetic study, though this genus does have similar pollen morphology as *M. maristellae* (pers. com. Javier Fuertes-Aguilar; Hanks and Fryxell, 1979). However, this taxon is recognized as a close relative of *Abutilon* (Tate et al., 2005), so it will likely occur within one of the three subclades that we have identified here. While future microscopy of pollen across Malvoideae (and, specifically, the Abutilinae subtribe of Malveae) will likely shed additional light into the phylogenetic placement of *M. maristellae*, the biogeographic implications of this taxon are consistent no matter to which of these subclades it belongs, as discussed below.

Historical biogeography of Malvoideae (Fig. 6): Biogeographic movements of Malvoideaeae were statistically inferred using the DEC model. The subfamily is approximately 56 Ma, and is ancestrally widespread, occurring in the North and Central America, Africa, and Australasia. From this ancestral distribution, cladogenesis resulted in two major lineages with disjunct distributions: Malvoideae in North America and Hibisceae + Gossypieae in Africa. Within Malveae, we infer 18 southward dispersal or range expansion events from North and Central America into South America. Of these, 14 dispersal events occur within Abutilinae. While we cannot attribute any one of these events specifically to the progenitor of *M. maristellae*, they share many similarities that allow us to make inference about this fossil pollen taxon. The three most likely events are marked by gray, black, and white stars in Fig. 6; these correspond to the *Abutilon* clade (dispersal ca. 14.1 Ma [HPD: 6.6–18.0 Ma]), the *Bakeridesia* clade (dispersal ca. 5.4 Ma [HPD: 2.4–8.2 Ma]), and the *Callianthe* clade (dispersal ca. 14 Ma [HPD: 6.8–22.5 Ma]). Because the earliest known appearance of *Malvacipolloides maristellae* is at 17.1–16.7 Ma (Jaramillo et al., 2011), the *Bakeridesia* clade is too young to represent the first movement of *M. maristellae* into South America, though *M. maristellae* may still represent a composite taxon that includes members of this group. Importantly, all dispersals into South America within Abutilinae occur from North and Central America, and are inferred to have occurred between 37 and 5 Ma. These results suggest a northern origin of South American Abutilinae, likely resulting from relatively recent dispersal from warm, dry climates where the clade thrives today. This contrasts with the South American origin of Grewioideae.

3.7. Phylogeny of Grewioideae

The final alignment for Grewioideae included 64 species (including four Byttneriodeae species used to root the phylogeny) and totaled 4902 base pairs. The concatenated Bayesian phylogenetic analyses using the best-fitting partitioning scheme (i.e., three partitions corresponding to matK + ndhF, psbA-trnH, and rbcL) yielded a topology that is not in conflict with previously published results (e.g., Brunken and Muellner, 2012) (Fig. 7; Appendix 4, Fig. 4.2). Within Grewioideae, we find support for the monophyly of Apeibeae and Grewieae sensu Brunken and Muellner (2012). *Trichospermum* and *Vasivaea*, our taxa of interest in Grewieae, both fall in a clade that also includes *Hydrogaster, Mollia,* and *Tetralix* (PP = 1.0). We can place *Rhoipites* within this clade based on morphological comparisons to extant pollen samples (see pollen discussion), as it includes its most likely extant relatives (Fig. 7, star).

Historical biogeography Grewioideae (Fig. 7): A stratified biogeographical maximum likelihood analysis was performed using a time-calibrated DEC model. We infer an South American origin of crown Grewioideae approximately 70.9 Ma (HPD: 59.9–80.7 Ma). The lineage that gave rise to *Rhoipites* is inferred to have occurred in South America from the origin of Grewioideae until the range of this subclade expanded to include Central America at the origin of the clade that includes *Trichospermum* and *Tetralix* at ca. 40.0 Ma (HPD: 15.8–51.9 Ma). Within *Trichospermum,* at least one intercontinental long-distance dispersal event to the Paleotropics occurred along the branch corresponding to *Trichospermum pleiostigma*. Overall, the biogeographic history of Grewioideae suggests a southern hemisphere origin of *R. guianensis*.

