The emergence of the tropical rainforest biome in the Cretaceous

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Abstract. Modern tropical rain forests (TRF) are one of the most ecologically important and species-rich biomes on the planet. However, the origin of modern TRF is still debated, especially due to the incongruence between the fossil record and molecular data. Here, we test whether Campanian assemblages from north-eastern Africa could represent fossil TRF vegetation. In so doing, we compare the investigated assemblages with other assemblages known to represent temperate forests, subtropical forests, and TRF in terms of leaf physiognomy, species richness, and taxonomic composition. We conclude based on fossil leaves that modern-looking TRF already existed about 80 Ma ago during the Campanian in north-eastern Africa in an area corresponding to 10% of the modern Amazonian or 25% of the Congolese TRF. The apparent conflict between the fossil record and phylogenetic evidence is due to the nearly complete absence of published tropical floras for the Cretaceous.

Keywords. tropical rainforests; Cretaceous; Campanian; Africa; Egypt; Sudan

Teaser. Eighty Ma old fossil leaf assemblages suggest a widespread distribution of tropical rainforest in north-eastern Africa.

1 Introduction

Modern tropical rain forests (TRF) are one of the most ecologically important and species-rich biomes on the planet. Rainforest environments have an enormous impact on global water and heat circulation and therefore play a major role in water distribution and rainfall patterns. This implies that the closed canopy is stratified, when the closed canopy is one of several layers, including the emergent and lower strata. The presence of woody angiosperms, abundant rainfall, and equable temperatures. The origin of modern TRF is still debated (Eiserhardt et al., 2017). Molecular phylogenetic studies of modern plants suggest that the earliest appearance of the TRF dated back to the Cenomanian (93.9-100.5 Ma). In contrast, fossil TRF, characterized by its (leaf) physiognomy, climate proxies, and high diversity, has not been identified so far before the Maastrichtian (66.0-72.1 Ma) (Carvalho et al., 2021). An alternative scenario implies an earlier origin of TRF at mid-latitudes (Morley, 2000; Davis et al., 2005). However, mid-latitude floras from the Dakota Formation (ca. 100 Ma) (Upchurch and Wolfe, 1987) and from the Olmos Formation (ca. 72 Ma) (Estrada-Ruiz et al., 2008) correspond to a paratropical/subtropical climate, the paratropical (20-25°C) being slightly cooler that truly tropical climate (>25°C) and exhibiting higher seasonal temperature amplitude.

Understanding the early development of TRF has been hampered by the fact that most previous information originated from mid- to high-latitude fossil sites reflecting more temperate climates, while low-latitude sites have hardly been studied. However, relevant material including Campanian fossil plants from Egypt and Sudan, which were located near or on the equator in paleogeographic reconstructions for the Campanian, was collected by the 'Sonderforschungsbereich 69' (a collaborative research centre located in Berlin funded by the DFG) in the 70s to 90s (Figure 1). The studied assemblages were preliminarily studied by

Klitzsch and Lejal-Nicol (1984), Lejal-Nicol (1987) and Kahlert et al. (2009). However; these contributions focused only on a few selected taxa and did not attempt to estimate the palaeoclimate or the palaeodiversity. The studied collection, from Baris Oasis in Egypt, comes from the Quseir Formation (Fm.) of early to middle Campanian age (ca. 84-76 Ma) (Mahmoud, 2003). In addition, other seven smaller assemblages from lateral and temporal equivalents of the Quseir Fm. were also studied. To test whether these assemblages correspond to fossil TRF vegetation, or at least a habitat suitable for stem lineages of modern TRF taxa, we compared them with contemporary and younger fossil assemblages known to represent temperate forests, subtropical forests, and TRF considering three aspects;

(1) Leaf physiognomy, dominated by entire margined taxa, reflecting mean annual temperature >24°C, and mesophyllous or larger leaves, implying rainfall >1500mm, corresponding to the limit of TRF in Africa (White, 1983).

(2) A high species richness, comparable to modern assemblages (Wing et al., 2009).

(3) A taxonomic composition similar to modern TRF (Wing et al., 2009).

1.1 Palaeoclimate background during the Campanian of NE Africa

1.1.1 Sedimentological evidence

In Southern Egypt and Northern Sudan, the shallow marine Campanian sediments are rich in kaolinite and sometimes contain phosphorites (Schwarz and Germann, 1999). However, equivalent continental facies comprise stacked paleosols consisting of quartz, kaolinite, iron hydroxides, and oxides. These paleosols are interpreted as laterites formed in situ or eroded and redeposited (Schwarz and Germann, 1999). The dominance of kaolinite in the clay mineral fraction in the sediments indicates a perennial warm and humid tropical palaeoclimate that promoted the hydrolysis of aluminosilicate minerals (Chamley, 1989; Thiry, 2000).

Phosphorite formation has also been ascribed to intense chemical weathering on the African continent due to a humid tropical palaeoclimate and fluvial transport of the weathering products into a shallow marine environment (Schwarz and Germann, 1999). Laterites are typically formed by intense tropical or subtropical weathering, although preferably in a warm climate with pronounced dry seasons (Widdowson, 2007).

