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Late Cretaceous (Turonian) angiosperm pollen from Tanzania: a glimpse of past vegetation from a warmer climate

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ABSTRACT

Exceptionally well-preserved palynomorphs were recovered from a Turonian section cored in Tanzania. Here we provide an in-depth evaluation of the terrestrial palynomorph assemblages recovered, discuss their environmental affinity, and provide taxonomic descriptions for seventeen angiosperm species. Forms present include various species of *Liliacidites*, *Tricolpites*, *Tricolporites*, *Tetracolpites*, *Syncolporites*, *Triporopollenites*, *Hexaporotricolpites*, and *Periporopollenites*. In addition to these angiosperm species, the palynological assemblage is dominated by gymnosperm genera that include *Classopollis*, *Ephedripites*, and *Exesipollenites*. This assemblage and the rarity of humidity-dependent bryophytes and pteridophytes clearly support the hypothesis that the Turonian climate in Tanzania was warm and relatively dry.

KEYWORDS

Angiosperms; climate; Cretaceous; gymnosperms; Tanzania; Turonian;

1. Introduction

Studies of exceptionally well preserved microfossils extracted from Turonian marine mudstones during the Cretaceous Tanzania Drilling Project (TDP) have provided many new insights on the taxonomy, evolution, biostratigraphy, and paleobiology of microfossil assemblages and the evolution of subtropical ocean temperatures (Jiménez Berrocoso et al. 2010; 2012, 2015; MacLeod et al. 2013; Wendler et al. 2013, 2016; Wendler and Bown 2013; Haynes et al. 2015; Huber et al. 2017). Key reasons for the excellent preservation of the Tanzanian microfossil *lagerstätte* have been linked to sedimentary factors controlling microbial activity and pore water chemistry (Haynes et al. 2017). Turonian palynofloras first documented in Haynes et al. (2017) and discussed herein in greater details are from two Turonian boreholes (TDP Sites 31 and 36) that range from the early Turonian through early Coniacian (~4.6 m.y.) and are stratigraphically continuous except for a brief (0.4–0.8 m.y.) hiatus in the late Turonian (Huber et al. 2017). The detailed stratigraphic and taxonomic analysis of terrestrial palynomorph assemblages in the present study provides the basis for in-depth interpretations of the changes in the regional terrestrial ecosystems.

The taxonomic analysis proposed here 2 is based on the work of Jarzen (1981) who identified 15 miospore taxa from the Upper Jurassic to Lower Cretaceous Saurian Beds at Tendaguru Hill in Tanzania. Jarzen's work suggested that the climate at the time of deposition (possibly Late Jurassic or Early Cretaceous) was likely warm and dry, and that the Tendaguru Hill site was not far from the ancient African coast. Few angiosperms were

reported in the study (Jarzen 1981), but those found included *Eucommidites*, *Clavatipollenites*, tricolpate, and stephanocolpate forms. Later, Schrank (1999) described terrestrially-derived palynomorphs from middle Saurian Beds and overlying Smeei Beds of Kimmeridgian to Tithonian age, providing a second reference for the Mesozoic palynomorphs from Tanzania.

In our study, gymnosperms are abundant, but rare specimens of a diverse suite of angiosperm pollen are also present among the well-preserved microfossils recovered from TDP Site 31 and TDP Site 36. Seventeen angiosperm pollen taxa, not previously described, coupled with habitat inferences suggested by the abundant gymnosperm palynomorphs, provide a basis for a better understanding of the terrestrial environmental conditions at the time of deposition.