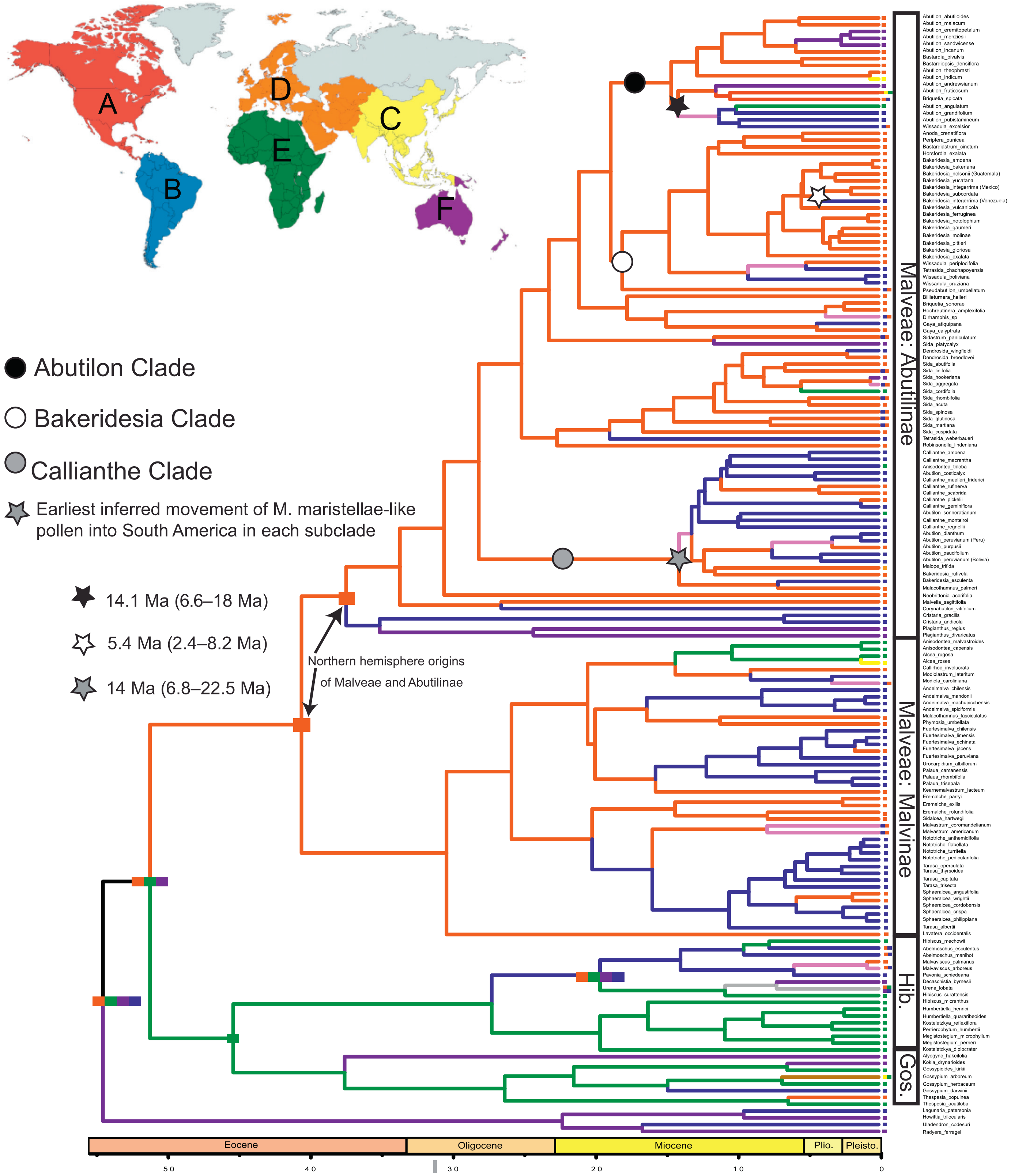


Fig. 6. Chronogram of Malvoideae showing biogeographic history and implications for fossil pollen taxa. The time-calibrated maximum clade credibility phylogeny of Malvoideae shows that the two major nested subdivisions that gave rise to *M. maristellae*, Malveae (40.5 MA [HPD: 30.1–52.5 Ma]) and Abutilinae (30.5 Ma [25.9–47.2 Ma]) have Laurasian (i.e., North + Central American) origins. The southward migration of taxa with this *M. maristellae*-type of pollen (i.e., in groups allied to *Abutilon*, including *Bakeridesia* and *Callianthe*) into South America is inferred to have occurred at one of three times (indicated by black, gray, and white stars), from as recently as 5.4 Ma (HPD: 2.4–8.2 Ma) in the *Bakeridesia* clade (black circle) to as long ago as 28 Ma (HPD: 18.6–36.2 Ma) in the *Callianthe* clade (gray circle). Map of world with biogeographic regions color-coded to the top left, with branches colored according to inferred ancestral range using BioGeoBEARS; boxes below map correspond to distributions of wide-spread lineages. Major taxonomic groupings are indicated in boxes to the side of the phylogeny. Geological timescale at bottom from Walker et al. (2015).