1.1.2 Palaeobotanical evidence

Records of gymnospermous charcoal, in sediments of the Quseir Fm., although rare, indicate the presence of wildfires during the Campanian in the surroundings of Baris (El Atfy et al., 2016). Although the occurrence of wildfires is often used as an indication of somewhat drier conditions, it is not clear whether such conditions occurred seasonally or just during an occasional dry spell (El Atfy et al., 2016). Even in modern rainforests such occasional dry spells can promote the ignition and spread of wildfires (Scott et al., 2013). Under conditions of higher than present oxygen concentrations in the atmosphere, which have been reconstructed by a number of models for the Cretaceous (Brown et al., 2012), it is even more likely that wildfires could also be ignited within ever-wet TRF and spread easily (Belcher et al., 2010).

Palynological data from the Quseir Fm. also point to a flora dominated by angiosperms, although pteridophytes and gymnosperms are present, but not diverse (Mahmoud, 2003). Based on the composition and diversity of the palynoflora, as well as data from palynofacies analysis, Mahmoud (2003) interpreted the source habitats of the recovered palynomorphs as a fluvio-lacustrine landscape with abundant moist and aquatic habitats as well as subordinate drier habitats (i.e., with *Araucaria*, ephedroids and other gymnosperms) in the hinterland, in which the plants grew under a warm and humid, tropical to subtropical palaeoclimate.

2 Geological and collecting information

The studied materials comprise fossil leaves collected by members of the 'Sonderforschungsbereich 69' in 1984 and 1987 that are housed now at the Natural History Museum of Berlin. They comprise collection B (Baris), which encompasses the material described here that was collected east of Baris (24°33'N, 30°43'E) in southern Egypt from the Quseir Fm., which has been dated as early to middle Campanian (Mahmoud, 2003). In addition, further eight assemblages were also studied, among them, four assemblages come from Egypt and three from the Bir Kiseiba area (pf12-81, pf3/82 and pf13/82) (Klitzsch and Lejal-Nicol, 1984; Lejal-Nicol, 1987) that were collected from the Kiseiba Fm., an equivalent to the Quseir Fm. (Klitzsch and Hermina, 1989) and only one from the Qena area (Schrank, 1992), also from the Quseir Fm. Moreover, four assemblages come from Sudan, one from the Jebel Abyad Plateau (pf82/23S) (Lejal-Nicol, 1987; Barazi, 1985) and three from the Bir Atrun-Nukheila area (pf8-84, pf9/84, pf10/84) (Lejal-Nicol, 1987; Barazi, 1985; Klitzsch and Wycisk, 1987), all of which are from the Kabbabish Fm. and its equivalents (Barazi, 1985). Concerning the dating of the studied assemblage, a lower age boundary is defined by a regional hiatus associated with a major unconformity between the Santonian and the Campanian, which has been dated palynologically (Wycisk, 1994 and references therein). An upper age boundary is defined by a transgression that covered the whole area. This transgression has been dated in Egypt as late Campanian based on palynology (El Beialy, 1995) and ammonites (Dominik and Schaal, 1984).

In addition to plant megafossils, the ecosystem in the Quseir Fm. is characterized by the presence of fragmented bones and other vertebrate remains of lungfishes, sawfishes, turtles, and crocodiles as well as dinosaurs (Abu El-Kheir, 2020).

3 Methods

3.1 Climate proxies and diversity analyses

For the diversity analyses and climate proxies, the leaves were grouped into morphotypes without considering formerly proposed taxa (a literature survey was done afterwards). Each morphotype differs from all others by at least one of the criteria described in the manual of leaf architecture described by Ellis et al. (2009). Although the biggest leaves are often fragmentary, all broken slabs are still recognized, e.g., by their tertiary venation (e.g., M-17 has horizontal tertiaries while in M-16 they are clearly at an obtuse angle to the midvein), or their shape (e.g., M-18 and M19 are very coriaceous, but differ in the base shape, which is cordate and rounded respectively). Considering the high proportion of simple, entire margined leaves, the most important distinguishing characters are found in the higher orders of venation.

Climate data were estimated using two kinds of climate proxies; the first is simple linear regressions between a physiognomic and a climate parameter, and the second is an artificial neural network approach based on 31 leaf characters and 13 palaeoclimate variables (CLANN). Each morphotype was evaluated for the physiognomic characters used (see Supplementary material).

As simple linear regressions between a physiognomic and a climate parameter, we used the regression by Kowalski and Dilcher (2003) and Miller et al. (2006) to calculate temperature estimates based on leaf margin analyses. For the rainfall estimates based on leaf size, we employed the regression by Wilf et al. (1998).

Climate proxies were also checked using the CLANN method (i.e., an artificial neural network approach to CLAMP) (Li et al., 2016) calibrated using the CLAMP global data set, which considers 378 sites worldwide (Spicer et al., 2009). As in Li et al. (2016), the spread for each climatic variable was calculated using 10-fold cross-validation, repeated 1000 times. The scoresheet for the Baris flora is given in supplementary material (Data S1) as well as the code used.

