

Earliest fossil pollen records of endemic African *Sclerosperma* palms and the palaeoecological aspects of the genus

Manuel Vieira^a, Johannes M. Bouchal^b, Christian Geier^b, Silvia Ulrich^{b,c}, Reinhard Zetter^d, Friðgeir Grímsson^{b,*}

^a NOVA School of Science and Technology, Department of Earth Sciences, GEOBIOTEC, Campus de Caparica, Caparica, Portugal

^b University of Vienna, Department of Botany and Biodiversity Research, Vienna, Austria

^c Austrian Academy of Sciences (OeAW), Austrian Archaeological Institute (OeAI), Department of Historical Archaeology, Vienna, Austria

^d University of Vienna, Department of Paleontology, Vienna, Austria

ARTICLE INFO

Keywords:

Arecaceae
Pollen morphology
Rainforest
Swamp elements
Tropical climates
Vegetation biomes

ABSTRACT

Palm diversity in present-day Africa is much less than in other tropical regions such as the Americas and Southeast Asia but comprises several endemic genera, including *Sclerosperma*. The origin and evolution of this small Arecaceae genus are still enigmatic, and every new fossil discovered helps fill the void in its palaeophytogeographic history. In this article, we report five different pollen morphologies assigned to *Sclerosperma* from the earliest Late Eocene (early Priabonian) of southeast Kenya, Africa. These pollen grains represent the earliest fossil records of *Sclerosperma* so far and add a new geographic region and time slot to the palaeophytogeographic history of this genus. The morphological variability observed in the fossil pollen suggests that the diversification within *Sclerosperma* was already underway by the onset of the Priabonian, c. 37 Ma. Detailed analysis of the distribution of the three extant *Sclerosperma* species shows that this genus occurs only under Equatorial/Tropical climates with MTCM ≥ 18 °C, such as fully humid Rainforest (Af), Monsoonal (Am), and winter dry Savannah (Aw) climates. *Sclerosperma* is also conservative when it comes to vegetation biomes and only occurs in three different but closely related biomes, the Tropical & Subtropical Moist Forests Biome, the Tropical & Subtropical Grasslands, Savannahs & Shrublands Biome, and the Mangroves Biome. No current outliners pinpoint to a wider ecological tolerance of this genus in the geological past. This suggests *Sclerosperma* to be an exceptionally reliable taxon for palaeoclimate estimations and when assigning palaeofloras to major vegetation biomes.

1. Introduction

The endemic African palm genus *Sclerosperma* G. Mann et H. Wendl (Arecaceae, Arecoideae) comprises only three extant species, *S. mannii* H. Wendl., *S. profizianum* Valk. et Sunderl., and *S. walkeri* A. Chev (Dransfield et al., 2008; Van Valkenburg et al., 2008a). All species show restricted and disjunct distributions in the Guineo-Congolian Region of tropical West and Central Africa. The patchy distribution of *S. mannii* stretches from Liberia and Nigeria in a south-eastwards direction towards the borders of the Democratic Republic of the Congo and Rwanda. *Sclerosperma profizianum* occurs only sporadically in Ghana, Gabon, the Republic of the Congo, the Democratic Republic of the Congo, and Angola. *Sclerosperma walkeri* has a similar distribution as *S. profizianum* but does not occur in Ghana (Dransfield et al., 2008; Van Valkenburg

et al., 2008b). Living *Sclerosperma* are pleonanthic and monoecious plants; they are small, usually between 2 to 6 m high, and often form groups as part of the forest understory. They grow in tropical lowland rainforests, on swampy sites, from sea level to an elevation of about 1400 m (Dransfield et al., 2008; Van Valkenburg et al., 2008a).

The pollen morphology of *Sclerosperma* is not only unique within the Arecaceae but within all angiosperms, and its diagnostic features have been pinpointed in numerous publications (e.g., Erdtman and Sing, 1957; Harley and Hall, 1991; Harley, 1996, 1999, 2004; Harley and Baker, 2001; Harley and Dransfield, 2003; Dransfield et al., 2008). The combined morphological features of extant *Sclerosperma* pollen observed with light microscopy (LM) and scanning electron microscopy (SEM) were conducted by Grímsson et al. (2019c). The authors showed that the three living *Sclerosperma* species produce four different pollen

* Corresponding author: University of Vienna, Department of Botany and Biodiversity Research, Rennweg 14, 1030 Vienna, Austria.

E-mail address: fridgeir.grimsson@univie.ac.at (F. Grímsson).

<https://doi.org/10.1016/j.revpalbo.2023.104954>

Received 5 July 2023; Received in revised form 18 July 2023; Accepted 19 July 2023

Available online 24 July 2023

0034-6667/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

morphologies, with *S. mannii* and *S. walkeri* sharing a coarsely reticulate pollen and *S. profizianum* producing three pollen types that are either microreticulate or fossulate or perforate (Grímsson et al., 2019c). *Sclerosperma* fossil records are rare and comprise only a handful of finds, mostly pollen, depicted from Late Oligocene to Miocene sediments of Africa (Grímsson et al., 2019b; Currano et al., 2020; Ulrich and Grímsson, 2020). Still, the uniqueness of *Sclerosperma* pollen and the conservative tropical preferences of the parent plants make its fossil pollen ideal for tracing the palaeophytogeographic history of this genus and for estimating both palaeoclimate and palaeovegetation in areas currently lacking this palm.

Here we describe fossil *Sclerosperma* pollen grains from the earliest Late Eocene of Kenya, Eastern Africa, the earliest records of this genus ever reported. The fossil pollen is compared to other, younger (Oligocene to Miocene) *Sclerosperma* records as well as to pollen from the three living species. Based on pollen morphology of the fossils, origins of morphotypes and evolutionary trends within *Sclerosperma* pollen are discussed in a time-related framework. Using detailed accounts on the climatic preferences of extant *Sclerosperma* and their current distribution in present-day vegetation biomes, we also estimate palaeoclimates endured at sites during burial of fossil *Sclerosperma* pollen. Similarly, we broadly speculate about the predominant palaeo-vegetation biomes in regions with *Sclerosperma* fossils during pollen dispersal.

2. Material and methods

2.1. Origin and preparation of sample

The fossil *Sclerosperma* pollen grains from Kenya, Africa (Fig. 1), were extracted from a silty mudstone sample, initially positioned c. 1.373 m below the surface, from core Dodori-1 (lat. 1° 48' 53.7" S, long 41° 11' 04.0" E), Lamu Basin, Kenya, Africa (Nyagah, 1995). The Dodori-1 core was drilled in 1964 to a depth of c. 4.340 m when searching for hydrocarbon reservoirs in Cretaceous and Cenozoic strata at the periphery of the Lamu Basin. The Dodori-1 core is named after a settlement in Kenya's Lamu County that is situated c. 21 km inland from the coast (Fig. 1). The sedimentary rock sample was processed, and fossil pollen was extracted according to the method explained in Grímsson et al. (2008). The fossil pollen grains were investigated with both LM and SEM using the single grain method as described by Zetter (1989) and Halbritter et al. (2018, pp. 121–123). Pollen descriptions include all morphological and diagnostic features observed with both LM and SEM. The pollen terminology follows Punt et al. (2007; LM) and Halbritter et al. (2018; LM and SEM). Part of the original sediment and the SEM stubs with the fossil pollen produced during this study are stored in the collection of the Department of Botany and Biodiversity Research, University of Vienna, Austria.

2.2. Geographic and geological background

The Lamu Basin (Fig. 1) is the largest basin in Kenya and covers a wide area (approximately 132,720 km²) extending across southeastern Kenya and into the southwestern part of Somalia (Nyaberi and Rop, 2014). The sedimentary filling comprises Permian to Cenozoic age rocks, including continental rift basin sandstones, fluvio-deltaic sandstones, marine shales, and carbonates. Nyagah (1995) divided the Mesozoic and Cenozoic sediments of the Lamu Basin into four Megasequences deposited during alternating periods of transgression and regression. Megasequence I (the Karroo Group) comprises Late Permian to Middle Jurassic age sediments. Megasequence II (the Sabaki Group) comprises strata deposited between the Late Jurassic and the Late Paleocene. Megasequence III (the Tana Group) consists of Eocene to Oligocene sediments. The Tana Group comprises, among others, the Kipini Formation and the Dodori limestone (Fig. 1) deposited during three pulses of sea-level rise and a single regressive phase. The Kipini Formation consists of interbedded nummulitic sands, poorly sorted and

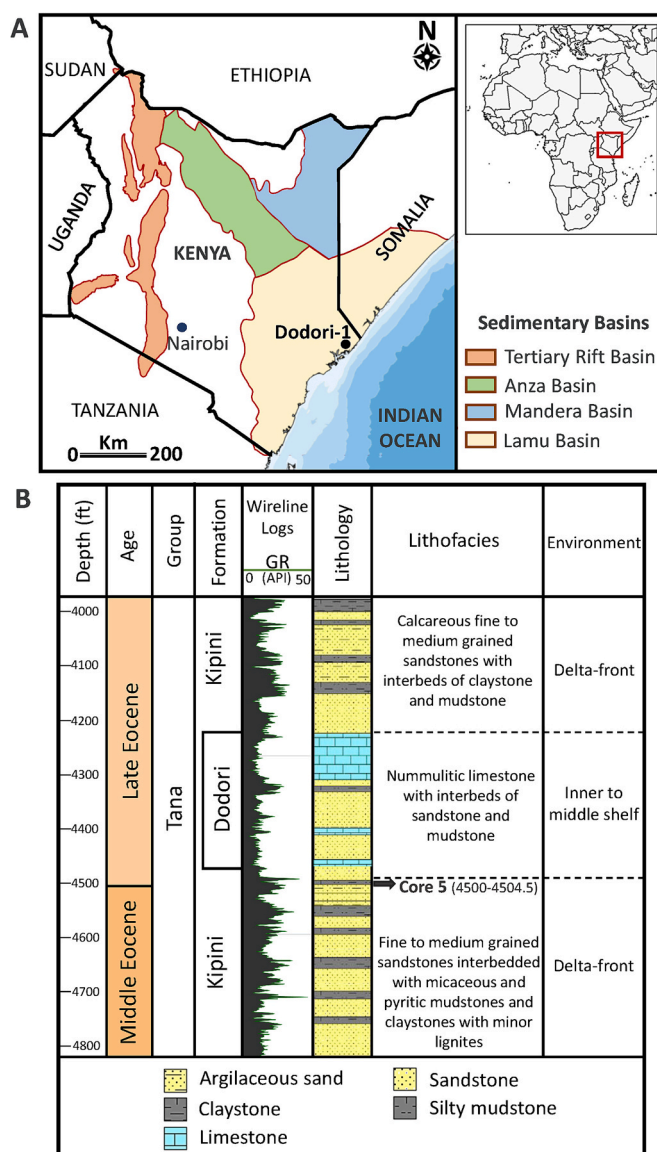


Fig. 1. Geography and geology of the sample site. A. Schematic maps showing the geographic position of the Dodori-1 well and major sedimentary basins. B. Compiled stratigraphic profile with lithofacies description and interpreted environment. Stratigraphic level of sample where the *Sclerosperma* pollen was identified is marked with an arrow (Core 5).

fine to very coarse-grained calcareous sandstones, nummulitic and micritic limestones, and dark olive-greenish grey shales and grey-green silty mudstones interpreted to have been deposited within a delta-front environment (Nyagah, 1995). The Dodori limestone is an expression of the shelf carbonate deposition that occurred in the area until the Late Eocene during a transgressive phase. The studied sample was collected from a greyish shale of the Kipini Formation, positioned just underneath the Dodori limestone (at c. 1373 m below the surface; Fig. 1). The interval where the sample containing the fossil *Sclerosperma* pollen grains was collected was assigned an earliest Late Eocene (earliest Priabonian) age (ca. ~37.71 Ma; following Cohen et al., 2013 [updated, v2022/10]) based on the consistent occurrence of the large foraminifera, *Nummulites fabianii* (from c. 1344 m upwards), as well as various species of dinoflagellate cysts (including *Cordosphaeridium fibrospinosum*) that are characteristic of the Late Eocene. The Megasequence IV (Coastal Group), resting unconformably on the Oligocene sediments of the Tana Group, constitutes the youngest sediment filling the Lamu Basin (Nyagah, 1995).