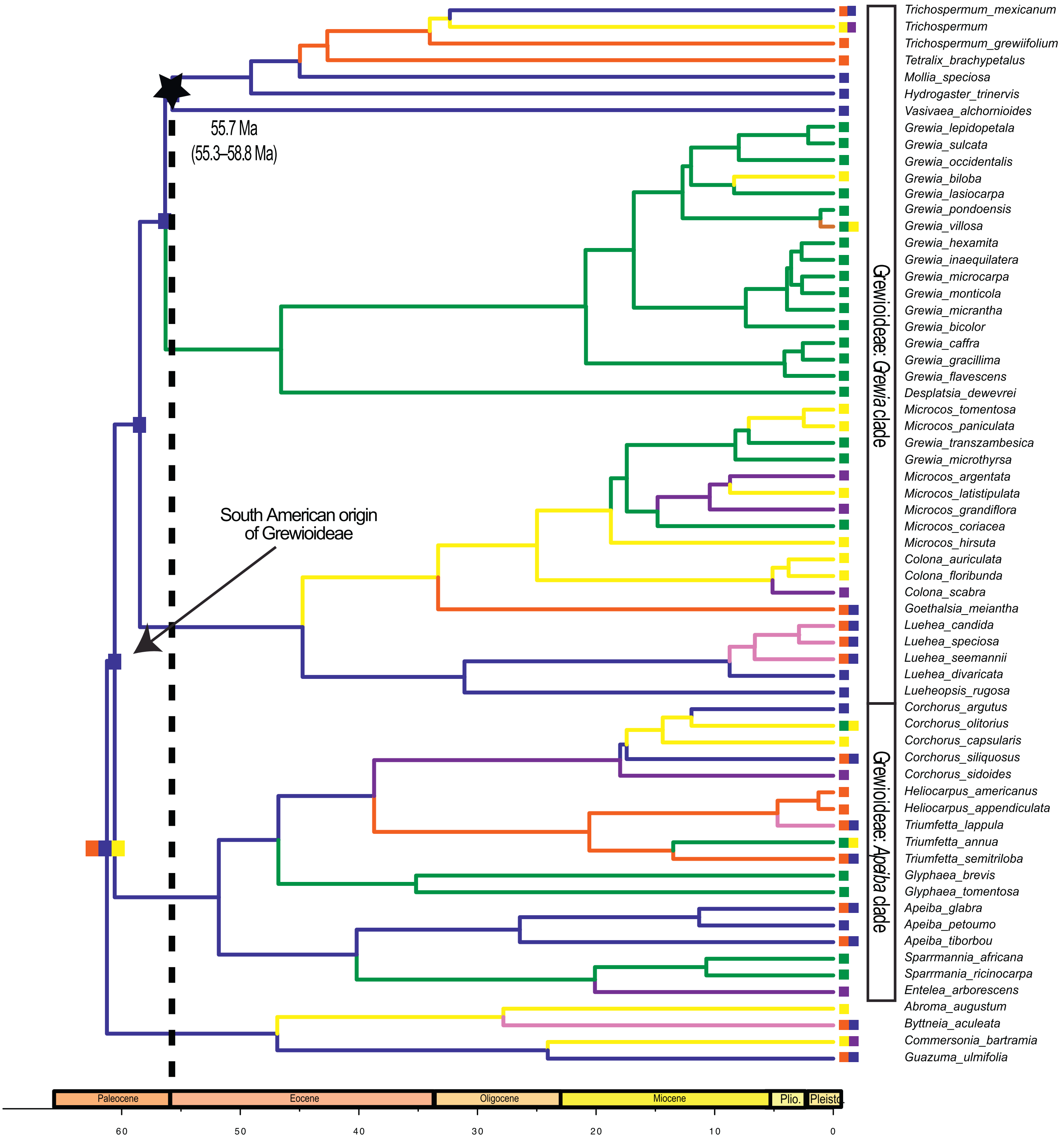


Fig. 7. Chronogram of Grewioideae showing biogeographic history and implications for fossil pollen taxa. The time-calibrated maximum clade credibility phylogeny shows that the early evolutionary history of Grewioideae occurred in the southern hemisphere, with an African origin of Grewioideae, followed by expansion into South America in the earliest divergence events. The clade including the nearest living relatives of *R. guianensis*, marked by a black star, originated ca. 47.9 MA (HPD: 23.2–60.8 Ma) in South America. Colored boxes at tips reflect modern biogeographic occurrence of extant species, while colors of branches reflect past biogeography as inferred via BioGeoBEARS; color scheme is shared with Fig. 6.

4. Discussion

Using a combination of palynological and molecular phylogenetic techniques, our study highlights the diverse histories underlying botanical diversity in northern South America during a period of dramatic climatic and geological change. We determined the nearest living relatives of two fossil pollen species belonging to the Malvaceae by comparison to modern pollen. We documented each taxon's occurrence through space and time, and correlated presence with environmental conditions based on co-occurring taxa and the sedimentological features of the geological formations. We then put this information into a macroevolutionary context by inferring molecular phylogenies of the closest extant relatives of our focal taxa. By integrating results from each of these analyses, we are able to more fully understand the response of these taxa to changing geological and climatic conditions that characterized northern South America.

The history of *Rhoipites guianensis* (Grewioideae) is marked by a Southern Hemisphere origin, followed by northward movement into new areas coincident with local extirpation. The fossil record of this taxon, whose origin in South America is supported by biogeographic analyses informed by molecular phylogenetics, shows that it began to decline in the lowlands during the Miocene (between 15 and 5 Ma; Fig. 2), preceding the movement of other Grewioideae into the emerging Andes in northern South America. Based on the combined information from the palynological and molecular phylogeographic results, we propose that both *Vasivaea* (*R. guianensis*, type 1) and the progenitors of *Trichospermum (R. guianensis*, type 2) declined in the tropical lowlands following changes in climate and paleoenvironment that were related to Andean uplift. Concurrently, the pioneering nature of *Trichospermum (R. guianensis*, type 2) enabled it to colonize the newly formed Eastern Cordillera, where it seemingly thrived in more suitable environmental conditions.

Our results suggest that *R. guianensis* became extirpated in regions with seasonal rainfall, as is indicated by its declining presence in fluvio-lacustrine formations with highly variable water tables and extensive paleosols (i.e., fossil soils that indicate past precipitation cycles) in western Amazonia, the Llanos Basin ~12–10 Ma and in the Middle Magdalena Valley ~33–25 Ma, including the Carbonera, Guayabo, and Mugrosa Formations (Cooper et al., 1995; Bayona et al., 2008; Gomez et al., 2005; Caballero, 2010). In addition, we hypothesize that the movements of *R. guianensis* into Central America during the early Miocene (~18.5 Ma), that are documented in the fossil record from Panama (Jaramillo et al., 2014), were a response to the incipient formation of the Panama Isthmus, which closed the Central American Seaway around 13–15 Ma (Montes et al., 2015).

Contrasting with the southern origin and northward migration of *R. guianensis,* Abutilinae (which includes *Malvacipolloides maristellae*) is characterized by a Northern Hemisphere origin and multiple southward migrations. Members of Abutilinae immigrated into South America from the northern hemisphere on multiple occasions from the Oligocene to the Pliocene, with the majority of dispersal events during the Miocene (Fig. 3). Many of these southward movements occurred before complete closure of the Panama Isthmus. This is consistent with findings from other studies that demonstrated that plant migration was possible with an incomplete isthmus, and generally preceded the migration wave of fauna (Cody et al., 2010; Bacon et al., 2012, 2015; Erkens et al., 2007; Iturralde-Vinent and MacPhee, 1999). The two scenarios that we have identified for the biogeographic history of *M. maristellae* (i.e., either in the *Abutilon* or *Callianthe* clade) are consistent with such early migration. The arrival of *M. maristellae* in northern South America is dated by means of biostratigraphy at 17.7 Ma (Jaramillo et al., 2011), which coincides with the establishment of the Andes as orographic barrier (Barnes et al., 2012). This makes the early Andes a plausible conduit for migration into South America.

As with *Rhoipites guianensis,* changing environmental conditions may have played a fundamental role in the changing distribution of *Malvacipolloides maristellae* through time. Abutilinae are generally drought tolerant taxa, evidenced both by palynological records from the early Miocene in which *M. maristellae* co-occurs with taxa with similar environmental preferences (e.g., Mimosoideae and Amaranthaceae; Salamanca et al., 2016), as well as Abutilinae's modern day distribution in dry habitats of northern South America, including the dry slopes of the Andes, Caatinga, and Cerrado (Fig. 5c). If indeed *M. maristellae* settled in the emerging Andes mountains, its later success there might have been promoted by climatic cooling and aridification that started in the late Miocene (Herbert et al., 2016) and progressive diversification of the Andean landscape throughout the Quaternary.

In response to the rising Andes, lineages persisted via in-situ evolution or movement into areas to which they were pre-adapted, a phenomenon that is widely documented in other lineages (Donoghue, 2008). In our study, the former strategy is exemplified by the descendants of the Miocene Abutilinae, which became extremely successful in the Andes, comprising species-rich radiations. As with *Malvacipolloides maristellae,* there was often a time lag between arrival to South America and subsequent species radiation in the clades that became diverse in the Andes. For example, Cinchonoideae (Rubiaceae) first arrived during the Eocene in the South American lowlands, but did not diversify until the Miocene, when the tribe Isertieae was concentrated in the lowlands and Cinchoneae in the highlands (Antonelli et al., 2009). Similarly, species richness in *Hedyosmum* (Chloranthaceae), a taxon that is found in Amazonia during the early-middle Miocene (Hoorn, 1994b; Da Silva-Caminha et al., 2010), did not begin to accumulate species diversity until the uplift of the Andes mountains took place (Antonelli and Sanmartin, 2013; Martínez et al., 2013).