2. Geology and locality

The Mesozoic and Cenozoic geologic evolution of southeastern Tanzania is dominated by rifting and passive margin deposition related to the breakup of Gondwana that began in the Permian and resulted in the subsequent formation and growth of the Indian Ocean (Kent et al. 1971; Nicholas et al. 2007). However, shifting positions of rifting centers as well as intervals of transform motion and more recent compressional stress resulted in a sedimentary record with more complexity than an Atlantic style passive margin. The Upper Jurassic and Lower Cretaceous deposits in the region are largely terrestrial to marginal marine in character, including the famous dinosaur-bearing Tendaguru Formation (Janensch 1914; Aberhan et al. 2002; Bussert et al. 2009; Heinrich et al. 2011). Sediments at

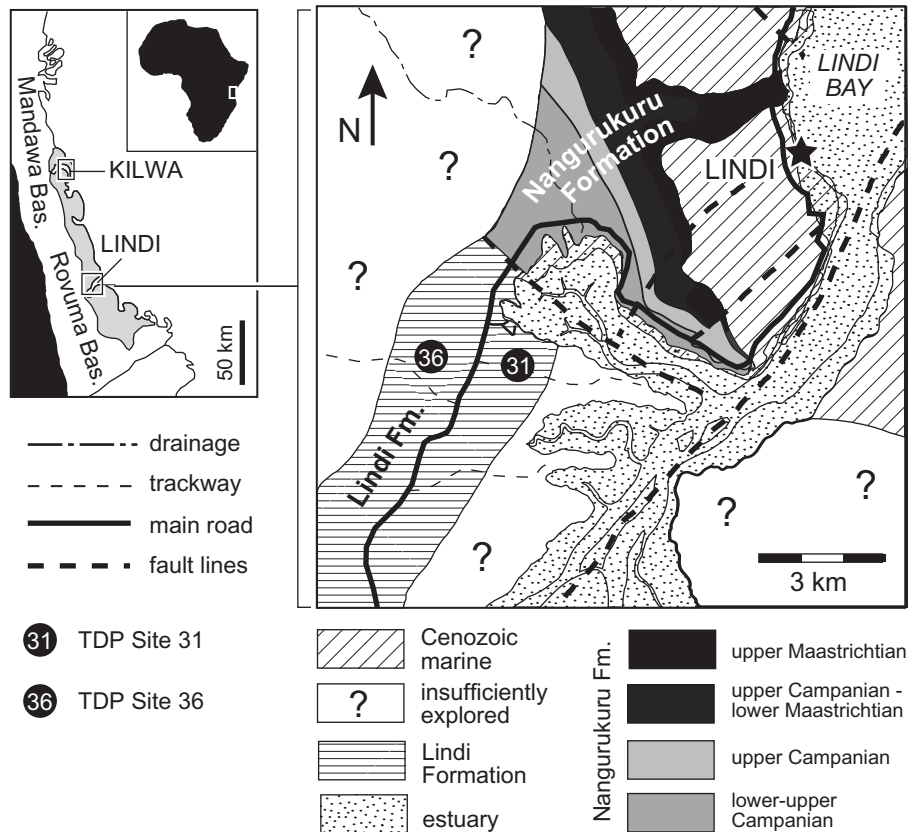


Figure 1. Location map of study region in southeast Tanzania (from Haynes et al. 2017, modified from Jiménez Berrocoso et al. 2010). TDP—Tanzania Drilling Project.

Tendanguru were deposited in the Mandawa Basin as a result of sea level changes in the Late Jurassic–Early Cretaceous (Aberhan et al. 2002; Bussert et al. 2009). Late Cretaceous–Miocene deposits, on the other hand, preserved marine fossils and sedimentary features typical of outer shelf to slope-style environments, that have experienced only shallow burial depths. These deposits commonly include exceptionally well-preserved calcareous microfossils, palynomorphs, and organic compounds such as lipids (e.g. Pearson et al. 2001; van Dongen et al. 2006; Wendler et al. 2016; Haynes et al. 2017). The younger Cretaceous–Miocene sediments accumulated in the Revuma and Mandawa basins, with deposition initiated by accelerated regional subsidence during the Cretaceous (Nicholas et al. 2006, 2007).

