1 **The emergence of the tropical rainforest biome in the Cretaceous**

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1 **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,

3 especially due to the incongruence between the fossil record and molecular data. Here, we are

4 testing whether Campanian assemblages from north-eastern Africa could represent fossil TRF vegetation. In so doing, we compare the investigated assemblages with others

6 known to represent temperate forests, subtropical forests, and TRF in terms of leaf

7 physiognomy, species richness, and taxonomic composition. We assume that modern-looking TRF already existed about 80 Ma ago during the Campanian in north-eastern Africa based on fossil leaves in an area corresponding to 10% of the modern Amazonian or 25% of the

10 Congolese TRF. The apparent conflict between the fossil record and phylogenetic evidence is due to the more or less absence of published tropical floras for the Cretaceous.

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

15 **Teaser.** Eighty Ma old fossil leaf assemblages suggest a widespread distribution of tropical

16 rainforests in north-eastern Africa.

1 **1 Introduction**

2 Modern tropical rain forests (TRF) are one of the most ecologically important and species-

3 rich biomes on the planet. Rainforest environments have an enormous impact on global water

4 and heat circulation and therefore play a major role in water distribution and rainfall patterns.

5 These forests are characterized by a stratified closed canopy, the presence of woody

6 angiosperms at least in the understory, abundant rainfall, and equable temperatures. The origin

7 of modern TRF is still debated (Eiserhardt et al., 2017). Studies based on modern plants

8 suggest that the earliest appearance of the TRF dated back to the Cenomanian (93.9-100.5

9 Ma). In contrast, fossil TRF, characterized by their (leaf) physiognomy, climate proxies, and

10 high diversity, have not been identified so far before the Maastrichtian (66.0-72. Ma)
11 (Carvalho et al., 2021). An alternative scenario implies an earlier origin of TRF at mid-
12 latitudes (Morley, 2000; Davis et al., 2005). However, mid-latitude floras from the Dakota Formation (ca. 100 Ma)
(Upchurch and Wolfe, 1987) and the Olmos Formation (ca.72 14 Ma) (Estrada-Ruiz et al., 2008) correspond

to a paratropical/subropical climate.

15 The early development of TRF has been hampered by the fact that most of the information originated from mid to high-
latitude fossil sites reflecting more temperate

17 climates, while low-latitude sites have hardly been studied. Nevertheless, material including Campanian fossil plants from
Egypt and the Sudan have been collected by the

19 'Sonderforschungsbereich 69' (a collaborative research centre located in Berlin funded by the (DFG) in the 70s to 90s
(Figure 1). The studied assemblages have been preliminarily studied by Klitzsch and Lejal-Nicol (1984), Lejal-Nicol (1987)
and Kahlert et al. (2009). Nonetheless, these contributions focused only on a few selected taxa and did not attempt to
estimate the palaeoclimate or the palaeodiversity. The studied collection, from the Baris Oasis in Egypt, comes from the
Quseir Formation (Fm.) of early to middle Campanian age (ca. 84 Ma)

1   (Mahmoud, 2003). In addition, other seven smaller assemblages from lateral and temporal

2   equivalents of the Quseir Fm. were also studied. To test whether these assemblages

3   correspond to a fossil TRF vegetation, or at least a habitat suitable for stem lineages of

4   modern TRF taxa, we compared them with contemporary and younger assemblages known to

5   represent temperate forests, subtropical forests, and TRF considering three aspects.

6   (1) Leaf physiognomy dominated by entire margined taxa, reflecting mean annual

7   temperature >24°C and mesophyllous or larger leaves, implying rainfall>1500mm

8   corresponding to the limit of TRF in Africa (White, 1983).

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

10 (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

14 In Southern Egypt and Northern Sudan, the shallow marine Campanian sediments are rich in kaolinite and partly contain phosphorites (Schwarz and Germann, 1999). However, equivalent

continental facies comprised stacked palaeosols consisting of quartz, kaolinite, iron hydroxides, and oxides. eroded
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).

21 Phosphorite formation was also ascribed to intense chemical weathering on

the African continent due to a humid tropical palaeoclimate and the fluvial transport of the

weathering solutions into the shallow marine environment (Schwarz and Germann, 1999).

Laterites are typically formed by intense tropical or subtropical weathering, but preferably in a

warm climate with pronounced dry seasons (Widdowson, 2007).