2.3. Climate/ecological data harvesting and analyses

The georeferenced distribution data for living *Sclerosperma* species were downloaded from GBIF.org (10.15468/dl.pvrnun) and compiled from literature (Supplementary Material 1). Each dataset was checked for natural distribution outliers (e.g., specimens from botanical gardens) using published chorological data (Van Valkenburg et al., 2008b; Bourobou Bourobou et al., 2016). Additionally, multiple occurrences with identical coordinates were merged, resulting in a dataset including 81 georeferenced occurrence data for the three extant *Sclerosperma* species. The revised dataset was then plotted onto 1 km² grid Köppen-Geiger maps (1979–2013 data; Cui et al., 2021) to establish Köppen

profiles for all modern species (e.g., Denk et al., 2013, 2023; Grímsson et al., 2018a; Bouchal et al., 2020). A Köppen profile reflects the proportional coverage of the various Köppen-Geiger climate zones (cf. Kottek et al., 2006; Peel et al., 2007) by a modern species based on gridded distribution data. The georeferenced data and the Köppen-Geiger maps with 1 km² resolution were processed using the ‘Sample Raster Values’ Toolbox in Qgis v.3.16.4-Hannover. The Köppen-Geiger climates occupied by extant members are shown as maps generated in Qgis and frequency (proportional distribution) diagrams (Supplementary Material 2). Excel files provide the raw data (Supplementary Material 1). We compiled climate diagrams for the three extant *Sclerosperma* species (revised data set) based on historical climate data

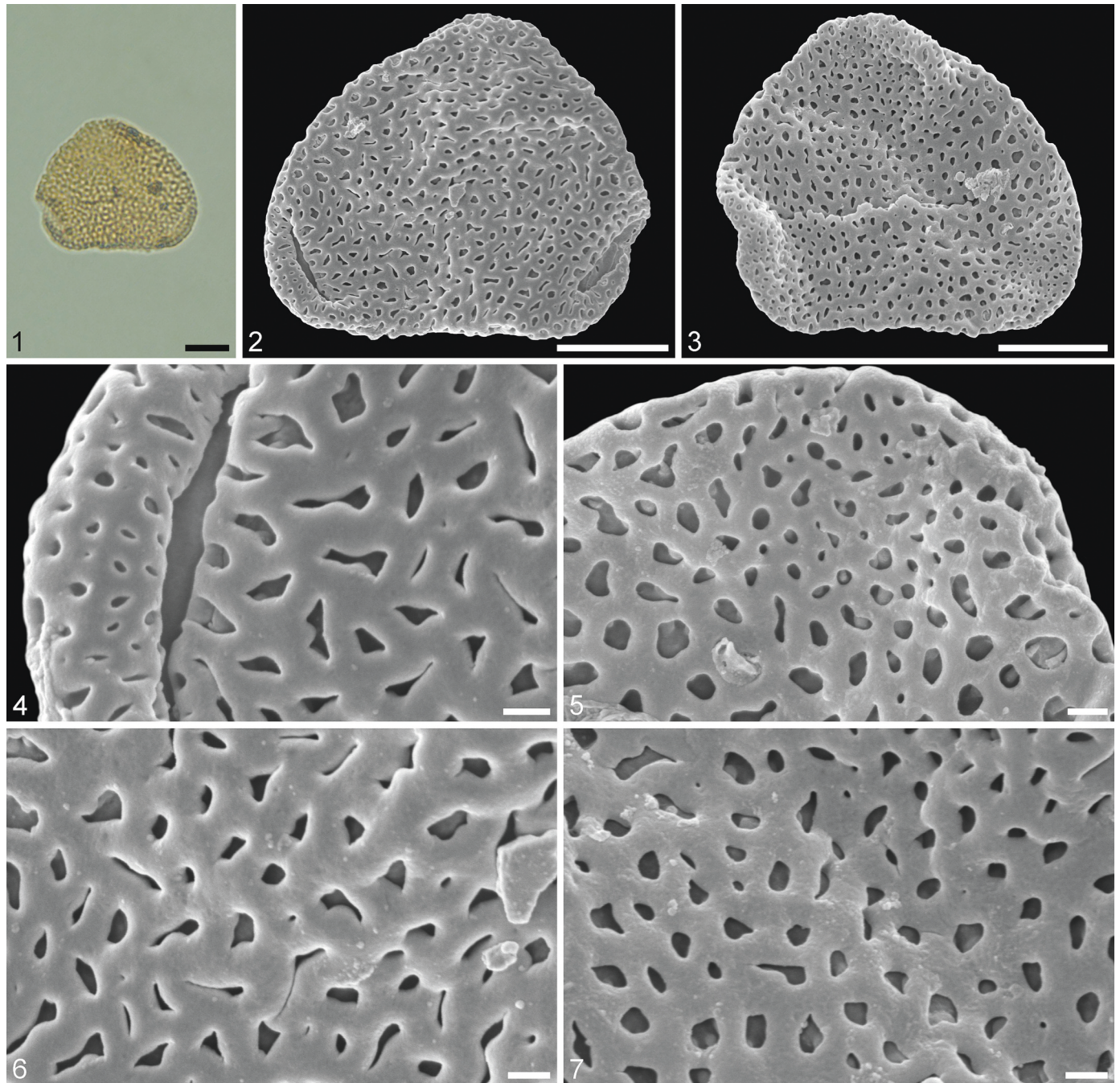


Plate I. Fossil *Sclerosperma* sp. Dodori MT 1 from Dodori, earliest late Eocene, southeast Kenya, Africa. Light microscopy (1), scanning electron microscopy (2–7) micrographs of the same pollen grain. (2). Distal face. (3). Proximal face. (4). Close up of the pores on the distal face. (5). Close-up of the apex on the proximal face. (6). Close-up of the distal central polar area. (7). Close-up of the proximal central polar area. Scale bars – 10 µm (1–2), 1 µm (4–7).

(1970–2000) using WorldClim v.2.1 (<https://www.worldclim.org/data/worldclim21.html>) at a resolution of 30s (c. 1 km²; Fick and Hijmans, 2017). The species data were normalized to avoid biases towards species with more georeferenced occurrences for the combined species climate diagram. Additionally, we compiled biome profiles for the modern species (revised data set) based on the world biome dataset of Olson et al. (2001) using the 'Intersection' Geoprocessing Tool in Qgis v.3.16.4-Hannover (Supplementary Material 2).

3. Results

3.1. Systematic and descriptive palynology

For practical reasons, the fossil pollen types are classified as morphotypes (MT's) one to five and named after the place/well where they were found.

Family: ARECACEAE Bercht, et J. Presl

Genus: *Sclerosperma* G. Mann et H. Wendt

Species: *Sclerosperma* sp. Dodori MT 1, pollen close to *S. profizianum* Type A (Plate I, Table 1).

Description: Pollen (2 grains measured), monad, heteropolar, P/E ratio oblate, outline convex-triangular in polar view; equatorial diameter 30–36 µm in LM, 29–35 µm in SEM; triporate, pori positioned sub-apically on the distal polar face, pori elliptic, 8.0–8.7 µm in diameter; exine ca. 1.9 µm thick in LM; pollen wall semitectate; sculpture reticulate in LM, microreticulate with perforations in SEM; distal face microreticulate to perforate with broad muri and polygonal to elliptic lumina or circular to slit-like perforations, 41–48 lumina per 100 µm² at central distal face; proximal face microreticulate to perforate, lumina/perforations elliptic to circular to polygonal, central polar area and mesoporum microreticulate to perforate, sculpture becoming nano-reticulate to perforate towards apices.

Remarks: Due to the flattened state of the pollen, it could not be studied in detail in equatorial view. The *Sclerosperma* sp. Dodori MT 1 pollen is comparable to the late Oligocene *S. protoprofizianum* Grímsson et R. Zetter pollen and that of extant *S. profizianum* Type A (Table 1). The Dodori MT 1 pollen differs from the late Oligocene *S. protoprofizianum* pollen in outline (being more convex), number of lumina (less per 100 µm²), and the absence of free-standing columellae. Remnants of the opercula seem to be present in one of our specimens, but the preservation does not allow a direct comparison to the opercula observed in *S. protoprofizianum* (Grímsson et al., 2019b; fig. 5I). Compared to extant *S. profizianum* Type A pollen (Grímsson et al., 2019c), the Dodori MT 1 pollen is more convex-triangular in outline and has a higher number of lumina (41–48 per 100 µm² vs. 30–35 per 100 µm²).

Species: *Sclerosperma* sp. Dodori MT 2, pollen close to *S. profizianum* Type B (Plate II, Table 1).

Description: Pollen (2 grains measured), monad, heteropolar, P/E ratio oblate, outline straight-triangular in polar view; equatorial diameter 28–36 µm in LM, 26–34 µm in SEM; triporate, pori positioned sub-apically on the distal polar face, pori circular to elliptic, 7.1–9.5 µm in diameter, pori equipped with opercula; exine 1.5–2.0 µm thick in LM; pollen wall tectate; sculpture scabrate/rugulate in LM, fossulate, rugulate and perforate in SEM, sculpture becoming finer towards apices; opercula with nanoverrucate to granulate sublayer and perforate supralayer (SEM).

Remarks: Compared to extant *S. profizianum* Type B pollen (Grímsson et al., 2019c), the Dodori MT 2 pollen exhibits a straight-triangular outline in polar view, shorter equatorial diameter, wider aperture diameter and a thinner exine. The operculum is very similar. There is a slight difference in sculpture observed with SEM, the Dodori MT 2 has a higher number of perforations that are not aligned with the fossulae, as evident in the *S. profizianum* Type B.

Species: *Sclerosperma* sp. Dodori MT 3, pollen close to *S. profizianum* Type B (Plate III, Table 1).