The rarefied diversity, i.e., the diversity expected for a subsample of the collection, was estimated for individual localities (single collection point) and for the bulk floras. Concerning possible collection biases, it is worth noting that the material was collected very carefully by sedimentologists who collected almost everything, including tiny unidentifiable plant fragments, which abound in the collection. To test whether our assemblages are more similar to TRFs than to other kinds of vegetation, we compared the diversity of fossil samples from NE Africa with tropical and warm temperate associations from the Cretaceous, Paleocene and Eocene. The data from Cerrejon, Castle Rock, Bison basin, Rio Negro, Barro Colorado were taken from Wing et al. (2009) and compiled with data from Laguna del Hunco (Wilf et al., 2005) and Grünbach (Herman and Kvaček, 2010). The data from Grünbach are based on the number of specimens of each taxon (see Supplementary material). Only the bulk flora diversity could be estimated for Grünbach due to the absence of data concerning individual collection points. The rarefaction curves were produced using PAST (Krebs, 1989; Hammer et al., 2001).

4 Results

4.1 Morphotypes

Previous works focused on the investigated material (Klitzsch and Lejal-Nicol, 1984; Lejal-Nicol, 1987; Kahlert et al., 2009) recorded only 37 taxa, while our current revision based on 361 specimens resulted in the identification of 70 morphotypes: 54 non-monocotyledon (dicots) angiosperms, 11 monocotyledons, 4 ferns, and a single conifer (Figure 2). The presence of some morphotypes present in several assemblages (Supplementary material; Table S1), especially monocotyledons, suggests homogeneous vegetation for the whole area and supports their contemporaneity.

4.2 Climate

The physiognomy of the Baris assemblage is similar to that of a modern TRF. Of the 20 terrestrial non-monocotyledonous angiosperms with a preserved margin, 85% are entire-margined, yielding estimates of mean annual temperature (MAT) ranging from >25°C (26 to 33°C) corresponding to a tropical climate (Wolfe, 1979). Furthermore, the average leaf size of the 23 terrestrial non-monocotyledonous angiosperms is 69 cm^2, yielding an estimate of the mean annual precipitation (MAP) of 2609 mm based on the regression model of Wing et al. (2009) which is comparable to >1500 mm precipitation found in the Guineo-Congolian evergreen rainforests (White, 1983). The CLANN analysis results in slightly lower temperatures (24°C) and precipitation (1795 mm).

The CLANN analysis also favors an equable climate with an annual amplitude of about 6°C (warm month mean temperature; WMMT: 27°C, cold month mean temperature, CMMT: 21°C). This reflects the continuous growing season (12 months). Nevertheless, the precipitation of the three wettest months (Three-Wet: 911 mm/ 304 mm per month) is about twice the mean monthly precipitation (MMGSP: 150 mm), while the three driest months (131 mm/ 44 mm per month) indicates a dry season (month with less than 50 mm). This suggests a strong seasonality with a short dry season. Nevertheless, such seasonality is comparable to the Guinean part of the Guineo-Congolian TRF (White, 1983).

4.3 Diversity

Despite the low number of specimens, the diversity of the Baris flora rarefied at 100 specimens (the averaged diversity of a subsample consisting of 100 specimens) and appears comparable to the richest floras of the Paleogene and modern TRF as well as subtropical assemblages and is richer and more diverse than the Paleocene temperate assemblages (Table 1). Moreover, the assemblages also rarefied at 20 specimens, in order to include most assemblages, the same applies to the remaining assemblages of NE Africa. The total diversity of the Campanian of NE Africa displays the same pattern (Figure 3).

4.4 Taxonomic composition

In terms of composition (Table 1), the African Campanian assemblages are characterized by the dominance of angiosperms, which account for 94% of the flora. Among the mid-latitude floras, the Campanian Grünbach flora has only 68% angiosperms, and only Paleogene assemblages exhibit more than 85% angiosperms (e.g., Castle Rock). Even among the angiosperm-dominated assemblages (i.e., >85% angiosperms), only the tropical assemblages of Guaduas, Cerrejon, and Africa are rich in monocots (11%, 20%, and 17% respectively), while other assemblages, although extremely rich, display no more than 2% monocots (i.e., Laguna del Hunco and Castle Rock). The high dominance of both monocots and other angiosperms and the near exclusion of other plant groups seem to be typical for both ancient and modern TRFs.

Furthermore, a closer comparison with the contemporaneous subtropical Grünbach flora, the Maastrichtian Guaduas flora, and the Paleocene Cerrejon TRF supports a closer affinity of the NE African vegetation with younger TRF than with coeval subtropical vegetation.

A thorough comparison with Grünbach based on Herman and Kvaček (2010) reveals the complete absence of taxa common to both assemblages. Of particular importance is the absence of platanoid taxa in NE Africa although they are very common in northern mid-latitudes floras. Among monocots, Araceae, which are abundant in NE Africa, also occur at Grünbach, but they are represented by Orontioideae, a subfamily that is currently restricted to the northern subtropical to temperate area (Mayo et al., 1997).