In contrast, *Rhoipites guianensis'* nearest living relatives illustrate the latter strategy: movement into pre-existing environments following environmental change. This subclade of Grewioideae currently represents species that are widespread in the Andes and Central America, and only limited species diversity in the low Andean forests, while largely lacking from their ancestral distribution in lowland northern South America. Similarly, *Cyclusphaera* (Araucariaceae) was once widely distributed across South America, and extended as far north as Venezuela until the late Miocene (Lorente, 1986; Dino et al., 2012; Jaramillo et al., 2013; Bermúdez et al., 2015). In the present day, *Cyclusphaera* is limited to forests of southern South America and associated with nutrient depleted soils, typically occupied by *Podocarpus* stands (Jaramillo et al., 2013). As with *R. guianensis*, the likely cause of the southward retreat of *Cyclusphaera* was humidification along the eastern slopes of the Andes and the tropical lowlands, following the emplacement of the orographic barrier.

The history of *Rhoipites guianensis* and *Malvacipolloides maristellae* and their nearest living relatives illustrates the implications of geological and climatic changes in the Neogene for floristic composition. The broader picture that emerges from this study is that changes in environment due to the uplift of the Andes coincided with the decline of long-lived fossil taxa such as *R. guianensis* that were adapted to the pre-Andean landscape in the tropical lowlands of northern South America. Instead, transient taxa such as *M. maristellae* only fully established and diversified with the onset of the geographic and climatic changes in the late Miocene when global cooling and aridification set in (e.g. Herbert et al., 2016). The emerging mountains thus also presented an ecological opportunity for these taxa, resulting in evolutionary diversification into newly formed habitats, particularly in Abutilinae. Alwyn Gentry (1982) famously observed that Amazonian biodiversity might be "*an accident of Andean orogeny*". He placed the effects of uplift into a broader geological context and compared the importance of mountain uplift with the estimated effects of the connection between the Americas and Plio-Pleistocene climatic fluctuations. His hypothesis about the importance of the Andean uplift was later supported through combined studies of molecular and geological records (Antonelli et al., 2009; Hoorn et al., 2010). Our study demonstrates that some aspects of Andean diversity (e.g., Abutilinae) may also be an "accident" of pre-existing diversity in the lowlands (or, perhaps, in emerging the uplands), while other taxa responded to Andean uplift and associated changes in the northern South American landscape, including marine incursions (Bernal et al., in press), by shifting their ranges (Hoorn, 1993, 1994b; Wesselingh and Salo, 2006; Hoorn et al., 2010). The interactive, often complicated roles that multiple geological and climatic events have played in generating modern patterns of species diversity in richness in northern South America are becoming increasingly appreciated, and this is greatly facilitated by the simultaenous application of methodology from palynology, geology, and phylogenetics.

5. Conclusions

Our study shows that two Malvacaeae fossil pollen taxa, which are important biostratigraphic markers, had very different biogeographic and evolutionary histories in South America, despite having similar distributions and ecological preferences. The lineage representing *Rhoipites guianensis* (Grewioideae), a taxon of southern hemisphere origin, now includes groups with a relic distribution in Amazonia (represented by the two extant species of *Vasivaea*), and others, such as Neotropical *Trichospermum*, that form outposts in the Andes, where a limited number of speciation events may have occurred in response to Andean uplift. Contrastingly, *Malvacipolloides maristellae* (Malvoideae), a taxon of northern hemisphere origin, entered South America from the north, following at least the earliest stages of uplift in the Andes. From this we infer that M. maristellae evolved in response to climatic cooling and diversification of the Andean landscape. As documented in many other lineages, when the descendants of *M. maristellae* moved into the newly formed Andes, they formed species-rich radiations. Interestingly, the regional palynological records show that exchange between the Americas took place during the early Miocene (ca. 18 Ma).

Through the study of these distinct histories, we are left with a clearer understanding of the evolution of the flora of northern South America in a period of extreme geological and climatic change. Across taxa, plant evolution in northern South America may have been driven by three important abiotic events: Andean uplift (20–15 Ma), the closure of the Central American Seaway (15–10 Ma), and climate aridification and cooling from late Miocene onwards (<10 Ma).

We demonstrate that integrating biogeographic and ecological information the fossil record with molecular phylogenetic analyses can provide a more complete perspective of the plant evolutionary history than either sub-discipline alone. By taking this approach, we elucidated aspects of history that would have otherwise remained invisible in molecular phylogenies.

Together, our results suggest that the tropical lowland forest is of transient nature and a product of intricate biotic and abiotic interaction on the million-year time scale. The evolution of both montane and lowland forests, and the origins of modern species diversity in northern South America can thus only be fully understood in the light of the combined geological and climatic history. If plant biogeography is, in fact, deeply influenced by the establishment of altitudinal gradients, the climatic system, reconnection of the Americas, and the exchange between mountain and lowland biota, then floristic composition must have strongly changed following mountain building.

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Appendix A. Supplementary data

See Appendix dataset https://data.mendeley.com/datasets/8yh5mk958j/1: Reserved DOI: doi:10.17632/8yh5mk958j.1. Supplementary data to this article can be found online at doi: https://doi.org/10.1016/j.revpalbo.2019.01.010.

References

Alverson, W.S., Whitlock, B.A., Nyffeler, R., Bayer, C., Baum, D.A., 1999. Phylogeny of the core Malvales: evidence from *NDHF* sequence data. AJB 86, 1474–1486.

Antonelli, A., Sanmartin, I., 2013. Why are there so many species in the tropics? Taxon 60 (2), 403–414.

Antonelli, A., Nylander, J.A.A., Persson, C., Sanmartin, I., 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. PNAS 106, 9749–9754.