Description: Pollen (1 grain measured), monad, heteropolar, P/E ratio

oblate, outline straight-triangular in polar view; equatorial diameter 28–30 µm in LM, 25–27 µm in SEM; triporate, pori positioned sub-apically on the distal polar face, pori circular to elliptic, 5.0–6.7 µm in diameter, pori equipped with opercula; exine 1.3–1.4 µm thick in LM, nexine slightly thinner than sexine; pollen wall tectate; sculpture scabrate in LM, fossulate, rugulate and perforate in SEM, distal face fossulate, fossulae outlining irregularly shaped rugulae (SEM); proximal face fossulate, rugulate with scattered perforations; opercula with granulate sublayer and rugulate supralayer (SEM).

Remarks: What differentiates *Sclerosperma* sp. Dodori MT 3 from MT 2 is the high density of fossulae per 100 µm² and the presence of scattered perforations observed on the proximal face.

When compared with extant *S. profizianum* Type B pollen (Grímsson et al., 2019c) the *Sclerosperma* sp. Dodori MT 3 exhibits a straight-triangular (vs. convex-triangular) outline in polar view, a shorter equatorial diameter, a wider aperture diameter, and a thinner exine.

Species: *Sclerosperma* sp. Dodori MT 4, pollen close to *S. mannii* and *S. walkeri* (Plate IV, Table 1, Supplementary Material 3).

Description: Pollen (5 grains measured), monad, heteropolar, P/E ratio oblate, outline straight-triangular to slightly concave-triangular in polar view, bean-shaped in equatorial view; equatorial diameter 38–42 µm in LM, 32–38 µm in SEM, polar axis 21–27 µm in LM; triporate, pori positioned sub-apically on the distal polar face, pori circular, 6.4–9.5 µm in diameter; exine 1.8–3.0 µm thick in LM, nexine thinner than sexine; pollen wall semitectate; sculpture reticulate in LM, reticulate to perforate in SEM; distal face reticulate with broad muri and elliptic to triangular to polygonal lumina, 12–23 lumina per 100 µm² at central distal face, 0–3 nanogemmae free-standing columellae per lumina (SEM); proximal face reticulate to perforate, lumina/perforations elliptic to triangular to polygonal, 0–3 nanogemmae free-standing columellae per lumina; proximal central polar areas and interapertural areas reticulate, sculpture becoming microreticulate to perforate towards apices.

Remarks: *Sclerosperma* sp. Dodori MT 4 closely resembles pollen from both *S. mannii* and *S. walkeri* (Grímsson et al., 2019c). The Dodori MT 4 pollen has a longer polar axis than both *S. manni* and *S. walkeri*. There is also a difference in the outline of the pori between the three taxa, the Dodori MT 4 has circular pori but the extant pollen has elliptic pori. The fossil pollen also has fewer nanogemmae free-standing columellae per lumina compared with *S. mannii* and *S. walkeri*. Still, showing more similarity to *S. mannii* that also has less conspicuous free-standing columellae and numerous lumina without such sculpture elements.

Species: *Sclerosperma* sp. Dodori MT 5 (Plate V, Table 1).

Description: Pollen (2 grains measured), monad, heteropolar, P/E ratio oblate, outline straight-triangular in polar view; equatorial diameter 28–41 µm in LM, 26–34 µm in SEM; triporate, pori positioned sub-apically on the distal polar face, pori elliptic, 7–8.6 µm in diameter, pori equipped with opercula; exine 1.7–2.0 µm thick in LM; pollen wall tectate; sculpture verrucate in LM, verrucate to microverrucate, fossulate, and perforate in SEM, sculpture becoming finer towards apices; opercula with verrucate to nanoverrucate suprasculpture (SEM).

Remarks: *Sclerosperma* sp. Dodori MT 5 exhibits unique features not observed in any extant or fossil species of *Sclerosperma* (Grímsson et al., 2019b, 2019c), including the ones described above. However, *Sclerosperma* sp. Dodori MT 2 shows the most comparable morphology but does not exhibit the verrucate sculpture defining this morphotype, and the operculum is different.

3.2. Climatic preferences and vegetation biomes of extant *Sclerosperma*

Sclerosperma mannii occurs only in two types of Equatorial/Tropical climates, more profoundly in the Monsoonal (Am) climate but also under typical winter dry Savannah (Aw) climates (Fig. 2; Supplementary Material 2). Most of the *S. mannii* populations are concentrated in coastal areas of the Guineo-Congolian region, hence their occurrence in the Mangroves Biome. Still, most of them thrive in the Tropical &

Table 1
Pollen morphology of fossil and extant *Sclerosperma*.

	<i>Sclerosperma</i> sp. Dodory MT1	<i>Sclerosperma</i> sp. Dodory MT2	<i>Sclerosperma</i> sp. Dodory MT3	<i>Sclerosperma</i> sp. Dodory MT4	<i>Sclerosperma</i> sp. Dodory MT5	<i>S. protomannii</i>	<i>S. protoprofizianum</i>	<i>Sclerosperma</i> sp.	<i>S. mannii</i>	<i>S. profizianum</i> (Type A)	<i>S. profizianum</i> (Type B)	<i>S. profizianum</i> (Type C)	<i>S. walkeri</i>
Distribution (or locality for fossil)	Dodori-1 core (4503 ft), Kenya	Dodori-1 core (4503 ft), Kenya	Dodori-1 core (4503 ft), Kenya	Dodori-1 core (4503 ft), Kenya	Dodori-1 core (4503 ft), Kenya	Chilga, northwestern Ethiopia	Chilga, northwestern Ethiopia	Mush Valley, Ethiopia	Liberia, Nigeria, Cameroon, Equatorial Guinea, Gabon, Angola, DR Congo	Ghana, Gabon, R Congo, DR Congo, Angola (species distribution)	Ghana, Gabon, R Congo, DR Congo, Angola (species distribution)	Ghana, Gabon, R Congo, DR Congo, Angola (species distribution)	Gabon, DR Congo
Age	Late Eocene	Late Eocene	Late Eocene	Late Eocene	Late Eocene	Late Oligocene	Late Oligocene	Early Miocene	Extant	Extant	Extant	Extant	Extant
Outline polar view	Convex-triangular	Straight-triangular	Straight-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular; apices often infolded towards proximal side (hexagonal appearance)	Straight-triangular to slightly concave-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular to slightly concave-triangular	Straight-triangular to slightly concave-triangular
Outline equatorial view	/	/	/	Bean-shaped	/	Bean-shaped	Bean-shaped	/	Bean-shaped	Bean-shaped	Bean-shaped	Bean-shaped	Bean-shaped
Equatorial diameter (µm in LM)	30–36	28–36	28–30	38–42	28–41	27–38	23–35	32–37	32–38	35–40	32–38	37–42	35–40
Equatorial diameter (µm in SEM)	29–35	26–34	25–27	32–38	26–34	24–35	21–29	30–34	27–34	29–35	30–34	31–39	30–35
Polar axis (µm in LM)	/	/	/	21–27	/	9–12	9–12	/	9–15	10–14	10–13	10–16	15–19
Aperture type	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate	Triporate
Aperture position	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face	Sub-apically, distal polar face
Aperture outline	Elliptic	Elliptic	Circular to elliptic	Circular	Elliptic	Elliptic	Elliptic	Elliptic	Elliptic	Elliptic	Elliptic	Elliptic	Elliptic
Aperture diameter (µm in SEM)	8.0–8.7	7.1–9.5	5.0–6.7	6.4–9.5	7–8.6	5.5–8.0	6.0–8.0	6.6–9.0	4.5–6.0	5.0–8.5	4.0–5.5	4.0–6.5	5.0–8.0
Exine thickness (µm in LM)	ca. 1.9	1.5–2.0	1.3–1.4	1.8–3.0	1.7–2.0	1.7–2.5	1.7–2.5	1.8–2.1	1.7–2.5	1.7–2.5	1.7–2.5	1.7–2.5	1.7–2.5
Pollen wall (SEM)	Semitectate	Tectate Scabrate to rugulate	Tectate	Semitectate	Tectate	Semitectate	Semitectate to tectate	Tectate Scabrate to rugulate	Semitectate	Semitectate	Tectate	Tectate	Semitectate
Sculpture (LM)	Reticulate	Fossulate, rugulate to perforate	Scabrate	Reticulate	Verrucate Verrucate to microverrucate, fossulate, perforate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate	Rugulate Fossulate, rugulate/verrucate, perforate	Scabrate Perforate, rugulate/verrucate and fossulate Perforate,	Reticulate
Sculpture (SEM)	Microreticulate to perforate	Microreticulate to perforate	Reticulate to perforate	Reticulate to perforate	Reticulate to perforate	Reticulate to perforate	Microreticulate to perforate	Fossulate, perforate	Reticulate to perforate	Microreticulate to perforate	Fossulate with tiny circular to slit-like perforations aligned within the fossulae, sinuous	Perforations elliptic to slit-like, often aligned in sinuous rows, rows of perforations outlining irregular shaped rugulae/verrucae	Reticulate with broad muri and elliptic to triangular to polygonal lumina, 0–6 nanogemmate free-standing columellae per lumina
Sculpture distal face (SEM)	Microreticulate to perforate with broad muri and polygonal lumina or circular to slit-like perforations	Fossulate, rugulate and perforate, sculpture becoming finer towards apices	Fossulate, fossulae outlining irregular shaped rugulae	Distal face reticulate with broad muri and elliptic to triangular to polygonal lumina, 0–3 nanogemmae free-standing columellae per lumina	Verrucate to microverrucate, fossulate, perforate; sculpture becoming finer towards apices	Reticulate with broad muri and elliptic to polygonal lumina	Microreticulate to perforate with broad muri and elliptic to polygonal lumina	Reticulate with broad muri and elliptic to triangular to polygonal lumina, 0–6 nanogemmate free-standing columellae per lumina	Reticulate with broad muri and elliptic to triangular to polygonal lumina, 0–6 nanogemmate free-standing columellae per lumina	Microreticulate with broad muri and elliptic to triangular to polygonal lumina	Fossulate with tiny circular to slit-like perforations aligned within the fossulae, sinuous	Perforations elliptic to slit-like, often aligned in sinuous rows, rows of perforations outlining irregular shaped rugulae/verrucae	Reticulate with broad muri and elliptic to triangular to polygonal lumina, 0–6 nanogemmate free-standing columellae per lumina

(continued on next page)

Table 1 (continued)