Considering its relation to the Guaduas assemblage (Carvalho et al., 2021), the Baris assemblage displays a piperalean morphotype (M15) quite similar to *Piper margaritae* (Guaduas morphotype GD05) as well as a fern (M36) similar to GD103. However, the monocots of Guaduas seem to be dominated by Zingiberales and palms, of which the latter have not been observed in NE Africa. Only two morphotypes have possible araceous affinities, but neither of them is similar to the Araceae of NE Africa. However, palynological evidence highlighted its occurrence in the Campanian in North Africa (e.g., Jardiné and Magloire, 1965; Meon, 1990; Mahmoud, 2003). The majority of palm and palm-like records in the Campanian (and Maastrichtian) are from coastal regions of western, northern, and eastern Africa (Somalia), e.g., Schrank (1994). These records also occurred in tropical south America and, to a lesser extent, in southeast Asia, forming the core of the Late Cretaceous Palmae Province (Herngreen et al., 1996; Morley, 2000; Pan et al., 2006).

In contrast to Guaduas, the monocot assemblage of Cerrejon based on Wing et al. (2009) is to that at Baris, displaying not only Zingiberales (especially morphotype CJ49) similar to M-32, but also *Montrichardia* (CJ3) a colocasioid member of Araceae similar to *Afrocasia* (M-31) (Coiffard and Mohr, 2016), a probable *Cobbania* (M-29) (Coiffard and Mohr, 2018) (CJ59) and a member of Araceae similar to *Lejalia* (M-30) (Coiffard and Mohr, 2015) (CJ47). In addition to similarities with Cerrejon, terrestrial Araceae at Baris show affinities with modern

TRF taxa. Furthermore, *Afrocasia* is a member of Aroideae with huge leaves that displays close affinity with taxa that are usually found in tropical rainforests but also occur in warm temperate forests. More important is *Lejalia*, which is closely related to *Homalomena* and *Philodendron*, both genera that belong to groups restricted to tropical rainforests. Furthermore, in contrast to the above-mentioned taxa, Aroideae growing in seasonal (monsoonal) tropical vegetation have compound leaves, such as *Amorphophallus*. The dicot morphotypes CJ5 (Lauraceae) and CJ48 (Salicaceae) are similar to M-03 and M-04 respectively. M-03 and CJ5 share the presence of one pair of acute basal secondaries, simple brochidodromous secondaries, and simple agrophic veins. Also, M-04 and CJ-48 share the same basal actinodromous venation, well-developed simple agrophic veins, and a toothed margin. The teeth of M-04 also display spherulate apices.

The Campanian floral assemblages from NE Africa are thus more similar, in terms of physiognomy, species richness, and taxonomic composition, to younger tropical assemblages than to contemporary and younger temperate and subtropical forests.

5 Discussion

The leaf physiognomy of the NE African Campanian leaf assemblages is consistent with a wet tropical climate comparable to that of modern African TRF. Wet tropics during the Late Cretaceous agree with models predicting increased precipitation during the Late Cretaceous (Chaboureau et al., 2014) and suggest that a seasonal intersecting overlap of the ITCZ existed at least during the Campanian (Spicer et al., 2013).

Considering their composition, the NE African Campanian floras display a set of Aroideae that belong to typical TRF clades (Nauheimer et al., 2012) and thus support the idea that the Late Cretaceous tropics already housed such lineages under conditions similar to their modern habitat. This reconciles an apparent conflict between the fossil record and phylogenetic evidence (Eiserhardt et al., 2017). Such conflict was due to the almost complete absence of published tropical floras for the Cretaceous, with the notable exception of the Crato flora (Mohr and Friis, 2000), and some preliminary reports from NE Africa (Kahlert et al., 2009) as well as the recent record from the Maastrichtian of Guaduas from the central Andes of Colombia (Carvalho et al., 2021).

The Aptian Crato flora in NE-Brazil is supposed to have grown in a rather (seasonally) dry climate and is dominated by gymnosperms (Mohr et al., 2006). The angiospermous component of this vegetation differs strongly from that of younger vegetation, consisting of magnoliids and early diverging eudicots and monocots (Coiffard et al., 2019). If the Crato flora is representative of tropical vegetation during the late Early Cretaceous, this implies that modern-looking TRF must have developed during the 120-80 Ma time interval.

Unfortunately, except for the Turonian floras of the Negev desert (Krassilov, 2005), fossil floras from this time interval are under-sampled, although new collections are planned in Egypt and Sudan. The Turonian flora of the Negev desert (Krassilov, 2005) apparently grew further away from the palaeoequator and seems to correspond to a drier climate, and it has rather low diversity (19 leaf morphotypes) and strong affinities to Laurasia.

To sum up, the present results show that TRF occurred in NE Africa during the Campanian in an area extending between 19°N and 26°N and between 26°E and 33°E, covering at least 550,000 km^2, which corresponds to 10% of the Amazonian or 25% of the Congolese TRF.