1 Laterites on the otherhand, are typically formed by intense tropical or subtropical weathering in a

4 1.1.2 Palaeobotanical evidence

5 Records of gymnospermous charcoal, despite rare, in sediments of the Quseir Fm. 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

8 conditions, it is not clear whether such conditions might have occurred seasonally or just

9 during an occasional dry spell (El Atfy et al., 2016). Even in modern rainforests such

10 occasional dry spells can promote the ignition and spread of wildfires (Scott et al., 2013).

11 Under conditions of higher than present oxygen concentrations in the atmosphere, which were

12 reconstructed by a number of models for the Cretaceous (Brown et al., 2012), it is even more

13 likely that also within ever-wet TRF wildfires could be ignited and spread easily (Belcher et

14 al., 2010).

15 Palynological data from the Quseir Fm. also point to a flora dominated by angiosperms,

16 although pteridophytes and gymnosperms are present, but not diverse (Mahmoud, 2003).

17 Based on the composition and diversity of the palynoflora, as well as data from palynofacies

18 analysis, Mahmoud (op. cit.) interpreted the source habitats of the recovered palynomorphs as

19 a fluvio-lacustrine landscape with abundant moist and aquatic habitats as well as

20 subordinately drier habitats (i.e., with *Araucaria*, ephedroids and other gymnosperms) in the

21 hinterland, in which the plants are grown under a warm and humid, tropical to subtropical,

22 palaeoclimate.

2 Geological and collecting information

2 The studied materials comprise fossil leaves collected by members of the

3 'Sonderforschungsbereich 69' in 1984 and 1987 that are housed now at the Natural History Museum of

Berlin. They comprised collection B (Baris) which encompasses the material

5 described here that was gathered east of Baris (24°33'N, 30°43'E) in southern Egypt from the Quseir

Fm. which was dated as early to middle Campanian age (Mahmoud, 2003). In

7 addition, seven additional assemblages were also studied, among them, four assemblages

8 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

10 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 the 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) from the

Kabbabish Fm. and its equivalents (Barazi, 1985).

15 A lower age boundary of the studied assemblage can be delimited by a regional hiatus associated with

16 a major unconformity between the Santonian and the

17 Campanian which has been dated palynologically (Wycisk, 1994

18 An upper age boundary has been dated in Egypt, based on the age of transgression which covered

19 the whole area in Egypt, as late Campanian, which has been confirmed palynologically (El Beialy, 1995

20 and macropalaeontologically (ammonites, Dominik and Schaal, 1984).

21 In addition to mega plant fossils, the ecosystem in the Quseir Fm. is characterized by the

presence of fragmented bones and other vertebrate remains of lungfishes, sawfishes, turtles, crocodiles as

well as dinosaurs (Abu El-Kheir, 2020).

1 **3 Methods**

2 3.1 Climate proxies and diversity analyses

3 For the diversity analyses and climate proxies, the leaves were grouped into morphotypes

4 without considering formerly proposed taxa (the literature survey was done afterwards). Each morphotype differs from others by at least one of the criteria described in the manual of leaf architecture (Ellis et al., 2009). Although the biggest leaves are often fragmentary, all

7 broken slabs are still recognized, e.g. by their tertiary venation (e.g., M-17 has horizontal

8 tertiaries while in M-16 they are clearly obtuse to the mid-vein), or their shape (e.g., M-18 and M19 are very coriaceous, but differ in the base shape, which is corded and rounded

10 respectively). Considering the high proportion of simple, entire margined leaves, the most 11 important distinguishing characters are found in the higher order of venation.

12 Climate data were estimated using two kinds of climate proxies, the first is simple linear

13 regressions between a physiognomic and a climate parameter, and the second is an artificial neural network approach, based on 31 leaf characters and giving, palaeoclimate variables (CLANN). Each morphotype was evaluated for the physiognomic characters used (see

16 Supplementary material).

17 We used the simple linear regressions between a physiognomic and a climate parameter, following Miller et al. (2006) and Kowalski and Dilcher (2003) to calculate temperature estimates, based on leaf margin analyses. For the rainfall estimates based on leaf size, we

20 employed the regression by Wilf et al. (1998).

21 Climate proxies were also checked using the CLANN method (i.e. an artificial neural network approach CLAMP) (Li et al., 2016) calibrated using the CLAMP global data set

23 considering 378 sites worldwide (Spicer et al., 2009). As in Li et al. (2016), the spread for each climatic variable was calculated using a 10-fold cross-validation, repeated 1000 times.

1 The scoresheet for the Baris flora is given in the supplementary material (Supplementary

2 material; Data S1) as well as the code used.