	<i>Sclerosperma</i> sp. Dodory MT1	<i>Sclerosperma</i> sp. Dodory MT2	<i>Sclerosperma</i> sp. Dodory MT3	<i>Sclerosperma</i> sp. Dodory MT4	<i>Sclerosperma</i> sp. Dodory MT5	<i>S. protomannii</i>	<i>S. protoprofizianum</i>	<i>Sclerosperma</i> sp.	<i>S. mannii</i>	<i>S. profizianum</i> (Type A)	<i>S. profizianum</i> (Type B)	<i>S. profizianum</i> (Type C)	<i>S. walkeri</i>
Number of lumina / perforations at central distal face (SEM)	41–48 per 100 μm^3	Not applicable	Not applicable	12–23 per 100 μm^3	Not applicable	10–20 per 100 μm^3	lumina when present 50–65 per 100 μm^3	Not applicable	18–25 per 100 μm^2	30–35 per 100 μm^2	Not applicable	45–55 per 100 μm^2	16–25 per 100 μm^2
Sculpture proximal face (SEM)	Microreticulate to perforate, lumina/ perforations elliptic to circular to polygonal, central polar area and mesopodium microreticulate to perforate, sculpture becoming nanoreticulate to perforate towards apices	Fossulate, rugulate and perforate, sculpture becoming finer towards apices	Fossulate, rugulate with scattered perforations	Proximal face reticulate to perforate, lumina/ perforations elliptic to triangular to polygonal, 0–3 nanogemmae free-standing columellae per lumina; central polar areas and interapertural areas reticulate, sculpture becoming microreticulate to perforate towards apices	Verrucate to microverrucate, fossulate, perforate; sculpture becoming finer towards apices	Reticulate central polar area and mesopodium with elliptic to polygonal lumina, nanogemmae free-standing columellae extremely rare and singular; becoming microreticulate to perforate towards apices	Microreticulate to perforate central polar area and mesopodium with elliptic to circular to polygonal or slit-like lumina/ perforations, free- standing columellae rare, up to 4 nanogemmae free- standing columellae per lumina when present; becoming nanoreticulate to perforate towards apices		Reticulate central polar area and mesopodium with elliptic to triangular to polygonal lumina, 0–6 nanogemmae free-standing columellae per lumina; becoming microreticulate to perforate towards apices	Microreticulate central polar area and mesopodium with elliptic to circular or slit- like lumina; becoming nanoreticulate to perforate towards apices	Fossulate central polar area and mesopodium with tiny circular to slit- like perforations aligned within the fossulae, sinuous fossulae outlining irregular shaped rugulae/ verrucae; becoming micro- to nanorugulate/ verrucate and perforate towards apices	Perforate and fossulate central polar area and mesopodium, perforations elliptic to slit- like, perforations often aligned in sinuous rows, rows of perforations and fossulae outlining irregular shaped rugulae/ verrucae; becoming micro- to nanorugulate/ verrucate and perforate towards apices	Reticulate central polar area and mesopodium with elliptic to triangular to polygonal lumina, 0–6 nanogemmae free-standing columellae per lumina; becoming microreticulate to perforate towards apices
Opercula (SEM)	Not preserved	Nanoverrucate to granulate sublayer and perforate supra-layer	Granulate sublayer and rugulate supralayer	Not preserved	Verrucate to nanoverrucate suprasculpture	Sublayer not observed, but with reticulate supra-layer	Nanoverrucate to granulate sublayer and microreticulate supra-layer		Nanoverrucate to granulate sublayer and microreticulate supra-layer	Nanoverrucate to granulate sublayer and reticulate supra-layer	Nanoverrucate to granulate sublayer and perforate supra-layer	Nanoverrucate to granulate sublayer and perforate supra-layer	Nanoverrucate to granulate sublayer and microreticulate supra-layer

Note: Data on fossil pollen from this study, Grímsson et al. (2019c, 2020), and Currano et al. (2020). Data on extant pollen from Grímsson et al. (2019b).

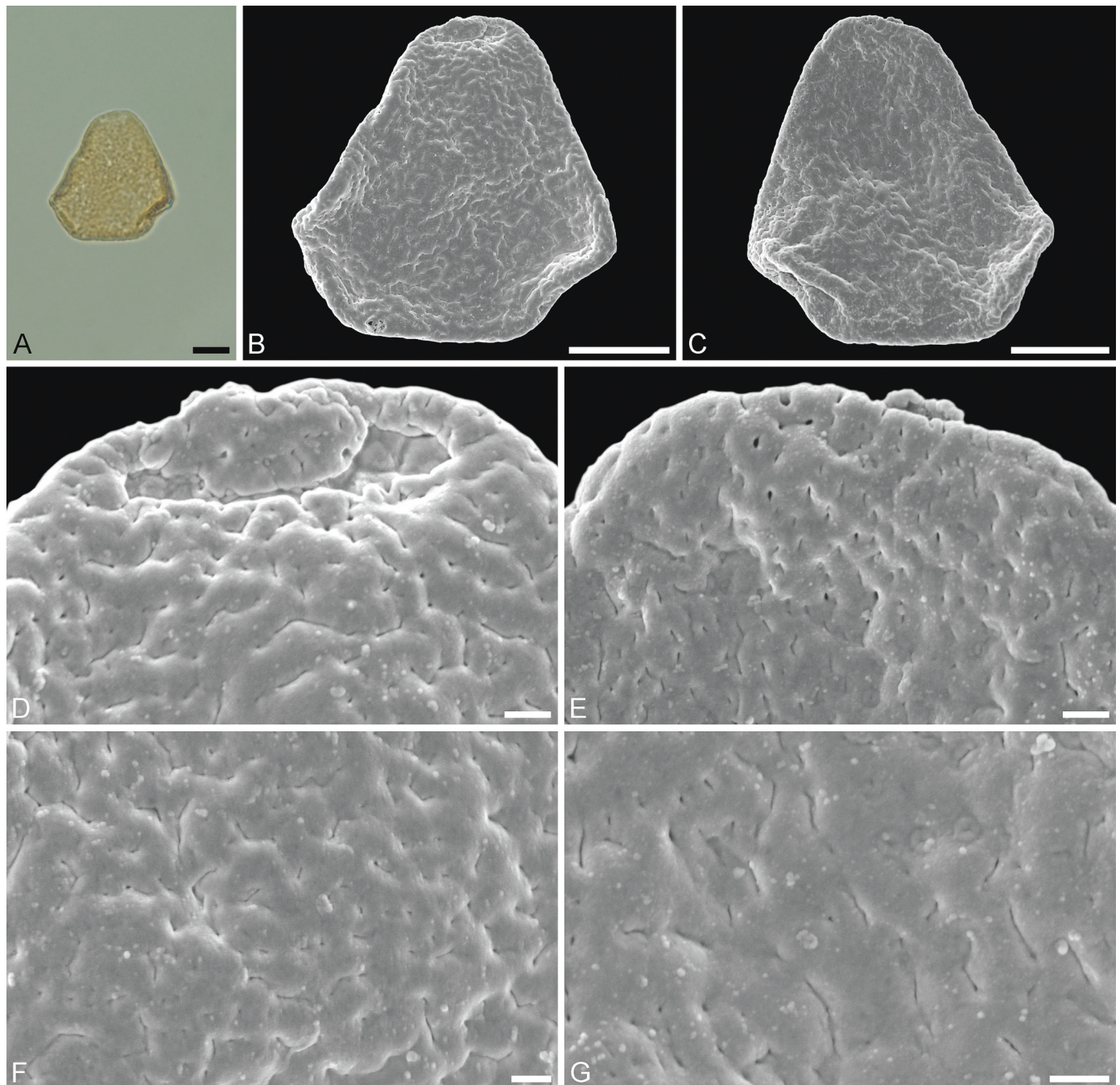


Plate II. Fossil *Sclerosperma* sp. Dodori MT 2 from Dodori, earliest late Eocene, southeast Kenya, Africa. Light microscopy (1), scanning electron microscopy (2–7) micrographs of the same pollen grain. (2). Distal face. (3). Proximal face. (4). Close up of the pores on the distal face. (5). Close-up of the apex on the proximal face. (6). Close-up of the distal central polar area. (7). Close-up of the proximal central polar area. Scale bars – 10 μm (1–3), 1 μm (4–7).

Subtropical Moist Broadleaf Forests Biome and follow waterbodies into marginal areas of the Tropical & Subtropical Grasslands, Savannahs & Shrublands Biome (Fig. 3). Despite the disjunct distribution of *S. profizianum*, the scattered populations occurring in Ghana and in the Congo Basin either endure a fully humid Rainforest (Af) or a Monsoonal (Am) climate as part of the Tropical & Subtropical Moist Broadleaf Forests Biome (Figs. 2 and 3; Supplementary Material 2). The *S. profizianum* populations occurring at the southern periphery of the Congo Basin, stretching across the Republic of the Congo, Democratic Republic of the Congo, and northern Angola, are growing under seemingly winter dry Savannah climate (Aw) (Fig. 2; Supplementary Material 2). These populations grow in the riparian areas of the Tropical &

Subtropical Grasslands, Savannahs & Shrublands Biome (Fig. 3). *Sclerosperma walkeri* predominantly occurs in Gabon and the western part of the Republic of the Congo, growing under winter dry Savannah (Aw) climate (Fig. 2; Supplementary Material 2) although concentrated in the Tropical & Subtropical Moist Broadleaf Forests Biome rather than the Grasslands, Savannah & Shrublands Biome (Fig. 3). *S. walkeri* also has minor occurrences in the central part of the Congo Basin, enduring a fully humid Rainforest (Af) climate (Fig. 2) as part of the Tropical & Subtropical Moist Broadleaf Forests Biome (Fig. 3).

In summary, all three extant *Sclerosperma* species show a similar preference regarding climate, especially the range of mean month temperatures throughout the year (Fig. 4) and vegetation biomes. All