6 Conclusions

A detailed investigation based on leaf physiognomy, species richness, and taxonomic composition was carried out on fossil leaf collections obtained from Baris Oasis, Egypt. The obtained results imply a wet tropical climate, comparable to that of modern African TRF. In terms of vegetation composition, the Campanian NE African floras display a set of Aroideae that belong to typical TRF clades and thus support the idea that Late Cretaceous tropics already housed such lineages under conditions similar to their modern habitat.

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Data availability. Data in this paper are available in the main text. Further data are available in the Supplement as follows.

Table S1: Morphotype catalogue of the NE African assemblages from the Campanian-Maastrichtian.

Table S2: Grünbach fossil collection.

Table S3: Results of the Climate Leaf Analysis with Neural Networks (CLANN).

Data S1: Original scoresheet filed for Baris and used for the CLANN.

Author contributions. CC contributed to the design and scope of the paper. JR provided the statistical and CLANN analysis. CC, HE, RB, and DU contributed to writing and revising the manuscript. CC and HE prepared the paper, with contributions from all co-authors.

Competing interests. The authors declare that they have no competing interests.

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Figures and Table captions:

Figure 1. Locations of the fossil assemblages studied. The location map shows the studied areas. The topographic map was created using the generic mapping tools of Wessel and Luis (2017) and the topographic dataset ETOPO1 of Amante and Eakins (2009).

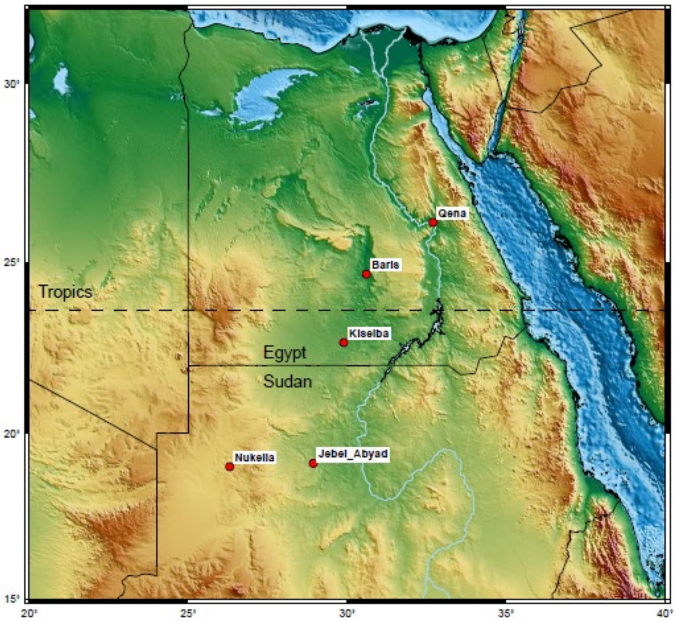

Figure 2. Line drawings of dicot (non-monocotyledonous angiosperm) leaf morphotypes, Baris, Egypt. The scale bar is 4 cm.