Anzótegui, L.M., Garralla, S., 1986. Estudio palinológico de la Formación Paraná (Mioceno supèrior) - "Pozo Josefina" - Provincia de Santa Fe, Argentina. I parte. Descripciones sistemáticas. FACENA 6, 101–178.

Bacon, C.D., Mora, A., Wagner, W.L., Jaramillo, C.A., 2012. Testing geological models of evolution of the Isthmus of Panama in a phylogenetic framework. Bot. J. Linn. Soc. 171, 287–300.

Bacon, C.D., Silvestro, D., Jaramillo, C.A., Tilston Smith, B., Chakrabarty, P., Antonelli, A., 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. PNAS 112 (19), 6110–6115.

Barnes, J.B., Ehlers, T.A., Insel, N., McQuarrie, N., Poulsen, C.J., 2012. Linking orography, climate, and exhumation across the central Andes. Geology 40 (12), 1135–1138.

Barreda, V.D., 1993. Late Oligocene? Miocene pollen of the families Compositae, Malvaceae and Polygonaceae from the Chenque Formation, Golfo San Jorge Basin, Southeastern Argentina. Palynology 17, 169–186.

Barreda, V.D., 1997. Palynomorph assemblage of the Chenque Formation, Late Oligocene? Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 3. Polycolpate and tricolporate pollen. Ameghiana (Rev. Asoc. Paleotol. Argent.) 34 (2), 131–144.

Baum, D.A., Smith, S.D., Yen, A., Alverson, W.S., Nyffeler, R., Whitlock, B.A., Oldham, R.L., 2004. Phylogenetic relationships of Malvatheca (Bombacoideae and Malvoideae; Malvaceae sensu lato) as inferred from plastid DNA sequences. AJB 91, 1863–1871.

Bayer, C., Fay, M.F., De Bruijn, A.Y., Savolainen, V., Morton, C.M., Kubitzki, K., Alverson, W.S., Chase, M.W., 1999. Support for an expanded family concept of Malvaceae within a recircumscribed order Malvales: a combined analysis of plastid atpB and rbcL DNA sequences. Bot. J. Linn. Soc. 129, 267–303.

Bayona, G., Cortes, M., Jaramillo, C., Ojeda, G., Aristizabal, J.J., Reyes-Harker, A., 2008. An integrated analysis of an orogen–sedimentary basin pair: latest Cretaceous–Cenozoic evolution of the linked Eastern Cordillera orogen and the Llanos foreland basin of Colombia. Geol. Soc. Am. Bull. 120 (9/10), 1171–1197.

Bercovici, A., Hadley, A., Villanueva-Amadoz, U., 2009. Improving depth of field resolution for palynological photomicrography. Pal. Electr. 12, 1–12.

Bernal, R., Bacon, C.D., Balslev, H., Hoorn, C., Bourlat, S.J., Tuomisto, H., Salamanca, S., Teunissen van Manen M., Romero, I., Sepulchre, P., Antonelli, A. (In press). Could coastal plants in western Amazonia be relicts of past marine incursions? Journal of Biogeography, Special issue: The legacy of Alexander von Humboldt: exploring the links between geo- and biodiversity. https://doi.org/10.1111/jbi.13560.

Bermúdez, M.A., Hoorn, C., Bernet, M., Carrillo, E., van der Beek, P.A., Garver, J.I., Mora, J.L., Mehrkian, K., 2015. The detrital record of late Miocene to Pliocene surface uplift and exhumation of the Venezuelan Andes in the Maracaibo and Barinas foreland basins. Bas. Res., 1–26 https://doi.org/10.1111/bre.12154.

Boonstra, M., Ramos, M.I.F., Lammertsma, E.I., Antoine, P.-O., Hoorn, C., 2015. Marine connections of Amazonia: evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). Palaeogeogr. Palaeoclim. Palaeoecology 417, 176–194.

Bouckaert, R., Heled, J., Kuhnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10, 1–6.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Brunken, U., Muellner, A.N., 2012. A new tribal classification of Grewioideae (Malvaceae) based on morphological and molecular phylogenetic evidence. Syst. Bot. 37, 699–711.

Caballero, V., 2010. Evolución tectono-sedimentaria del Sinclinal de Nuevo Mundo, Cuenca Valle Medio del Magdalena Colombia, durante el Oligoceno-Mioceno. Msc. thesis. Universidad Industrial de Santander, p. 148.

Carvalho, M.R., Herrera, F.A., Jaramillo, C.A., Wing, S.L., Callejas, R., 2011. Paleocene Malvaceae from northern South America and their biogeographical implications. AJB 98 (8), 1337–1355.

Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics 62, 361–371.

Christensen, P.B., 1986. Pollen morphological studies in the Malvaceae. Grana 25, 95–117.

Cody, S., Richardson, J.E., Rull, V., Ellis, C., Pennington, R.T., 2010. The great American biotic interchange revisited. Ecography 33, 326–332.

Coetzee, J., van der Schijff, H.P., 1979. Pollen morphology of South African Malvales. I. Characteristics useful for keying and for numerical analysis. J. South Afr. Bot. 45, 93–126.

Cooper, M.A., Addison, F.T., Alvarez, R., Coral, M., Graham, R.H., Hayward, A.B., Howe, S., Martinez, J., Naar, J., Peñas, R., Pulham, A.J., Taborda, A., 1995. Basin development and tectonic history of the Llanos Basin, Eastern Cordillera, and middle Magdalena Valley, Colombia. AAPG Bull. 79, 1421–1443.

Da Silva-Caminha, S.A.F., Jaramillo, C., Absy, M.L., 2010. Neogene palynology of the Solimões Basin. Palaeontographica Abt. B 283, 1–67.

D'Apolito, C., 2016. Landscape evolution in western Amazonia: palynostratigraphy, palaeoenvironments and diversity of the Miocene Solimões Formation, Brazil. University of Birmingham, p. 350 Thesis.

Dino, R., Soares, E.A.A., Antonioli, L., Riccomini, C., Nogueira, A.C.R., 2012. Palynostratigraphy and sedimentary facies of Middle Miocene fluvial deposits of the Amazonas Basin, Brazil. J. South Am. Earth Sc. 34, 61–80.