The palynomorphs discussed here were extracted from samples collected from two sites drilled by the Tanzania Drilling Project (TDP) near Lindi in southeastern coastal Tanzania (Figure 1). The primary site studied, TDP Site 31, was drilled in 2008 (Jiménez Berrocoso et al. 2012) with complementary samples from a second site, TDP 36, drilled in 2009 (Jiménez Berrocoso et al. 2015). Sediments recovered from TDP Sites 31 and 36 are part of the Cretaceous Lindi Formation (upper Albian–Coniacian), which is the basal unit of the Kilwa Group (Jiménez Berrocoso et al. 2015). The Lindi Formation conformably underlies the Upper Cretaceous (Santonian–Maastrichtian) Nangurukuru Formation and overlies the Lower Cretaceous Kingongo Marls (Nicholas et al. 2006; Jiménez Berrocoso et al. 2015). The upper contact (between the Lindi Formation and the Nangurukuru Formation) is gradational, whereas the nature of the contact

between the Lindi Formation and underlying Kingongo Marls is not well resolved by existing data. Specifically, incomplete recovery in cores, lack of outcrop control, structural complications, and poor age control for relevant samples compromises interpretations. Alternative interpretations include a conformable contact in Albian sediments and a hiatus locally spanning much or all of the Cenomanian (Jiménez Berrocoso et al. 2015).

TDP Sites 31 and 36 are dominantly Turonian and have been targeted for study due to the excellent preservation of microfossils present as well as, at TDP Site 31, a relatively long, continuous and well-recovered section. These attributes motivated a number of studies on calcareous microfossil systematics, biostratigraphy, and paleoceanography (MacLeod et al. 2013; Wendler and Bown 2013; Wendler et al. 2013, 2016; Huber and Petrizzo 2014; Haynes et al. 2015, 2017; Huber et al. 2017). The lithology at TDP Site 31 ($10^{\circ}1'49.80''S$, $39^{\circ}38'44.00''E$) consists of olive to gray and black marine claystones and siltstones that are generally finely bedded or laminated (Jiménez Berrocoso et al. 2012). The borehole was cored to 115 m and ranges from the lower to mid-Turonian foraminiferal *Helvetoglobotruncana helvetica* Zone up to the lower Coniacian *Dicarinella concavata* Zone (Figure 2; Jiménez Berrocoso et al. 2012; Huber and Petrizzo 2014; Huber et al. 2017). Sediments recovered from TDP Site 36 ($10^{\circ}1'45.36''S$, $39^{\circ}38'12.42''E$) typically consist of interbedded claystones and sandy siltstones and commonly contain laminated intervals (Jiménez Berrocoso et al. 2015). This borehole was cored to 98 m and ranges from the lower/mid-Turonian