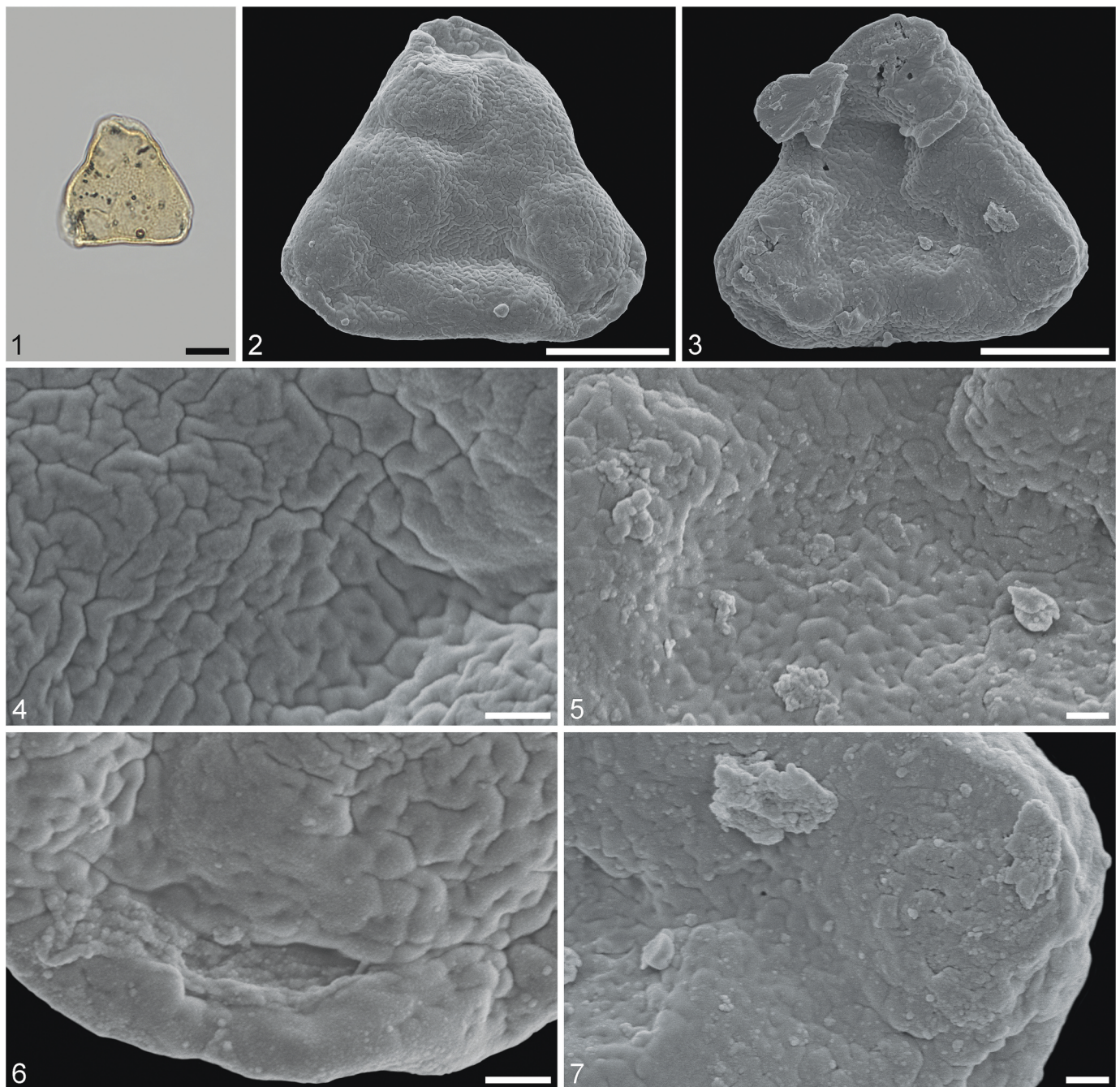


Plate III. Fossil *Sclerosperma* sp. Dodori MT 3 from Dodori, earliest late Eocene, southeast Kenya, Africa. Light microscopy (1), scanning electron microscopy (2–7) micrographs of the same pollen grain. (2). Distal face. (3). Proximal face. (4). Close-up of the distal central polar area. (5). Close-up of the proximal central polar area. (6). Close up of the porus on the distal face. (7). Close-up of the apex on the proximal face. Scale bars – 10 μm (1–3), 1 μm (4–7).

Sclerosperma populations are confined to Equatorial/Tropical climates, including fully humid Rainforest (Af), Monsoonal (Am), and winter dry Savannah (Aw) climates (Figs. 2 and 4; Supplementary Material 2). Note that in tropical Africa, where *Sclerosperma* is growing, the “coldest” months include June to August (Fig. 4) and are considered the “winter” period, hence the application of the term “winter dry Savannah (Aw) climate” above. In direct relation to the climate preferences of *Sclerosperma*, most of the populations are confined to the Tropical & Subtropical Moist Broadleaf Forests Biome, with some occurrences in riparian environments of the Tropical & Subtropical Grasslands, Savannahs & Shrublands Biome. Only *S. mannii* occurs in natural coastal wetlands of the Mangroves Biome (Fig. 3).

4. Discussion

4.1. Pollen morphology and species diversity of *Sclerosperma* through time

Surprisingly, we discovered a high morphological diversity in fossil *Sclerosperma* pollen from Kenya’s earliest Late Eocene sediments. It is evident that already c. 37 Ma, the vegetation in the Dodori region of Kenya sustained different species of *Sclerosperma*. How many is uncertain, but somewhere between three to five. As we know from living *Sclerosperma*, two species (*S. mannii* and *S. walkeri*) can produce morphologically similar pollen, and allegedly the same species (*S. profizianum*) can produce different pollen morphologies but see

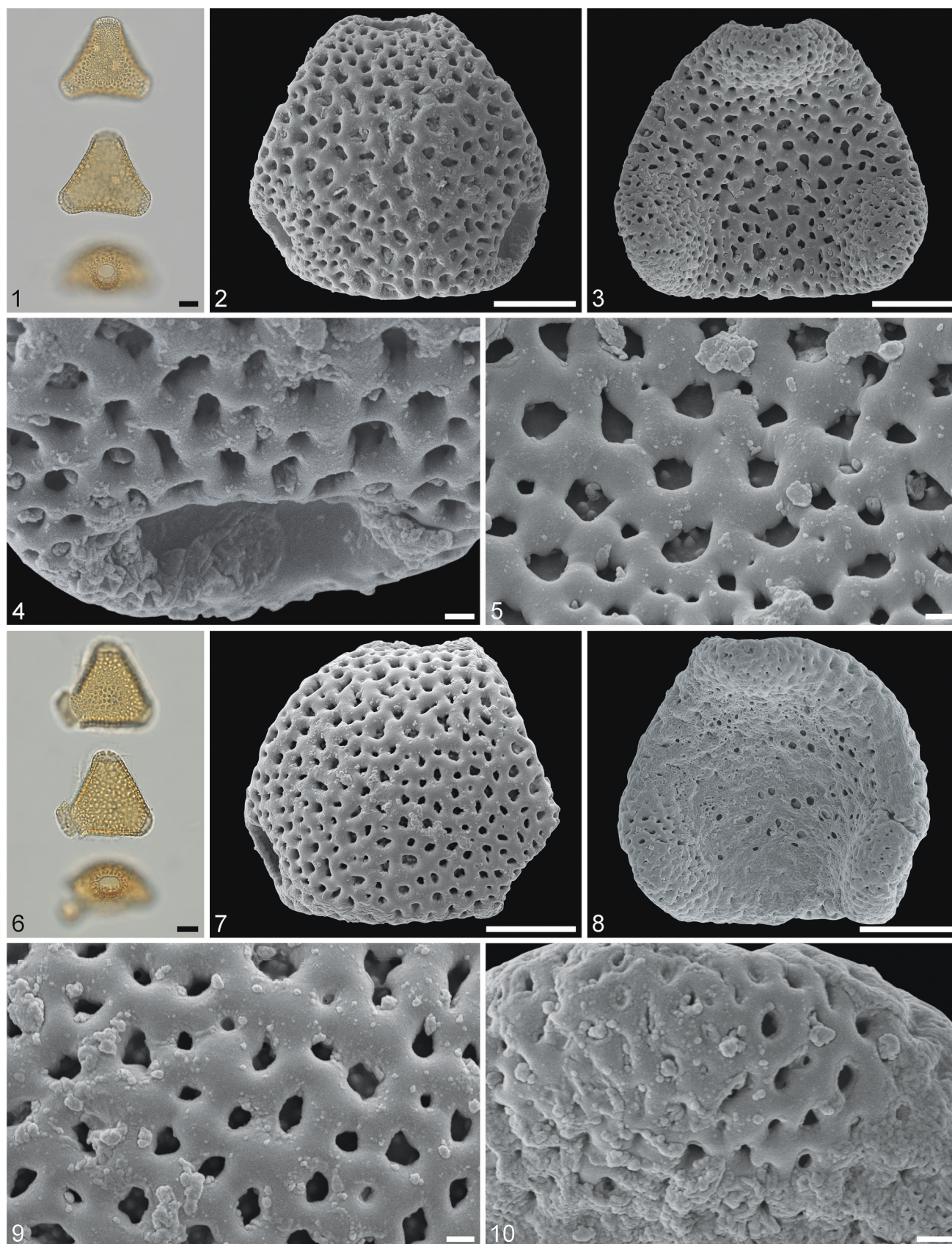


Plate IV. Fossil *Sclerosperma* sp. Dodori MT 4 from Dodori, earliest late Eocene, southeast Kenya, Africa. Light microscopy (1, 6), scanning electron microscopy (2–5, 7–10) micrographs. (1–5). Same grain. (2). Distal face. (3). Proximal face. (4). Close up of porus on the distal face. (5). Close-up of proximal central polar area. (6–10) Same grain. (7). Distal face. (8). Proximal face. (9). Close-up of the distal central polar area. (10). Close-up of the apex on the proximal face. Scale bars – 10 μ m (1–3, 6–8), 1 μ m (4, 5, 9, 10).

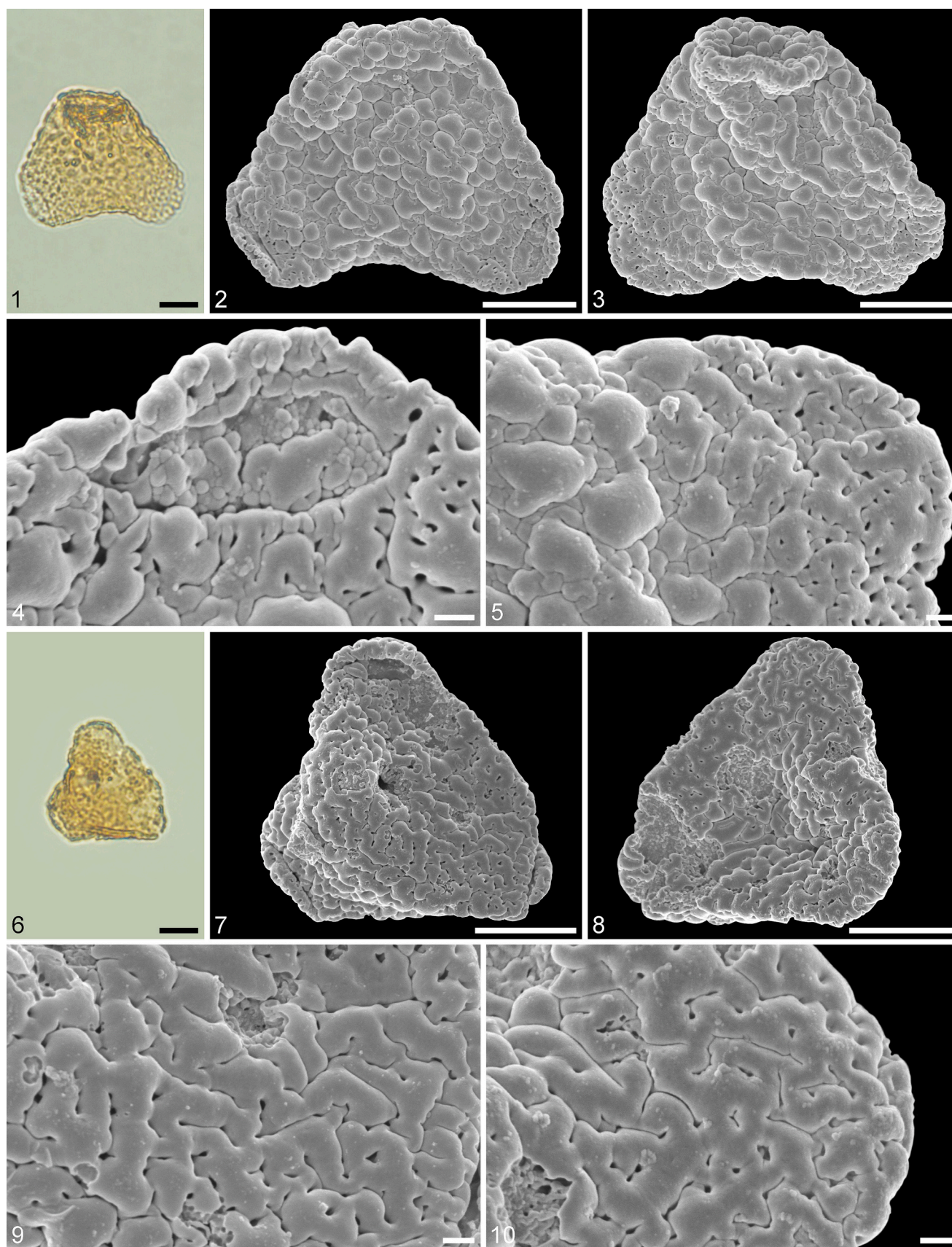


Plate V. Fossil *Sclerosperma* sp. Dodori MT 5 from Dodori, earliest late Eocene, southeast Kenya, Africa. Light microscopy (1, 6), scanning electron microscopy (2–5, 7–10) micrographs. (1–5). Same grain. (2). Distal face. (3). Proximal face. (4). Close up of the porus on the distal face. (5). Close-up of apex on the proximal. (6–10) Same grain. (7). Distal face. (8). Proximal face. (9). Close-up of the distal central polar area. (10). Close-up of the apex on the proximal face. Scale bars – 10 μ m (1–3, 6–8), 1 μ m (4, 5, 9, 10).