Donnell, A.A., Ballard Jr., H.E., Cantino, P.D., 2012. *Callianthe* (Malvaceae): a new genus of Neotropical Malveae. Syst. Bot. 37 (3), 712–722.

Donoghue, M.J., 2008. A phylogenetic perspective on the distribution of plant diversity. PNAS 105, 11549–11555.

Dueñas, H., 1980. Palynology of Oligocene-Miocene strata of borehole Q-E-22, Planeta Rica, Northern Colombia. Rev. Palaeobot. Palyn. 30, 313–328.

Edgar, R.C., 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32, 1792–1797.

Erdtman, G., 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm.

Erkens, R.H.J., Chatrou, L.W., Maas, J.W., van der Niet, T., Savolainen, V., 2007. A rapid diversification of rainforest trees (*Guatteria*; Annonaceae) following dispersal from Central into South America. Mol. Phyl. Evol. 44 (1), 399–411.

Gentry, A.H., 1982. Neotropical floristic diversity: phytogeographical connections between Central and South American, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Miss. Bot. Gard. 69 (3), 557–593.

Germeraad, J.H., Hopping, C.A., Muller, J., 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palyn. 6, 189-348.

Gomez, E., Jordan, T., Hegarty, K., Kelley, S., 2005. Syntectonic Cenozoic sedimentation in the northern middle Magdalena Valley Basin of Colombia and implications for exhumation of the Northern Andes. GSA Bull. 17 (5), 547–569.

Gomez, A., Jaramillo, C., Parra, M., Mora, A., 2009. Huesser Horizon: A lake and a marine incursion in Northwestern South America during the Early Miocene. Palaios 24, 199–210.

Gonzalez-Guzman, A.E., 1967. A Palynologic Study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene), Tibú Area, Colombia. E.J. Brill, Leiden, p. 68.

Hanks, S., Fryxell, P.A., 1979. Palynological studies of *Gaya* and *Herissantia* (Malvaceae). AJB 66 (5), 494–501.

Hayek, L.-A.C., Buzas, M.A., 2010. Surveying Natural Populations, Quantitative Tools for Assessing Biodiversity. 2nd edition. Columbia University Press.

Herbert, T.D., Lawrence, K.T., Tzanova, A., Cleaveland-Peterson, L., Caballero-Gill, R., Kelly, C.S., 2016. Late Miocene global cooling and the rise of modern ecosystems. Nat. Geosci. 9, 843–847.

Ho, S.Y.W., Phillips, M.J., 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. Syst. Bot. 58, 367–380.

Hoorn, C., 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. Palaeogeogr. Palaeoclim. Palaeoecol. 105, 267–309.

Hoorn, C., 1994a. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (Early Miocene-early Middle Miocene, Colombia). Palaeogeogr. Palaeoclim. Palaeoecol. 109, 1–54.

Hoorn, C., 1994b. An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia). Palaeogeogr. Palaeoclim. Palaeoecol. 112, 187–238.

Hoorn, C., 2006. Mangrove Forests and Marine Incursions in Neogene Amazonia (Lower Apaporis River, Colombia). Palaios 21, 197–209.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermúdez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D.D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. Science 330, 927–931.

Horn, H.S., 1966. Measurement of "overlap" in comparative palynological studies. Am. Nat. 100, 419–424.

Hughes, C., Eastwood, R., 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. PNAS 103, 10334–10339.

Iturralde-Vinent, M., MacPhee, R.D.E., 1999. Palaeogeography of the Caribbean Region: Implications for Cenozoic biogeography. Bull. Am. Mus. Nat. Hist. 238, 87.

Jaramillo, C.A., Dilcher, D.L., 2001. Middle Paleogene palynology of Central Colombia, South America: A study of pollen and spores from tropical latitudes. Palaeontographica Abt. B 258 (4–6), 87–213.

Jaramillo, C.A., Rueda, M., 2008. A morphological electronic database of cretaceous Tertiary fossil pollen and spores from northern South America. Colombian Petroleum Institute & Smithsonian Tropical Research Institution. Available at: http://biogeodb.stri.si.edu/jaramillo/palynomorph/ (accessed March 2017).

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M., De la Parra, F., Moron, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, A., Schouten, S., Bermudez, H., Navarrete, R.E., Parra, F., Alvaran, M., Osorno, J., Crowley, J.L., Valencia, V., Vervoort, J., 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. Science 330, 957–961.

Jaramillo, C.A., Rueda, M., Torres, V., 2011. A palynological zonation for the Cenozoic of the Llanos and Foothills of Colombia. Palynology 35 (1), 46–84.

Jaramillo, C., Zavada, M., Ortiz, J., Pardo, A., Ochoa, D., 2013. The biogeography of the Araucarian dispersed pollen *Cyclusphaera*. Int. J. Plant Biol. 174, 489–498.

Jaramillo, C., Moreno, E., Ramirez, V., da Silva, S., Barrera, At., Ad, Barrera, Moron, S., Herrera, F., Escobar, J., Koll, R., Manchester, S., Hoyos, N., 2014. Palynological record of the last 20 Million years in Panama. In: Stevens, W.D., Montiel, O.M., Raven, P. (Eds.), Paleobotany and Biogeography: A Festschrift for Alan Graham in his 80th Year. Miss. Bot. Gard. Press, St. Louis, pp. 134–251.

Jaramillo, C., Montes, C., Cardona, A., Silvestro, D., Antonelli, A., Bacon, C.D., 2017a. Comment (1) on "Formation of the Isthmus of Panama" by O'Dea et al. Sc. Adv. Technical Comment 3 e e1602321.

Jaramillo, C., Romero, I., D'Apolito, C., Bayona, G., et al., 2017b. Miocene flooding events of western Amazonia. Sci. Adv. 3 (5), e1601693.

Klitgård, B.B., Edwards, S.L., Biggs, N., Frisby, S., 2011. Neotropical Malvaceae (Malvoideae). In: Milliken, W., Klitgård, B. and Baracat, A. (2009 onwards), Neotropikey - Interactive key and information resources for flowering plants of the Neotropics. http://www.kew.org/science/tropamerica/neotropikey/families/Malvaceae_(Malvoideae).html

Koopman, M.M., Baum, D.A., 2008. Phylogeny and biogeography of Tribe Hibisceae (Malvaceae) on Madagascar. Syst. Bot. 33, 364–374.