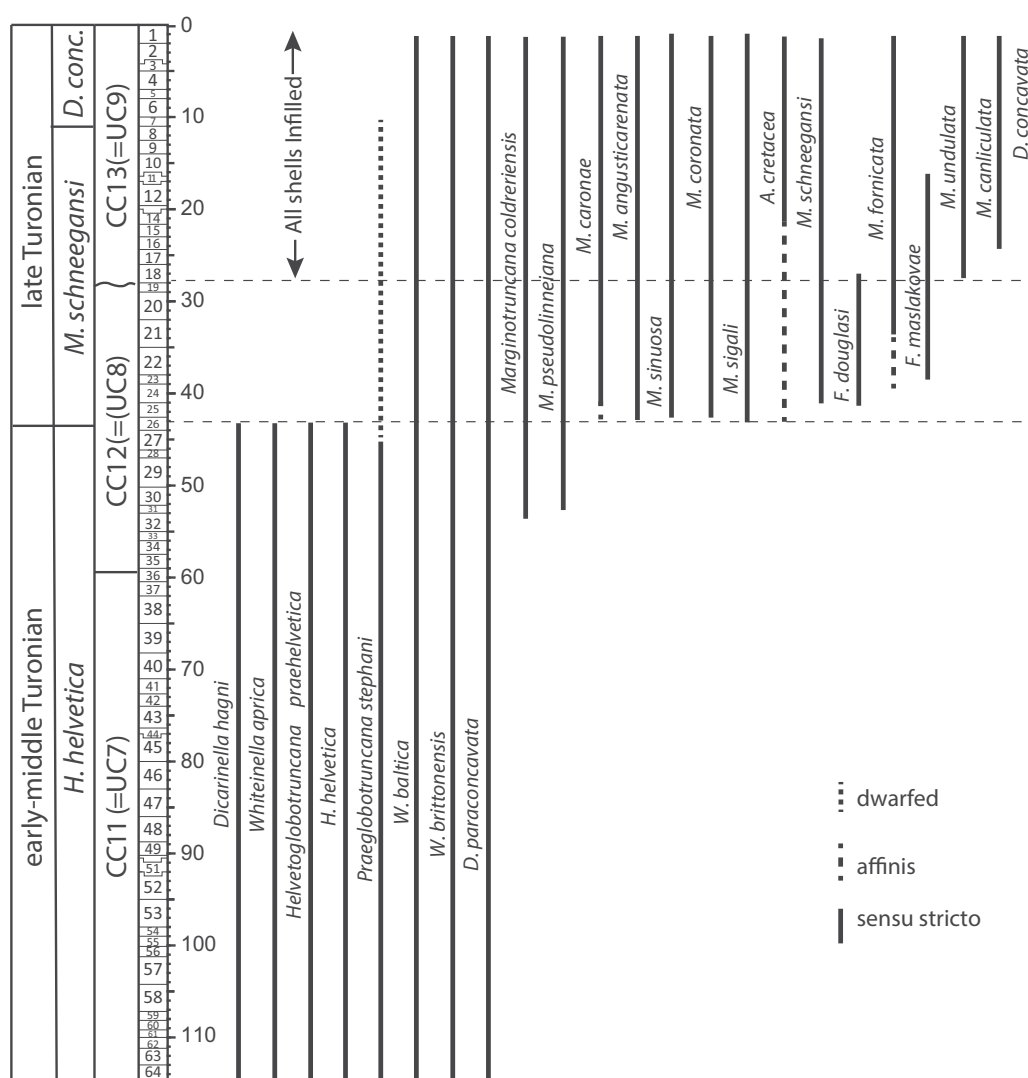


Figure 2. Biostratigraphic chart summarizing the ranges of key common trochospiral planktic foraminifera species recovered at Tanzania Drilling Project (TDP) Site 31. For full biostratigraphy of non-biserial planktic foraminifera for TDP Site 31, refer to Huber et al. (2017). Abbreviations are as follows: A.—*Archaeoglobigerina*, D.—*Dicarinella*, F.—*Falsotruncana*, H.—*Helvetoglobotruncana*, M.—*Marginotruncana*, and W.—*Whiteinella*, CC—Cretaceous Coccolith zonation of Perch-Nielsen (1985), and UC—Upper Cretaceous zonation (from Haynes et al. 2017).

upper *Whiteinella archaeocretacea* Zone through the mid-Turonian *H. helvetica* Zone (Jiménez Berrocoso et al. 2015; Huber et al. 2017).

TDP Site 31 contains the most complete record of the Turonian yet recovered in Tanzania; however, the nannofossil distribution indicates that there is a possible hiatus spanning up to ~0.4 m.y. between cores 18 and 19 in the upper portion of the section (Haynes et al. 2017; Huber et al. 2017). The excellent preservation of foraminifera, calcareous nannofossils, calcareous dinoflagellate cysts, organic carbon compounds, and palynomorphs found in most of the section generally declines across the proposed hiatus (Haynes et al. 2017). This shift in preservation has been attributed to changes in local depositional conditions that have been associated with evidence for increased early diagenetic microbial activity in the upper cores from this section (Haynes et al. 2017). This shift notwithstanding, biomarkers in well-preserved intervals suggest minimal thermal alteration and an organic sedimentary budget dominated by terrestrial input, particularly long-chained *n*-alkanes derived from leaf waxes. Consistent with the dominant terrestrial input among

biomarkers, pollen and spores dominate over dinoflagellate cysts and other marine palynomorphs.

3. Methods and materials

A total of 24 samples were processed for palynological evaluation. Twenty of these samples are from TDP Site 31 and 4 samples are from TDP Site 36 (see Table 1 for sampling distribution and depths). Samples were dried, weighed and spiked with a known quantity of *Lycopodium* spores prior to processing to allow for concentration computation following the procedures outlined in Stockmarr (1971). The samples were treated with hydrochloric (HCl) and hydrofluoric (HF) acids and washed to neutrality. To extract the palynomorphs from the remaining organic fraction, the residue underwent heavy liquid separation using zinc bromide (ZnBr₂) and was sieved through a 10 µm mesh sieve (Brown 2008). The final residue was mounted on standard microscope slides using glycerine jelly.