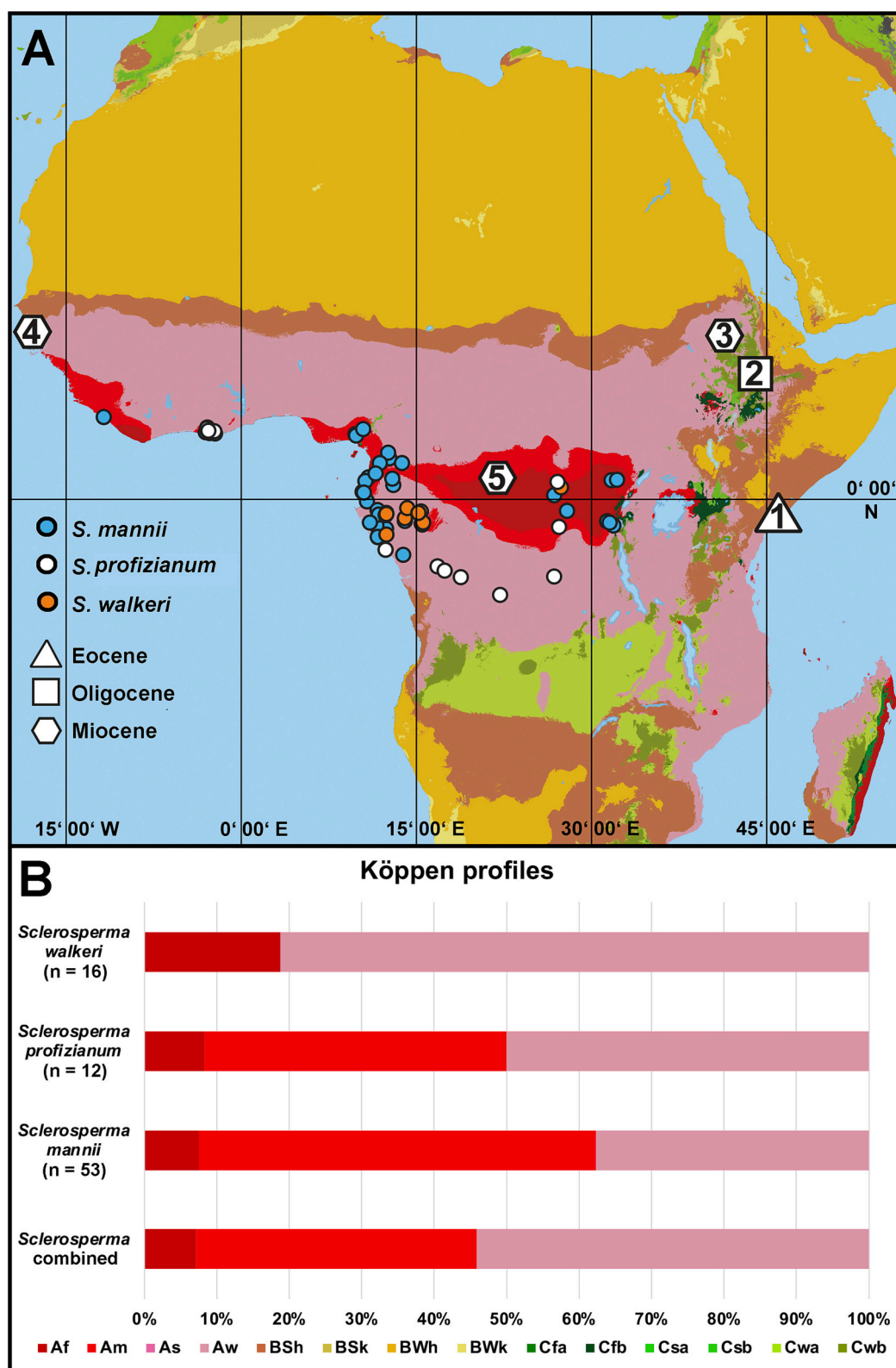


Fig. 2. Geographic distribution (A) and Köppen profiles (B) of *Sclerosperma*.

Fossil locality numbers refer to Table 2. Extant distribution of *Sclerosperma* and Köppen profiles are based on geo-referenced data provided in Supplementary Material 1. The Köppen climate classification, species distributions, and climate profiles are available in Supplementary Material 2. The climate map was generated in Qgis based on Cui et al. (2021). Af = fully humid equatorial rainforest climate, Am = equatorial monsoonal climate, As = summer dry equatorial savannah climate, Aw = winter dry equatorial savannah climate, BSh = hot arid steppe climate, BSk = cold arid steppe climate, BWh = hot arid desert climate, BWk = cold arid desert climate, Cfa = fully humid warm temperate climate with hot summer, Cfb = fully humid warm temperate climate with warm summer, Csa = summer dry warm temperate climate with hot summer, Csb = summer dry warm temperate climate with warm summer, Cwa = winter dry warm temperate climate with hot summer, Cwb = winter dry warm temperate climate with warm summer.

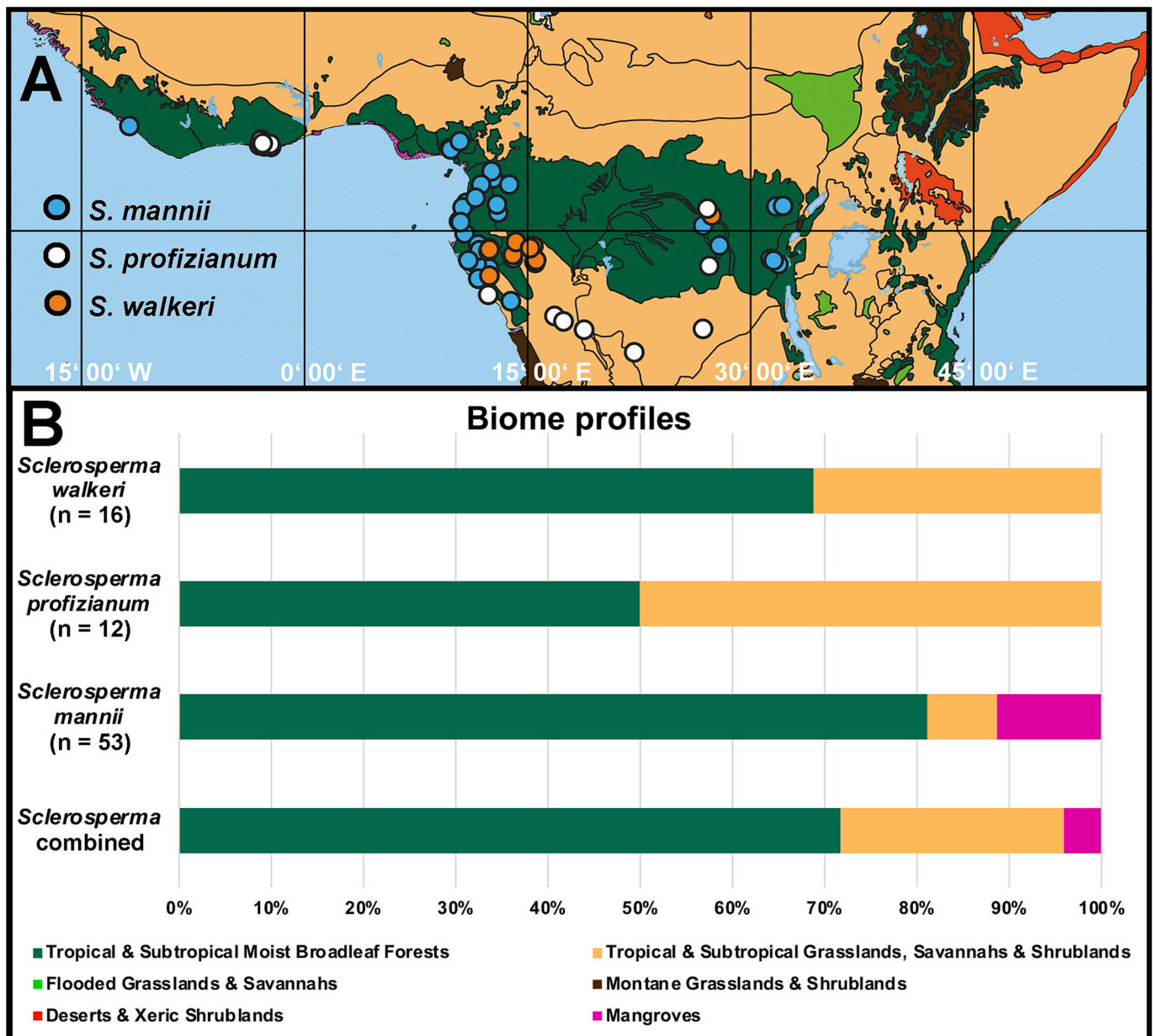


Fig. 3. Tropical African vegetation biomes (A) and Biome profiles (B) of *Sclerosperma*.