3 The rarefied diversity 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

7 assemblages are more similar to TRFs than to other kinds of vegetation, we compared the

8 diversity of fossil samples from NE Africa with tropical and warm temperate associations

9 from the Cretaceous, Paleocene and Eocene. The data from Cerrejon, Castle Rock, Bison

10 basin, Rio Negro, Barro Colorado were taken from Wing et al. (2009) and compiled with data

11 from Hunco (Wilf et al., 2005) and Grünbach (Herman and Kvaček, 2010). The data from

12 Grünbach are based on the number of specimens of each taxon mentioned as material given

13 (see Supplementary material). Only the bulk flora diversity could be estimated for Grünbach

14 due to the absence of data concerning individual collection points. The rarefaction curves

15 were done using PAST (Krebs, 1989; Hammer et al., 2001).

17 **4 Results**

18 4.1 Morphotypes

19 Previous works focused on the investigated material (Klitzsch and Lejal-Nicol, 1984; Lejal-

Nicol, 1987; Kahlert e al., 2009) recorded only 37 taxa while our current revision based on 361

specimens, resulted in the identification of 70 morphotypes: 54 non-monocotyledon

angiosperms, 11 monocotyledons, 4 ferns, and a single conifer (Figure 2). The presence of some

morphotypes occurring in several assemblages (Supplementary material; Table S1),

1 especially monocotyledons, suggests homogeneous vegetation for the whole area and supports

2 their contemporaneity.

4 4.2 Climate

5 The physiognomy of the Baris assemblage is similar to that of a modern TRF. Of the 20

6 terrestrial non-monocotyledonous angiosperms with preserved margin, 85% are entire-

7 margined, yielding estimates of mean annual temperature (MAT) ranging from 26°C to 33°C

8 corresponding to a tropical climate (Wolfe, 1979). Whereas, the average leaf size of the 23

9 terrestrial non-monocotyledonous angiosperms is 69 cm² (Wing et al., 2009), yielding

10 estimates of the mean annual precipitation (MAP) of 2609 mm which is alike to >1500 mm

11 precipitation found in the Guineo-Congolian evergreen rainforests (White, 1983). The

12 CLANN analysis results in slightly lower temperatures (24°C) and precipitation (1795 mm).

13 The CLANN analysis also advocates an equable climate with an annual amplitude of about

14 6°C (warm month mean temperature; WMMT): 27°C, cold month mean temperature; CMMT:

15 21°C. This is reflected by the continuous growing season (12 months). Nevertheless, the

16 precipitation of the three wettest months (Three-Wet: 911 mm/ 304 mm per month) is about

17 twice the mean monthly precipitation (MMGSP: 150 mm) while the three driest months (131

18 mm/ 44 mm per month) indicate a dry season (month with less than 50 mm). This suggests a

19 strong seasonality with a short dry season. Nevertheless, such seasonality is comparable to the

20 Guinean part of the Guineo-Congolian TRF (White, 1983).

22 4.3 Diversity

23 Despite the low number of specimens, the diversity of the Baris flora rarefied at 100

24 specimens and appear comparable to the richest floras of the Paleogene and modern TRF as

1 well as subtropical assemblages and richer and more diverse than the Paleocene temperate

2 assemblages (Table 1). Moreover, the assemblages also rarefied at 20 specimens, in order to

3 include most assemblages, the same applies to the remaining assemblages of NE Africa. The

4 total diversity of the Campanian of NE Africa displays the same pattern (Figure 3).

6 4.4 Taxonomic composition

7 In terms of composition (Table 1), the Campanian African assemblages are characterized by

8 the dominance of angiosperms accounting for 94% of the flora. Among the mid-latitude

9 floras, the Campanian Grünbach flora has only 68% angiosperms and only Paleogene

10 assemblages exhibit more than 85% angiosperms (e.g. Castle Rock). Even among the

11 angiosperm-dominated assemblages (i.e. >85% angiosperms), only the tropical assemblages

12 of Guaduas, Cerrejon, and Africa are rich in monocots (11%, 20%, and 17% respectively)

13 while other assemblages, although extremely rich, display no more than 2% monocots (i.e.

14 Hunco and Castle Rock). The high dominance of dicots and monocots and the near exclusion

15 of other plant groups seem to be typical for both ancient and modern TRFs.