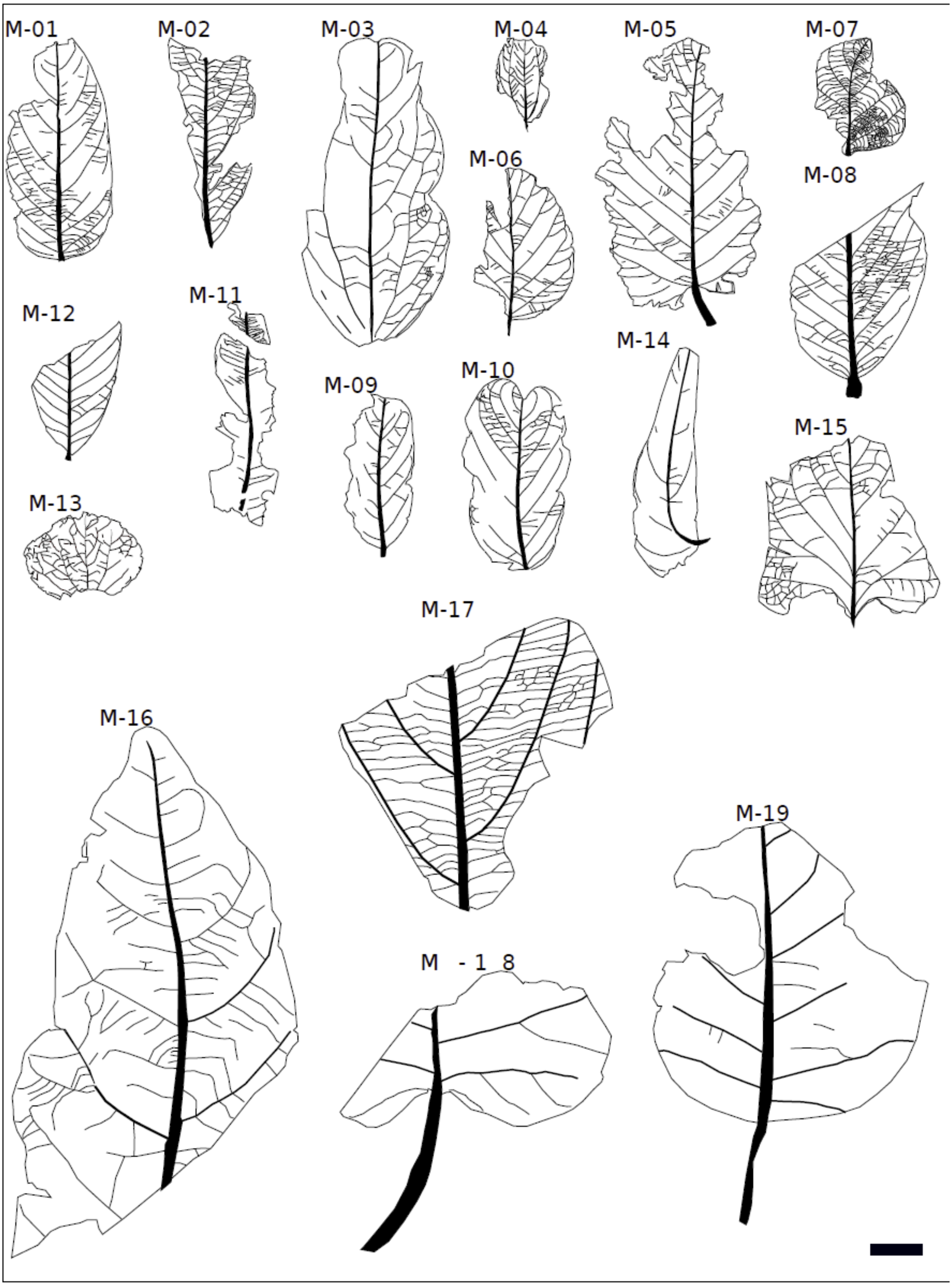

Figure 3. Line drawings of dicot leaf morphotypes, Baris, Egypt. The scale bar is 4 cm.