Lagomarsino, L.P., Condamine, F.L., Antonelli, A., Mulch, A., Davis, C.C., 2016. The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytol. 210, 1430–1442.

Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701.

Lattar, E.C., Galati, B.G., Ferrucci, M.S., 2012. Ultrastructural study of pollen and anther development in *Luehea divaricata* (Malvaceae, Grewioideae) and its systematic implications: Role of tapetal transfer cells, orbicules and male germ unit. Flora 207, 888–894.

Leite, F.P., Paz, J., do Carmo, D.A., Silva-Caminha, S.A., 2017. The effects of the inception of Amazonian transcontinental drainage during the Neogene on the landscape and vegetation of the Solimoes Basin, Brazil. Palynology 41 (3), 412–422.

Li, D.-Z., Gao, L.-M., Li, H.-T., Wang, H., Ge, X.-J., Liu, J.-Q., Chen, Z.-D., Zhou, S.-L., Chen, S.-L., Yang, J.-B., Fu, C.-X., Zeng, C.-X., Yan, H.-F., Zhu, Y.-J., Sun, Y.-S., Chen, S.-Y., Zhao, L., Wang, K., Yang, T., Duan, G.-W., 2011. Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. PNAS 108, 19641–19646.

Lorente, M., 1986. Palynology and Palynofacies of the Upper Tertiary in Venezuela. J. Cramer, Berlin, p. 222.

Luebert, F., Muller, L.A.H., 2015. Effects of mountain formation and uplift on biological diversity. Front. Gen. https://doi.org/10.3389/fgene.2015.00054.

Luebert, F., Weigend, M., 2014. Phylogenetic insights into Andean plant diversification. Front. Ecol. Evol. https://doi.org/10.3389/fevo.2014.00027.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Science, Oxford.

Mambrín, M.V., Avanza, M.M., Ferrucci, M.S., 2010. Análisis morfológico y morfométrico del polen de *Corchorus*, *Heliocarpus*, *Luehea*, *Mollia* y *Triumfetta* (Malvaceae, Grewioideae) en la Región austral de América del Sur. Darwiniana 48 (1), 45–58.

Mao, K., Milne, R.I., Zhang, L., Peng, Y., Liu, J., Thomas, P., Mill, R.R., Renner, S.S., 2012. Distribution of living Cupressaceae reflects the breakup of Pangea. PNAS 109, 7793–7798.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivendvoorden, J., Kappelle, M., De Oliveira, P., Texeira de Oliveira Filho, A., Lozano-Garcia, S., Hooghiemstra, H., Ledru Marie-Pierre, Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., Salgado-Labouriau, M.L., 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. Rev. Palaeobot. Palyn. 121 (1), 1–75.

Martínez, C., Madriñán, S., Zavada, M., Jaramillo, C.A., 2013. Tracing the fossil pollen record of Hedyosmum (Chloranthaceae), an old lineage with recent Neotropical diversification. Grana 52, 161–180.

Martínez-Ramos, M., Pingarroni, A., Rodríguez-Velázquez, J., Toledo Chelala, L., Zermeño-Fernández, I., Bongers, F., 2016. Natural forest regeneration and ecological restoration in human modified tropical Landscapes. Agricultural land uses and forest regeneration. Biotropica 48 (6), 745–757.

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Front. Biogeogr. 26, 217–220.

Mautino, L.R., Cuadrado, G.A., Anzótegui, L.M., 2004. Novedades taxonómicas, diversidad y significado evolutivo del polen de Malvaceae en el Terciario de Argentina. Rev. Esp. Micropal. 36 (3), 467–483.

Meseguer, A.S., Lobo, J.M., Ree, R., Beerling, D.J., Sanmartin, I., 2015. Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: the case of Hypericum (Hypericaceae). Syst. Biol. 64 (2), 215–232.

Molnar, P., 2017. Comment (2) on "Formation of the Isthmus of Panama" by O'Dea et al. Sc. Adv. Technical Comment 3, e1602320.

Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodriguez-Parra, L.A., Ramirez, V., Niño, H., 2015. Middle Miocene closure of the Central American Seaway. Science 248 (6231), 226–229.

Muller, J., Di Giacomo, E., van Erve, A.W., 1985. A palynological zonation for the cretaceous, Tertiary, and Quaternary of northern South America. In: Maraven, S.A. (Ed.), Internal report. Simplified and condensed in: VI Congreso Geologico Venezolano, Memorias, Tomo 2, 1042-1070 Caracas, Venezuela.

Muller, J., Di Giacomo, E., van Erve, A.W., 1987. A palynological zonation for the Cretaceous, Tertiary, and Quaternary of northern South America. AASP Contrib. Ser. 19, 76. www.ncbi.nlm.nih.gov/genbank/ accessed October 2014.

Nuttall, C.P., 1990. A review of the Tertiary non-marine molluscan faunas of the Pebas and other inland Basins of North-Western South America. Bull. Brit. Mus. (Natural History), Geology 45, 165–371.

Ochoa, D., Hoorn, C., Jaramillo, C., Bayona, G., de la Parra, F., 2012. The final phase of tropical lowland conditions in the axial zone of the Eastern Cordillera of Colombia: evidence from three palynological records. J. South Am. Earth Sc. 39, 157–169.

O'dea, A., Lessios, H.A., Coates, A.G., et al., 2016. Formation of the Isthmus of Panama. Sc. Adv. 2 (8), e1600883. https://doi.org/10.1126/sciadv.1600883 (35 authors).

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H., Wagner, H., 2015. Vegan: community ecology. R package version 2.3-0 http://CRAN.R-project.org/package=vegan.

Perveen, A., Siddiqui, S., Fatima, A., Qaiser, M., 1994. Pollen flora of Pakistan. 1. Malvaceae. Pakistan J. Bot. 26, 421–440.

Perveen, A., Grafström, E., El-Ghazaly, G., 2004. World Pollen and Spore Flora 23. Malvaceae Adams. P.P. Subfamilies: Grewioideae, Tilioideae, Brownlowioideae. Grana 43, 129–155.