16 Furthermore, a closer comparison with the contemporaneous subtropical Grünbach flora, the

17 Maastrichtian Guaduas flora, and the Paleocene Cerrejon TRF support a close affinity of the

18 NE African vegetation with younger TRF.

19 A thorough comparison with Grünbach based on Herman and Kvaček (2010) reveals the

20 complete absence of taxa common to both assemblages. Of particular importance is the

21 absence of platanoid taxa in NE Africa although they are very common in northern mid-

22 latitudes floras. Among monocots, Araceae do occur, but they are represented by

23 Orontioideae, a subfamily that is currently restricted to the northern subtropical to the

24 temperate area (Mayo et al., 1997).

1   Compared to the Guadas assemblage (Carvalho et al., 2021), the Baris assemblage displays a

2   piperalean morphotype (M15) quite similar to *Piper margaritae* (GD05) as well as a fern

3   (M36) similar to GD103. However, the monocots of Guadas seem to be dominated by

4   Zingiberales and palms, the latter apparently lacking in NE Africa. Only two morphotypes

5   could have araceous affinities but none of them is similar to the Araceae of NE Africa.

6   However, palynological evidence from the Maastrichtian of Somalia introduced the exclusive

7   occurrence of palms (Schrank, 1994).

8   In contrast to Guadas, the monocot assemblage of Cerrejon based on Wing et al. (2009) is

9   quite similar to Baris, displaying Zingiberales (especially CJ49) similar to M-32, but also

10 colocasioid Araceae similar to *Afrocasia* (M-31) (Coiffard and Mohr. 2016) (*Montrichardia*,

11 CJ3), a probable *Cobbania* (M-29) (Coiffard and Mohr. 2018) (CJ59) and an Araceae similar

12 to *Lejalia* (M-30) (Coiffard and Mohr. 2015) (CJ47). In addition to similarities with Cerrejon,

13 the terrestrial Araceae show affinities with modern TRF taxa. Furthermore, *Afrocasia* is an

14 Aroideae with huge leaves that displays close affinity with taxa usually found in tropical

15 rainforests but also in warm temperate forests. More important is *Lejalia*, which is closely

16 related to *Homalomena* and *Philodendron*, both taxa and their relatives being restricted to

17 tropical rainforests. Furthermore, Aroideae growing in seasonal (monsoonal) tropical

18 vegetation have compound leaves, such as *Amorphophallus*. The dicots morphotypes CJ5

19 (Lauraceae) and CJ48 (Salicaceae) are similar to M-03 and M-04 respectively. M-03 and CJ5

20 share the presence of one pair of acute basal secondaries, simple brochidodromous

21 secondaries and simple agrophic veins. Also, M-04 and CJ-48 share the same basal

22 actinodromous venation, well-developed simple agrophic veins, and a toothed margin. The

23 teeth of M-04 also display spherulate apices.

1   The Campanian floral assemblages from NE Africa are thus more similar, in terms of

2   physiognomy, species richness, and taxonomic composition, to younger tropical assemblages

3   than to contemporary and younger temperate and subtropical forests.

5   **5 Discussion**

6   The leaf physiognomy of the Campanian NE African leaf assemblages is consistent with a wet

tropical climate comparable to that occurring in modern African TRF. Wet tropics during the late

Cretaceous agree with increased precipitation during the Late Cretaceous (Chaboureau et al.,

2014) and suggest that a seasonal overlap of the ITCZ existed at least during the Campanian

10 (Spicer et al., 2013).

11   The composition of the Campanian NE African floras displays a set of aroids that belong to

typical TRF clades (Nauheimer et al., 2012) and thus support the idea that Late Cretaceous tropics

already housed such lineages under conditions similar to their modern

14 habitat. This reconciles the apparent conflict between the fossil record and phylogenetic

15 evidence (Eiserhardt et al., 2017). Such conflict was due to the near 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 (Carvalho et al., 2021).

19 The Barremian-Aptian Crato flora in NE-Brazil is supposed to have grown in a rather

20 (seasonally) dry climate and is dominated by gymnosperms (Mohr et al., 2006). The

21 angiosperms component of this vegetation differs strongly from younger vegetation,

22 consisting of Magnoliids and early diverging eudicots and monocots (Coiffard et al., 2019). If

23 the Crato flora is representative of the tropical vegetation during the late Early Cretaceous,

24 this implies that modern-looking TRF must have developed during the 120-80 Ma time

1   interval. Unfortunately, except for the Turonian floras of the Negev desert (Krassilov, 2005), fossil flora from this time interval are insufficient despite that new collections are planned in Egypt and the Sudan. The Turonian flora of the Negev desert (Krassilov, 2005) apparently grew further away from the palaeoequator. It seems to have a drier climate and a rather low diversity (19 leaf morphotypes) and strong affinities to Laurasia.