Extant distribution of *Sclerosperma* and Biome profiles (proportional occupied biomes) are based on geo-referenced data provided in Supplementary Material 1. The Biome map was generated in Qgis based on Olson et al. (2001). Biome profiles for each *Sclerosperma* species are available in Supplementary Material 2.

comments in Grímsson et al. (2019c) on the present species concepts within *Sclerosperma*. The Dodori MT 1 pollen is comparable to *S. protoprofizianum* pollen from the Late Oligocene of Ethiopia (Grímsson et al., 2019b) and to that of extant *S. profizianum* Type A (Grímsson et al., 2019c), suggesting that this pollen morphology or taxon lineage has been present in Africa since at least the Late Eocene. It is a similar scenario with the Dodori MT's 2 and 3, both pollen types are comparable to *Sclerosperma* sp. pollen from the Early Miocene of Ethiopia (Currano et al., 2020; Ulrich and Grímsson, 2020) and to pollen of extant *S. profizianum* Type B (Grímsson et al., 2019c). Insinuating that this pollen morphology/taxon lineage has also been present since the Late Eocene. The Dodori MT 4 is similar to *S. protomannii* pollen from the Late Oligocene of Ethiopia (Grímsson et al., 2019b) and comparable to extant pollen from both *S. mannii* and *S. walkeri* (Grímsson et al., 2019c). Again, suggesting that this morphology/taxon lineage has been part of the African flora since at least the Late Eocene. Considering also the Dodori MT

5, which seems unique among both fossil and extant *Sclerosperma* pollen, we determine that pollen diversity within this genus was higher in the Eocene than at present. Based on all *Sclerosperma* pollen MT's discovered so far in the fossil record (Table 1) we conclude that the genus comprised between three to five species already during the Late Eocene. These lineages seem to have survived in tropical regions of Africa during the late Paleogene and up through the Neogene and until present-day and are currently represented by at least three different species.

4.2. Palaeophytogeographic history of *Sclerosperma*

All alleged *Sclerosperma* pollen records older than Eocene and also those outside of Africa have so far been rejected by the main expert on palm pollen, Madeline M. Harley, see p. 67 in Harley and Baker (2001), p. 109 to 110 in Harley (2004), and appendix 2 in Harley (2006). Except for one, all currently accepted *Sclerosperma* fossil records (Table 2,

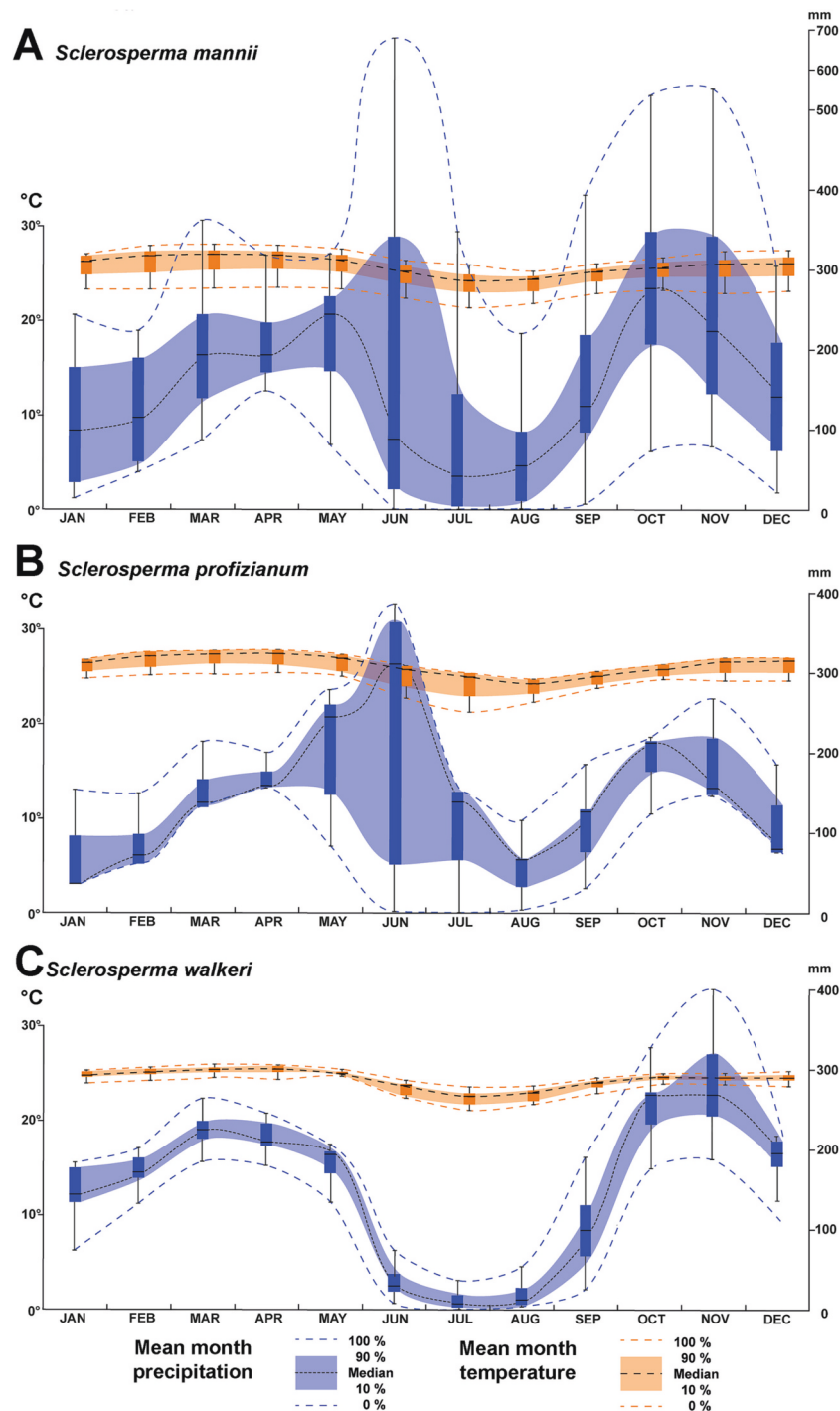


Fig. 4. Climate diagrams for extant *Sclerosperma* species.

S. mannii (n = 53), *S. profizianum* (n = 12), *S. walkeri* (n = 16). Based on raw climate data that is provided in Supplementary Material 1.

Fig. 2) appear outside the genus's present-day distribution zone. The earliest records presented here expand not only the palaeodistribution but also the stratigraphic range of this taxon considerably. It is apparent that *Sclerosperma* was already thriving along the coast of Eastern Africa during the earliest Late Eocene. We suspect these records are only remnant evidence of a much wider genus distribution across Equatorial Africa during the Eocene. This distribution would be consistent with the transcontinental extension of humid rainforests prior to the onset of the orogenic uplift of the Eastern African plateau (e.g., [Moucha and Forte, 2011](#); [Wichura et al., 2015](#)). Adding the Oligocene and the Miocene fossil records of *Sclerosperma* ([Table 2](#), *Fig. 2*), it is evident that the

tropical climate and the vegetation biomes sustaining this group during that time had a much wider latitudinal extension, when compared with the present, probably lasting until the Middle Miocene climatic optimum. Following the Middle Miocene, when orogenic uplift increased in Eastern Africa, large parts of the African realm became drier (summarized in [Wichura et al., 2015](#), fig. 4), resulting in the retreat of the pan-African rainforest. Consequently, *Sclerosperma* became restricted to the Guineo-Congolian region.

Currently, there are no records of *Sclerosperma* pollen reported outside of Africa. Based on the unique morphology of *Sclerosperma* pollen and the known Eocene American, European, and Asian floras

Table 2
Fossil record of *Sclerosperma*.

Taxon	Organ	Locality (Nr)	Age	Country	Reference
<i>Sclerosperma</i> sp. Dodori MT 1	Pollen	Dodori well (1)	late Eocene (c. 37 Ma)	Kenya	This study
<i>Sclerosperma</i> sp. Dodori MT 2	Pollen	Dodori well (1)	late Eocene (c. 37 Ma)	Kenya	This study
<i>Sclerosperma</i> sp. Dodori MT 3	Pollen	Dodori well (1)	late Eocene (c. 37 Ma)	Kenya	This study
<i>Sclerosperma</i> sp. Dodori MT 4	Pollen	Dodori well (1)	late Eocene (c. 37 Ma)	Kenya	This study
<i>Sclerosperma</i> sp. Dodori MT 5	Pollen	Dodori well (1)	late Eocene (c. 37 Ma)	Kenya	This study
<i>Sclerosperma protomannii</i>	Pollen	Guang River, Chilga (2)	late Oligocene (28–27 Ma)	Ethiopia	Grímsson et al. (2019a, figs. 3, 4, and 5A–E)
<i>Sclerosperma protoprofizianum</i>	Pollen	Guang River, Chilga (2)	late Oligocene (28–27 Ma)	Ethiopia	Grímsson et al. (2019b, figs. 5F–J and 6)
<i>Sclerosperma</i> sp.	Pollen	Mush Valley (3)	early Miocene (c. 21.73 Ma)	Ethiopia	Currano et al. (2020, figs. 4H–J), Grímsson et al. (2019c, figs. 3 and 4E–F)
<i>Sclerosperma</i> sp.	Pollen	Bignona borehole (4)	late Miocene (10–5 Ma)	Senegal	Medus (1975, pl. 4, figs. 2, 3)
<i>Sclerosperma safiannikoffii</i>	Leaves, cuticle	Mero camp (5)	?Miocene	Democratic Republic of the Congo	Lakhanpal (1966, pl. 1, fig. 1; pl. 2, fig. 1; pl. 3, figs. 1, 2)

Note: This list includes all *Sclerosperma* records verified using illustrated material (pollen, leaves, and cuticle). All other records have been excluded.

studied from several locations (e.g., Krutzsch, 1970; Muller, 1981; Graham, 1999, 2010; Song et al., 1999, 2004; Parmar et al., 2023), we postulate that this genus never dispersed outside the African continent. Even though Africa was an island during the Eocene, some plant taxa managed to disperse between Eurasia and Africa (e.g., Grímsson et al., 2018b; Grímsson et al., 2019a). This was not the case for *Sclerosperma* due to its narrow climatic preferences (strictly tropical), and we assume that the present African endemism of the genus has been the same throughout its palaeophytogeographic history.

4.3. Palaeoecological estimations based on extant *Sclerosperma* and fossil counterparts

The fossil pollen morphologies we discovered in the early Priabonian sediments from Kenya are comparable to that of modern *Sclerosperma*, suggesting survival of these lineages in tropical Africa over the last c. 37 million years. Currently, extant *Sclerosperma* strictly occurs across Equatorial/Tropical climates (Figs. 2 and 4) with a primary distribution in the Tropical & Subtropical Moist Broadleaf Forests Biome (Fig. 3). Based on this, we presume that the Dodori region endured an Equatorial/Tropical (A) climate during the early Priabonian. This assumption is further supported by the palynomorph assemblage, comprising pollen from numerous other palm taxa, including *Nypa* (F. Grímsson, pers. obs.), that is considered a typical tropical mangrove element (Reichgelt et al., 2018). Considering the geological evidence, we know that the sediments comprising the *Sclerosperma* pollen accumulated within a delta-front environment (Nyagah, 1995). Therefore, the palynoflora reflects a mixture of taxa originating from the coastal mangroves (occurrence of *Nypa* and dinoflagellate cysts), the delta plain, and the tropical forests growing along rivers towards the hinterland. This could explain the number of different *Sclerosperma* pollen morphotypes identified that likely reflect different vegetation units from where they originated. The parent plants producing the Dodori MT 4 pollen, comparable with that of *S. mannii* and *S. walkeri*, is likely to have been part of the coastal mangroves and possibly extended into the humid rainforest growing in the surrounding lowland areas. The plants producing the Dodori MT's 1–3, comparable with that of *S. profizianum*, are likely to have been part of the lowland rainforest and extending into the drier hinterland belonging to the Tropical & Subtropical Grasslands, Savannas & Shrublands Biome.