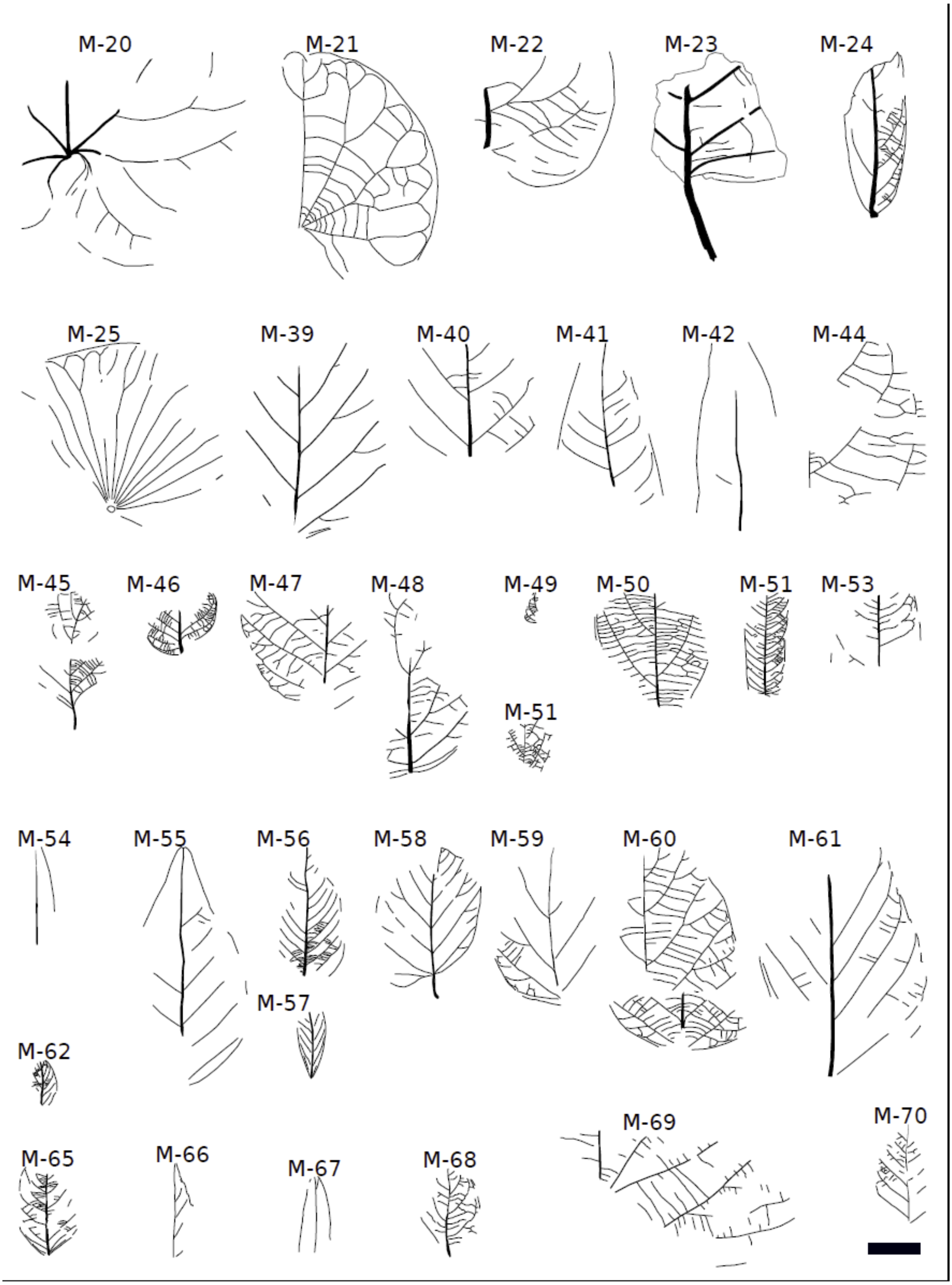

Figure 4. Line drawings of monocot, conifer (only M-43), and fern (M-36, M-37, M-38, M-64) morphotypes, Baris, Egypt. The scale bar is 4 cm.

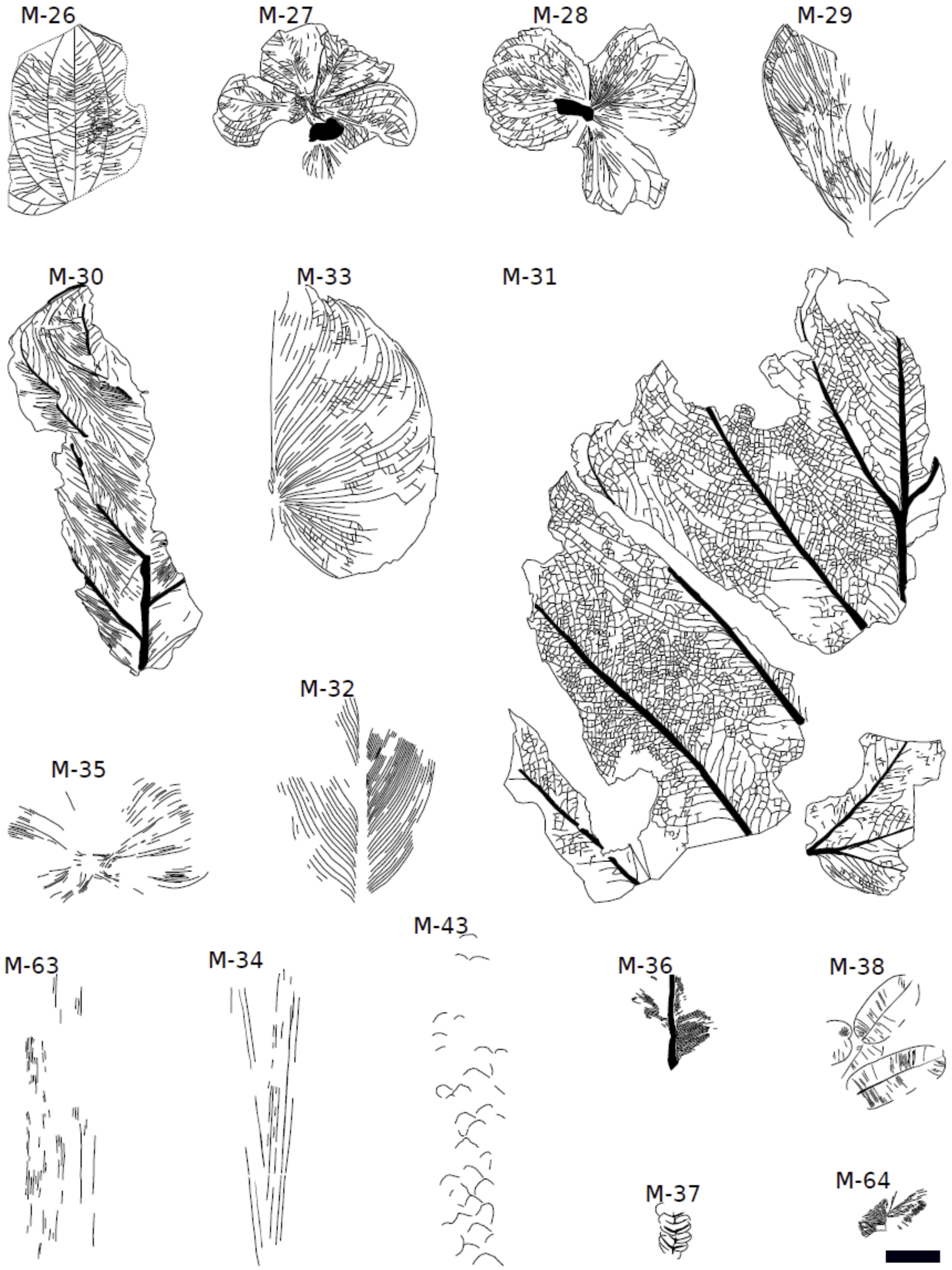

Figure 5. Rarefaction curves; information on the sites is given in the Supplementary material.