6   To sum up, the present results show that TRF occurred in NE Africa during the Campanian in an area expanding between 19°N and 26°N and between 26°E and 33°E, covering at least

8   550,000 km² which corresponds to 10% of the Amazonian or 25% of the Congolese TRF.

6 Conclusions

11   A detailed investigation based on leaf physiognomy, species richness, and taxonomic

12   composition was carried out on fossil leaf collection, recovered from the Baris Oasis, Egypt. The results obtained infer a wet tropical climate, comparable to that occurring in modern African TRF. In terms of vegetation composition, the Campanian NE African floras display a set of 15 aroids 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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1 **Data availability.** All data in this paper are available in the main text. Further data are

2 available in the Supplement as follows.

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

4 Maastrichtian.

5 Table S2: Grünbach fossil collection.

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

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

9 **Author contributions.** CC contributed to the design and scope of the paper. JR provided the

10 statistical and CLANN analysis. CC, HE, RB, and DU contributed to writing and revising the

11 manuscript. CC and HE prepared the paper, with contributions from all co-authors.

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

15 **Acknowledgements.** We would like to thank the institutions and researchers who made this

publication possible.

18 **Financial support.** This work has been supported by the Deutsche Forschungsgemeinschaft

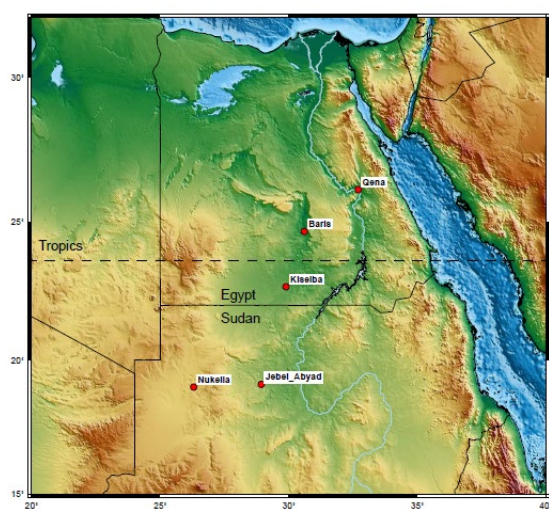
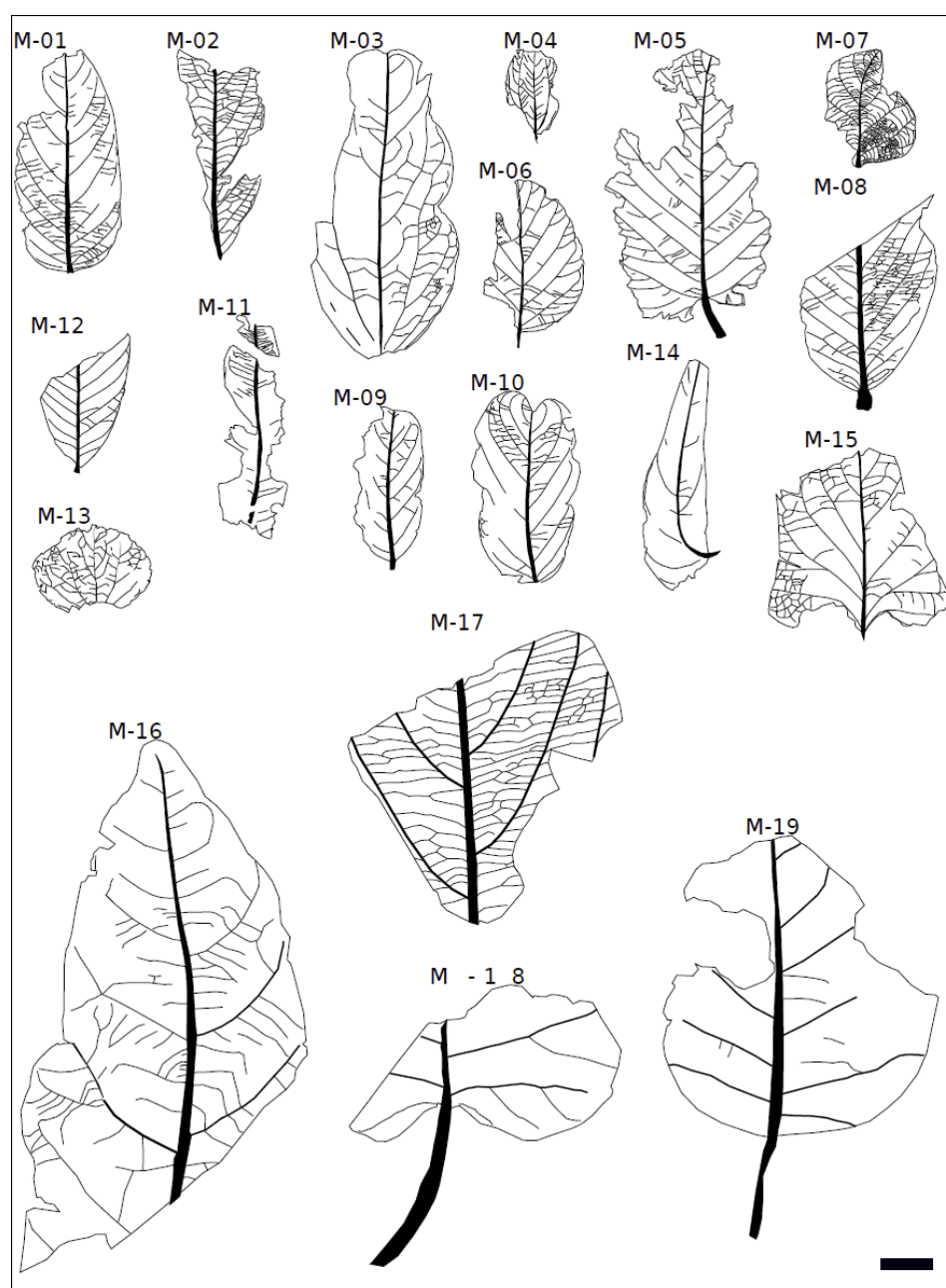
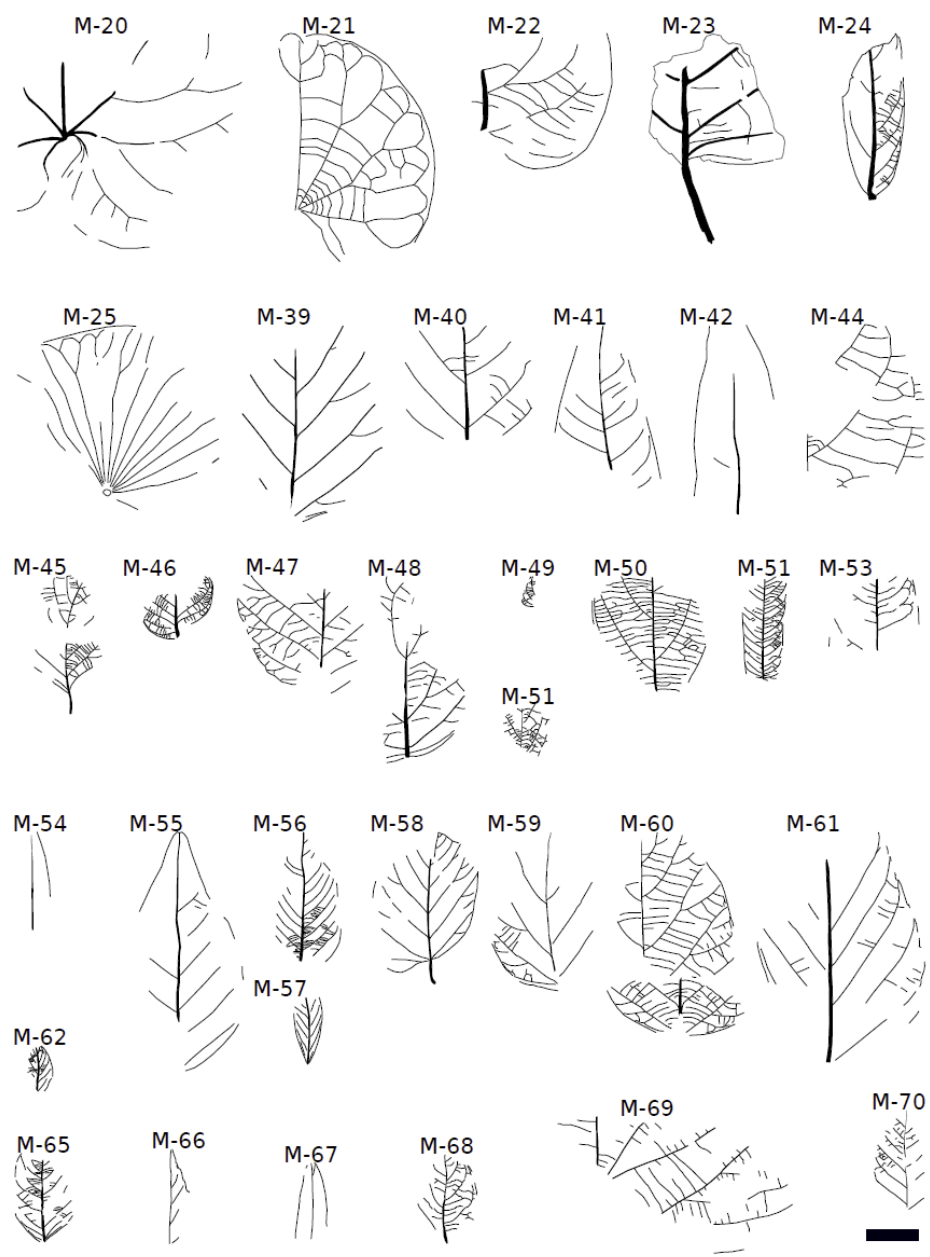
19 (grant number CO1060/3-1 to CC) and the Alexander von Humboldt Foundation (grant