Pilsbry, H.A., Olsson, A.A., 1935. Tertiary fresh-water mollusks of the Magdalena embayment. Colombia: Proc. Acad. Nat. Sc. Philadelphia 7, 7–39.

Pocknall, D.T., Crosbie, Y.M., 1982. Taxonomic revision of some Tertiary tricolporate and tricolpate pollen grains from New Zealand. New Zealand J. Bot. 20, 7–15.

Popma, J., Bongers, F., Martinez-Ramos, M., Veneklaas, E., 1988. Pioneer species distribution in treefall gaps in neotropical rain forest; a gap definition and its consequences. J. Trop. Ecol. 4 (1), 77–88.

Poulsen, C.J., Ehlers, T.A., Insel, N., 2010. Onset of convective rainfall during gradual late Miocene rise of the central Andes. Science 328, 490–493.

Presting, D., Straka, H., Friedrich, B., 1983. Palynologia Madagassica et Mascarenica. Fam. 128–146. Tropische und subtropische Pflantzenwelt 44, 7–93.

Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., le Thomas, A., 2007. Glossary of pollen and spore terminology. Rev. Palaeobot. Palyn. 143, 1–81.

QGIS Development Team, 2016. QGIS Geographic Information System. Open Source Geospatial Foundation URL. http://qgis.osgeo.org.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL. http://www.R-project.org/.

Rabosky, D.L., 2010. Extinction rates should not be estimated from molecular phylogenies. Evolution (N. Y). 64, 1816–1824.

Ree, R.H., Sanmartin, I., 2018. Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. J. Biogeogr. 45, 741–749.

Ree, R.H., Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst. Biol. 5, 4–14.

Richardson, J.E., Whitlock, B.A., Meerow, A.W., Madriñán, S., 2015. The age of chocolate: a diversification history of *Theobroma* and Malvaceae. Front. Ecol. Evol. 3, 120.

Rodriguez-Forero, G., Oboh-Ikuenobe, F., Jaramillo, C., Rueda, M., Cadena, E., 2012. Palynology of the Eocene Esmeraldas Formation, Middle Magdalena Valley, Colombia. Palynology 36 (s1), 96–111.

Rull, V., 2001. A quantitative palynological record from the early Miocene of western Venezuela, with emphasis on mangroves. Palynology 25, 109–126.

Sá, N., De, P., Absy, M.L., Soares, E.A.A., 2016. Late Holocene paleoenvironments of the floodplain of the Solimões River, Central Amazonia, based on the palynological record of Lake Cabaliana. Acta Bot. Bras. 30 (3), 473–485.

Saba, M.D., Santos, F.A.R., Esteves, G.L., 2004. Palinotaxonomia das tribos Byttnerieae DC., Hermannieae DC. e Helictereae DC. (Malvaceae s.l.) da flora da Bahia, Brasil. Hoehnea 31, 189–214.

Salamanca, S., van Soelen, E.E., Teunissen-van Manen, M.L., Flantua, S.G.A., Santos, R.V., Roddaz, M., Dantas, E.L., Van Loon, E., Sinninghe-Damste, J.S., Kim, J.-H., Hoorn, C., 2016. Amazon forest dynamics under changing abiotic conditions in the early Miocene (Colombian Amazonia). J. Biogeogr. 43, 2424–2437.

Sepulchre, P., Sloan, L.C., Fluteau, F., 2010. Modelling the response of Amazonian climate to the uplift of the Andean mountain range. In: Hoorn, C., Wesselingh, F. (Eds.), Amazonia: Landscape and Species Evolution: A Look into the Past. Blackwell, Oxford, pp. 211–222.

Skvarla, J.J.A.N.D., Turner, B.L., 1966. Systematic implications from electron microscopic studies of Compositae pollen, a review. Ann. Miss. Bot. Gard. 53, 220–256.

Stevens, P.F., 2012. Angiosperm Phylogeny Website. Version 12. http://www.mobot.org/MOBOT/research/APweb/.

Tate, J.A., Fuertes Aguilar, J., Wagstaff, S.J., La Duke, J.C., Bodo Slotta, T.A., Simpson, B.B., 2005. Phylogenetic relationships within the tribe Malveae (Malvaceae, subfamily Malvoideae) as inferrerd from ITS sequence data. AJB 92 (4), 584–602. https://doi.org/10.3897/phytokeys.56.5432.

Thanikaimoni, K., van der Ham, R.W.J.M., 1999. Eighth bibliographic index to the pollen morphology of angiosperms. Publ. Dép. Écol. Inst. Fr. Pondichéry 39, 346.

Thornhill, A.H., Popple, L.W., Carter, R.J., Ho, S.Y., Crisp, M.D., 2012. Are pollen fossils useful for calibrating relaxed molecular clock dating of phylogenies? A comparative study using Myrtaceae. Mol. Phyl. Evol. 63, 15–27.

Van der Hammen, T., Wijmstra, T.A., 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. Leidse. Geol. Meded. 30, 182–241.

Van der Hammen, T., Werner, J.H., van Dommelen, H., 1973. Palynological record of the upheaval of the Northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. Rev. Palaeobot. Palyn 16, 1–122.

Wei, T., 2013. corrplot: Visualization of a correlation matrix. R package version 0.73 http://CRAN.R-project.org/package=corrplot.

Wesselingh, F.P., Salo, J., 2006. A Miocene perspective on the evolution of Amazonian biota. Script. Geol. 133, 439–458.

Wittmann, F., Schöngart, J., Junk, W.J., 2010. Phytogeography, species diversity, community structure and dynamics of Central Amazonian floodplain forests. In: Junk, W.J., Piedade, M.T.F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), Amazonian floodplain forests. Springer, The Netherlands, pp. 61–102.

Wodehouse, R.P., 1933. The oil shales of the Eocene Green River formation. Bull. Torrey Bot. Club 60, 479–535.

Wolda, H., 1981. Similarity indices, sample size and diversity. Oecologia 50, 296–302.

Zetter, R., Hesse, M., Huber, K.H., 2002. Combined LM, SEM and TEM studies of late cretaceous Pollen and Spores from Gmünd, Lower Austria. Stapfia 80, 201–230.