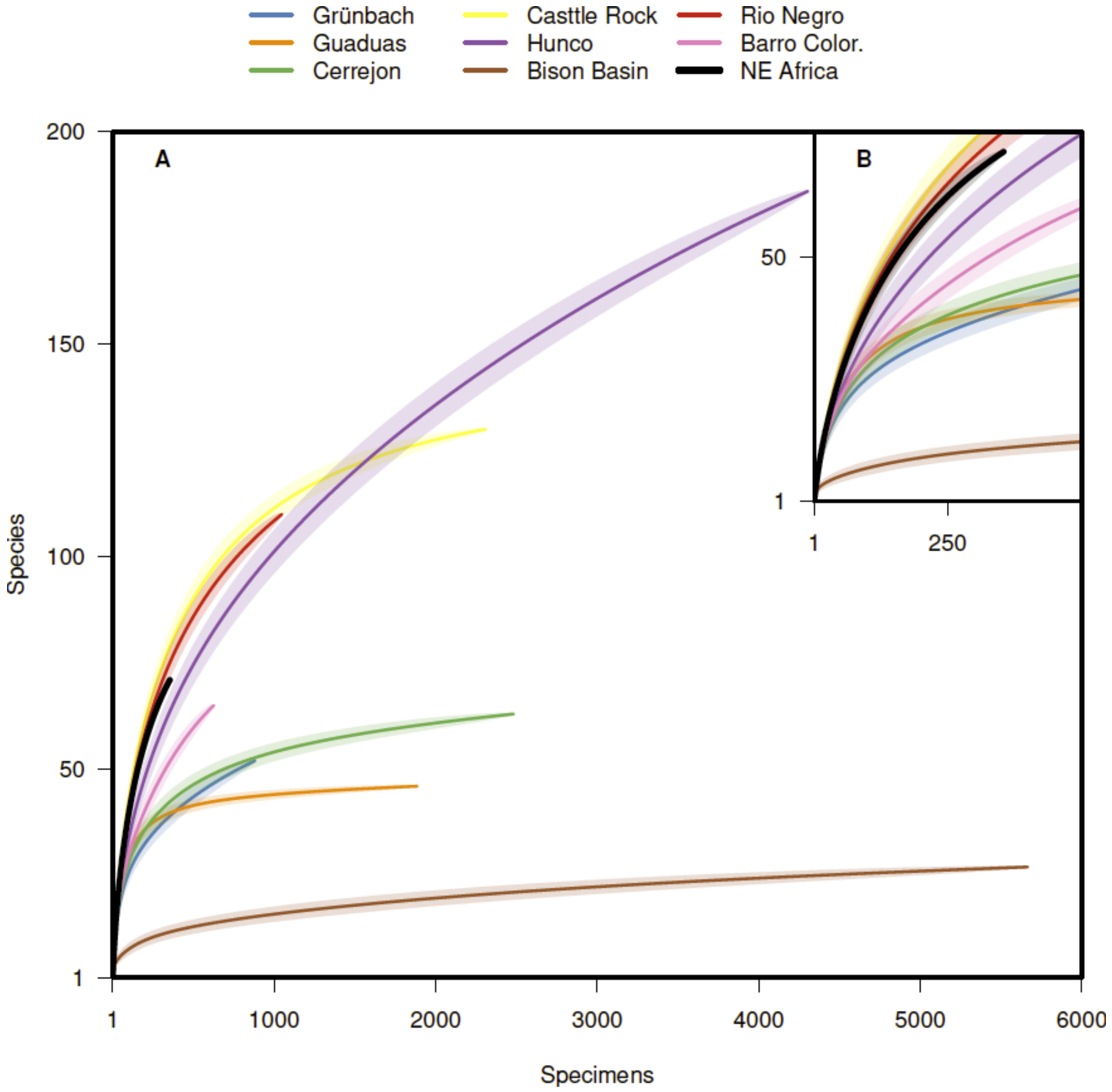

Table 1. Diversity and composition. Information on the sites is given in the Supplementary material. S_{total}, number of species in all samples; $S_{alpha}10$, number of species in sample rarefied to 10 specimens; $S_{alpha}100$, number of species in sample rarefied to 100 specimens; $S_{total}100$, number of species in all samples rarefied to 100 specimens.

	Grünbach	NE Africa	Guaduas	Cerrejon	Castle Rock	Laguna del Hunco	Bison basin	Rio Negro	Barro Color
	Late Cretaceous	Late Cretaceous	Late Cretaceous	Paleogene	Paleogene	Paleogene	Paleogene	modern	modern
No. sites	NA	8	5	16	5	25	10	7	3
No. specimens	881	354		2191	1015	4303	5664	1048	672
Stotal	52	60	46	65	104	191	23	110	79
Salpha100	NA	*28*	17	18	30	28	7	21	20
Stotal100	26	40	29	28	43	34	8	42	30
dicots (%)	56	77	80	71	92	86	91	NA	NA
monocots (%)	12	17	11	20	0	2	0	NA	NA
ferns (%)	23	5	9	8	3	4	4	NA	NA
cycads (%)	2	0	0	0	3	1	0	NA	NA
Ginkgoes (%)	0	0	0	0	0	1	0	NA	NA
conifers (%)	8	2	0	2	2	7	4	NA	NA