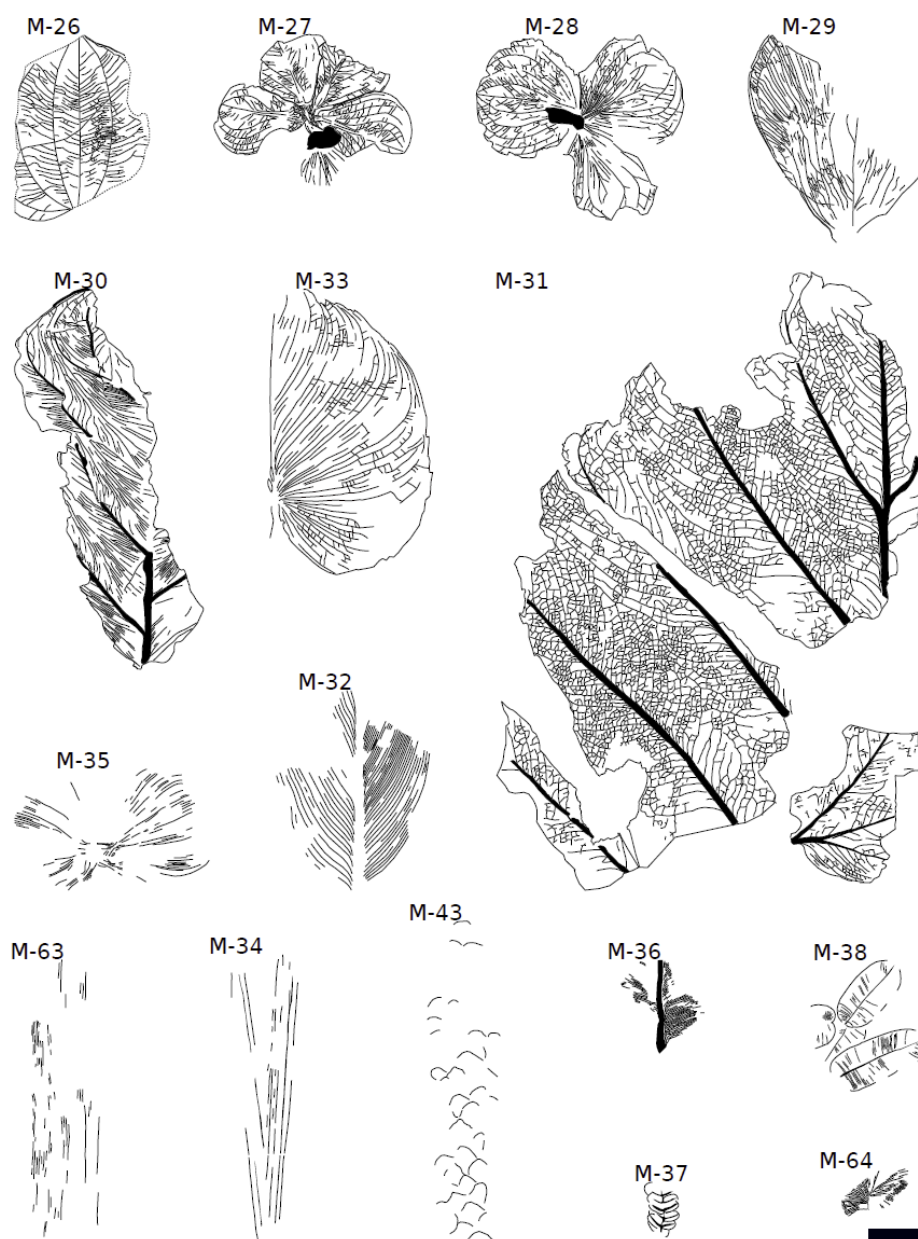
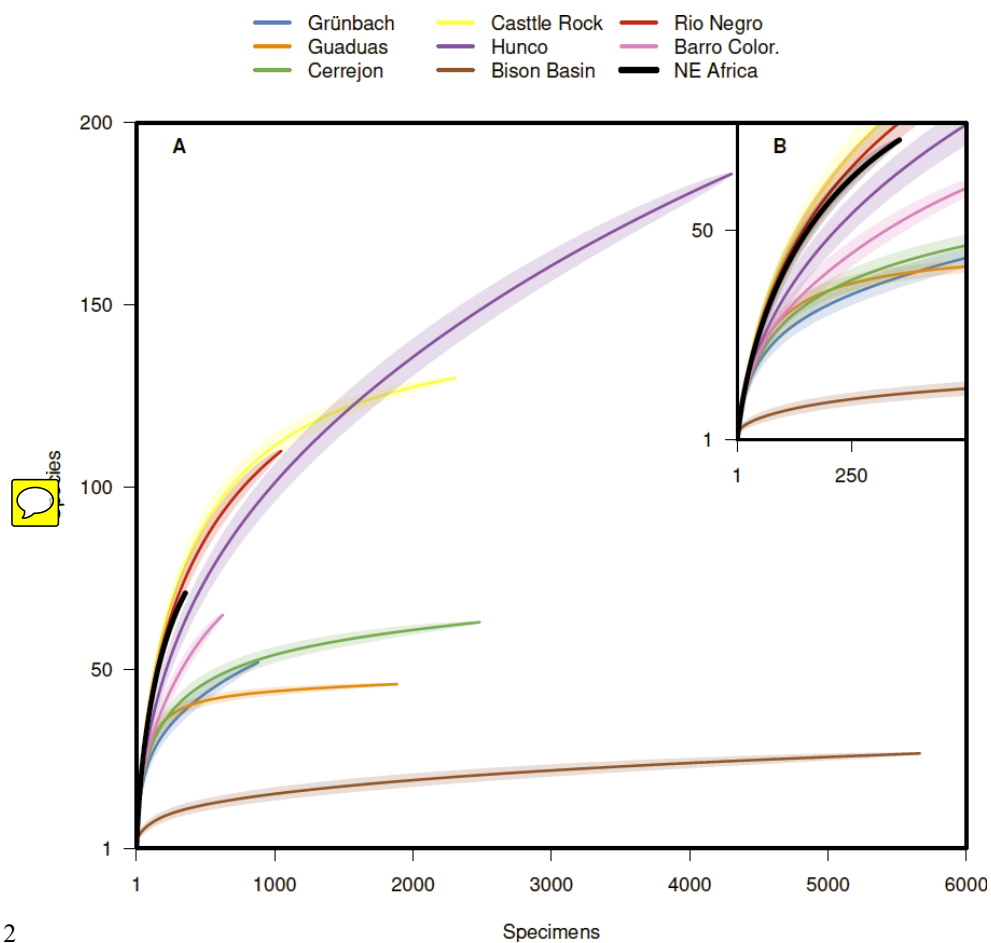
20 number EGY-1190326-GF-P to HE).

1 **Figures and Table captions:**

2 **Figure 1.** Location of the fossil assemblage used. The location map shows the studied areas.

3 The topographic map is created using generic mapping tools of Wessel and Luis (2017) and

4 the topographic dataset ETOPO1 of Amante and Eakins (2009).

1   **Figure 2.** Line drawings of dicot leaf morphotypes, Baris, Egypt. The scale bar is 4 cm.

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

1   **Figure 4.** Line drawings of monocots, conifers (only M-43), and ferns (M-36, M-37, M-38,

2   M-64) morphotypes, Baris, Egypt. The scale bar is 4 cm.

1   **Figure 5.** Rarefaction curves, information on the sites is given in the supplementary material.

1 **Table 1.** Diversity and composition. Information on the sites is given in the ==spplementary== material.

S_{total}, number of species in all samples; $S_{alpha}10$, number of species in sample

3 rarefied to 10 specimens; $S_{alpha}100$, number of species in sample rarefied to 100 specimens;

4 $S_{total}100$, number of species in all samples rarefied to 100 specimens.

	Grünbach	NE Africa	Guaduas	==Cerrejon==	Castle Rock	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