5. Conclusions and outlook

This study presents the oldest known records of the enigmatic palm genus *Sclerosperma*, a peculiar tropical wetland understory plant presently confined to the Guineo-Congolian region of Africa. The unique morphologic characters of *Sclerosperma* pollen make it easy to identify in palynofloras using only LM or combined LM and SEM. Assuming that fossil *Sclerosperma* had similar environmental requirements as extant members of the genus, one can infer tropical climates (Af, Am, Aw) for palynofloras based on their presence in the fossil assemblage. To fully understand the geographical origin and early dispersal of *Sclerosperma*, future studies must focus on Upper Cretaceous to Paleogene palynofloras from tropical Africa, a currently understudied region.

Funding

This study was not funded by any third party.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

We thank the reviewer and editor for their constructive comments that improved this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2023.104954>.

References

- Bouchal, J.M., Güner, T.H., Velitzelos, D., Velitzelos, E., Denk, T., 2020. Messinian vegetation and climate of the intermontane Florina–Ptolemais–Servia Basin, NW Greece inferred from palaeobotanical data: how well do plant fossils reflect past environments? R. Soc. Open Sci. 7, 192067 <https://doi.org/10.1098/rsos.192067>.

- Bouroubou Bouroubou, P., Niangadouma, R., Issembe, Y., Couvreur, T., 2016. Two new records of palm species for Gabon: *Sclerosperma profizianum* Valk. & Sunder. and *Eremospatha quiquecostulata* Becc. Biodivers. Data J. 4, e10187 <https://doi.org/10.3897/BDJ.4.e10187>.
- Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. (updated, v2022/10). The ICS International Chronostratigraphic Chart. Episodes 36, 199–204. <https://stratigraphy.org/ICSChart/ChronostratChart2022-10.pdf>.
- Cui, D., Liang, S., Wang, D., Liu, Z., 2021. A 1 km global dataset of historical (1979–2013) and future (2020–2100) Köppen-Geiger climate classification and bioclimatic variables. Earth Syst. Sci. Data 13, 5087–5114. <https://doi.org/10.5194/essd-13-5087-2021>.
- Curran, E.D., Jacobs, B.F., Bush, R.T., Novello, A., Feseha, M., Grímsson, F., McInerney, F.A., Michel, L.A., Pan, A.D., Phelps, S.R., Polissar, P., 2020. Ecological dynamic equilibrium in an early Miocene (21.73 Ma) forest, Ethiopia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 539, 109425.
- Denk, T., Grimm, G.W., Grímsson, F., Zetter, R., 2013. Evidence from 'Köppen signatures' of fossil plant assemblages for effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling. Biogeosciences 10, 7927–7942. <https://doi.org/10.5194/bg-10-7927-2013>.
- Denk, T., Grimm, G.W., Hipp, A.L., Bouchal, J.M., Schulze, E.-D., Simeone, M.C., 2023. Niche evolution in a northern temperate tree lineage: biogeographical legacies in cork oaks (*Quercus* section *Cerris*). Ann. Bot. 131, 769–787.
- Dransfield, J., Uhl, N.W., Asmussen, C.B., Baker, W.J., Harley, M.M., Lewis, C.E., 2008. Genera Palmarum. The Evolution and Classification of Palms. Kew Publishing, Kew.
- Erdtman, G., Sing, G., 1957. On the pollen morphology in *Sclerosperma mannii*. Bull. Jard. Bot. État Bruxelles 27, 217–220. <https://doi.org/10.2307/3666958>.
- Fick, S.E., Hijmans, R.J., 2017. WORLDCLIM2: new 1 km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.
- Graham, A., 1999. Late Cretaceous and Cenozoic History of North American Vegetation North of Mexico. Oxford University Press, New York.
- Graham, A., 2010. Late Cretaceous and Cenozoic History of Latin American Vegetation and Terrestrial Environments. Missouri Botanical Garden Press, St. Louis, Missouri.
- Grímsson, F., Denk, T., Zetter, R., 2008. Pollen, fruits, and leaves of *Tetracetrion* (Trochodendraceae) from the Cainozoic of Iceland and western North America and their palaeobiogeographic implications. Grana 47, 1–14. <https://doi.org/10.1080/00173130701873081>.
- Grímsson, F., Grimm, G.W., Potts, A.J., Zetter, R., Renner, S.S., 2018a. A Winteraceae pollen tetrad from the early Paleocene of western Greenland, and the fossil record of Winteraceae in Laurasia and Gondwana. J. Biogeogr. 45, 567–581.
- Grímsson, F., Xafis, A., Neumann, F.H., Scott, L., Bamford, M.K., Zetter, R., 2018b. The first Loranthaceae fossils from Africa. Grana 57, 249–259.
- Grímsson, F., Graham, S.A., Coiro, M., Jacobs, B.F., Xafis, A., Neumann, F.H., Scott, L., Sakala, J., Curran, E.D., Zetter, R., 2019a. Origin and divergence of Afro-Indian Picrodendraceae: linking pollen morphology, dispersal modes, fossil records, molecular dating and paleogeography. Grana 58, 227–275.
- Grímsson, F., Jacobs, B.F., Van Valkenburg, J.L., Wieringa, J.J., Xafis, A., Tabor, N., Pan, A.D., Zetter, R., 2019b. *Sclerosperma* fossils from the late Oligocene of Chilga, north-western Ethiopia. Grana 58, 81–98.
- Grímsson, F., van Valkenburg, J.L., Wieringa, J.J., Xafis, A., Jacobs, B.F., Zetter, R., 2019c. Pollen morphology of the African *Sclerosperma* (Arecaceae). Grana 58, 99–113.
- Halbritter, H., Ulrich, S., Grímsson, F., Weber, M., Zetter, R., Hesse, M., Buchner, R., Svojtka, M., Frosch-Radivo, A., 2018. Illustrated Pollen Terminology, 2nd edn. Springer, Vienna, Austria.
- Harley, M.M., 1996. Palm Pollen and the Fossil Record. PhD Thesis, University of East London, London, UK.
- Harley, M.M., 1999. Tetrad variation: Its influence on pollen form and systematics in the Palmae. In: Kurmann, M.H., Hemsley, A.R. (Eds.), Evolution of Plants Architecture. Kew Publishing, Kew, UK, pp. 289–304.
- Harley, M.M., 2004. Triaperturate pollen in the monocotyledons: configurations and conjectures. Plant Syst. Evol. 247, 75–122. <https://doi.org/10.1007/s00606-003-0107-x>.
- Harley, M.M., 2006. A summary of fossil records for Arecaceae. Bot. J. Linn. Soc. 151, 39–67. <https://doi.org/10.1111/j.1095-8339.2006.00522.x>.
- Harley, M.M., Baker, W.J., 2001. Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of the fossil record of palm-like pollen. Grana 40, 45–77. <https://doi.org/10.1080/00173130152591877>.
- Harley, M.M., Dransfield, J., 2003. Triporate pollen in the Arecaceae. Grana 42, 3–19. <https://doi.org/10.1080/00173130310008535>.
- Harley, M.M., Hall, D.H., 1991. Pollen morphology of the African palms. Palaeoecol. Afr. 22, 11–25.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. Meteorol. Z. 15, 259–263.
- Krutzsch, W., 1970. Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen-sowie der Mikroplanktonformen des nördlichen Mitteleuropas VII. VEB Gustav Fischer Verlag, Jena, Germany.
- Lakhanpal, R.N., 1966. Some middle Tertiary plant remains from South Kivu, Congo. Annales du Musée Royal de l'Afrique Centrale Serie 8 (52), 21–30.
- Medus, J., 1975. Palynologie de sédiments Tertiaires du Sénégal méridional. Pollen et Spores 17, 545–601.
- Moucha, R., Forte, A., 2011. Changes in African topography driven by mantle convection. Nat. Geosci. 4, 707–712. <https://doi.org/10.1038/ngeo1235>.
- Muller, J., 1981. Fossil pollen records of extant Angiosperms. Bot. Rev. 47, 1–142.
- Nyaberi, M.D., Rop, B.K., 2014. Petroleum prospects of Lamu Basin, South-Eastern Kenya. J. Geol. Soc. India 83, 414–422.
- Nyagah, K., 1995. Stratigraphy, depositional history and environments of deposition of Cretaceous through Tertiary strata in the Lamu Basin, southeast Kenya and implications for reservoirs for hydrocarbon exploration. Sediment. Geol. 96, 43–71.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.L., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecosystems of the world: a new map of life on Earth. BioScience 51, 933–938.
- Parmar, S., Morley, R.J., Banal, M., Singh, B.P., Morley, H., Prasad, V., 2023. Evolution of Arecaceae in the Indian Plate modulated by Early Palaeogene climate and tectonics. Rev. Palaeobot. Palynol. 313, 104890.
- Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>.
- Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., Le Thomas, A., 2007. Glossary of pollen and spore terminology. Rev. Palaeobot. Palynol. 143, 1–81. <https://doi.org/10.1016/j.revpalbo.2006.06.008>.
- Reichgelt, T., West, C.K., Greenwood, D.R., 2018. The relation between global palm distribution and climate. Sci. Rep. 8, 4721. <https://doi.org/10.1038/s41598-018-23147-2>.
- Song, Z.-C., Zheng, Y., Li, M., Zhang, Y., Wang, W., Wang, D., Zhao, C., Zhou, S., Zhu, Z., Zhao, Y., 1999. Fossil Spores and Pollen of China, vol 1: The Late Cretaceous and Tertiary Spores and Pollen. Science Press, Beijing.
- Song, Z.-C., Wang, W.-M., Huang, F., 2004. Fossil pollen records of extant angiosperms in China. Bot. Rev. 70, 425–458.
- Ulrich, S., Grímsson, F., 2020. The single-grain method: adding TEM to the equation. Grana 59, 44–57. <https://doi.org/10.1080/00173134.2019.1666915>.
- Van Valkenburg, J.L.C.H., Sunderland, T.C.H., Couvreur, T.L.P., 2008a. A revision of the genus *Sclerosperma* (Arecaceae). Kew Bull. 63, 75–86. <https://doi.org/10.1007/s12225-007-9002-x>.
- Van Valkenburg, J.L.C.H., Sunderland, T.C.H., Couvreur, T.L.P., 2008b. A revision of the genus *Sclerosperma* (Arecaceae). Kew Bull. 63, 75–86.
- Wichura, H., Jacobs, L.L., Lin, A., Polcyn, M.J., Manthi, F.K., Winkler, D.A., Strecker, M. R., Clemens, M., 2015. A 17-My-old whale constrains onset of uplift and climate change in East Africa. PNAS 112, 3910–3915.
- Zetter, R., 1989. Methodik und Bedeutung einer routinemäßig kombinierten lichtmikroskopischen und rasterelektronenmikroskopischen Untersuchung fossiler Mikroflora. Cour. Forsch. Inst. Senckenberg 109, 41–50.