Recovery in all but three samples was excellent and, a minimum of 300 palynomorphs was counted per sample.

Table 1. Sample distribution, concentration, and relative abundance (%) of palynomorphs at TDP Sites 31 and 36.

Palynological samples	SITES																							
	TD 31																							
Sample name	1	2	3	4	5	7	8	9	10	11	13	14	16	17	18	19	20	21	22	23	24	25	12	15
Sample depth	4-1	10-2	17-2	20-1	24-1	27-1	29-3	32-1	38-3	42-2	45-1	46-1	47-2	51-2	53-1	55-1	57-2	61-1	63-1	64-2	39-3	40-2	45-1	46-2
Marine cc	5.05	15.12	25.89	29.01	39.19	44.55	49.52	53.19	64.05	73.32	77.10	80.01	84.76	91.47	95.10	99.11	102.25	109.78	111.70	114.04	91.51	93.01	106.25	108.59
Terrestrial cc	0	0	2498	1284	380	123	605	503	248	2528	0	1694	557	191	835	683	1711	755	913	175	174	765	538	0
ratio (%) marine vs. ter.	0	0	17600	7575	4769	8072	12709	4558	13516	6807	0	11267	7172	7642	2592	7336	12060	8166	5648	11547	28319	10540	6709	170537
Dinocysts and Acritarchs	0	0	0	3	2	0	0	0	0	1	0	1	1	1	0	3	2	2	5	0	0	1	1	0
Spiniferites spp.	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dinogymnium sp.	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Florentinia sp.	0	0	2	1	0	0	1	3	1	18	0	6	5	2	9	4	6	2	2	1	0	0	1	0
Veyachium sp.	0	0	0	0	1	0	1	4	0	0	0	1	1	1	1	0	2	4	3	0	0	3	2	0
All spores	0	0	15	3	4	4	1	2	2	1	0	2	1	2	3	0	1	0	2	2	2	2	4	0
Bryophytes and Pteridophytes	0	0	35	10	11	36	3	7	1	5	0	4	3	9	5	6	3	9	9	2	4	3	10	1
Gymnosperms	0	0	17	39	45	6	14	24	23	25	0	28	15	38	29	40	41	30	30	22	21	28	31	97
Ephedripites group	0	0	0	5	14	5	61	23	63	25	0	37	61	21	26	34	32	35	28	53	57	49	28	0
Classopollis sp.	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Exesporites sp.	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other coniferous pollen	0	0	1	3	2	7	3	4	2	1	0	2	2	2	1	1	2	1	1	4	1	1	2	0
Hexaparticolpites sp.	0	0	9	19	10	23	13	22	7	11	0	12	8	22	10	9	8	13	12	13	11	5	18	0
All periporate grains	0	0	13	15	11	20	3	10	2	12	0	6	3	5	9	3	3	4	6	2	2	3	6	5
All other angiosperms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Identification and description of the palynomorphs was carried out using an Olympus BX 41, or Leitz Dialux 20, transmitted light microscope at the Center for Excellence in Palynology (CENEX), Louisiana State University, Baton Rouge, Louisiana, and the Paleobotany Paleoecology Laboratory, Cleveland Museum of Natural History, Cleveland, Ohio. The results were tabulated in Microsoft Excel™ spreadsheets and plotted on biostratigraphic distribution charts with StrataBugs™ software (see Haynes et al. 2017 for charts). Angiosperm palynomorph types discussed in this paper are illustrated in Plate 1. Unused portions of the samples, processed residues, and slides are stored at the Louisiana State University (LSU) Center for Excellence in Palynology (CENEX), LSU Museum of Natural History, Baton Rouge, Louisiana, USA.

Palynomorph concentrations were calculated as follows:

$$cc = (P_c \times L_t \times T) / (L_c \times W)$$

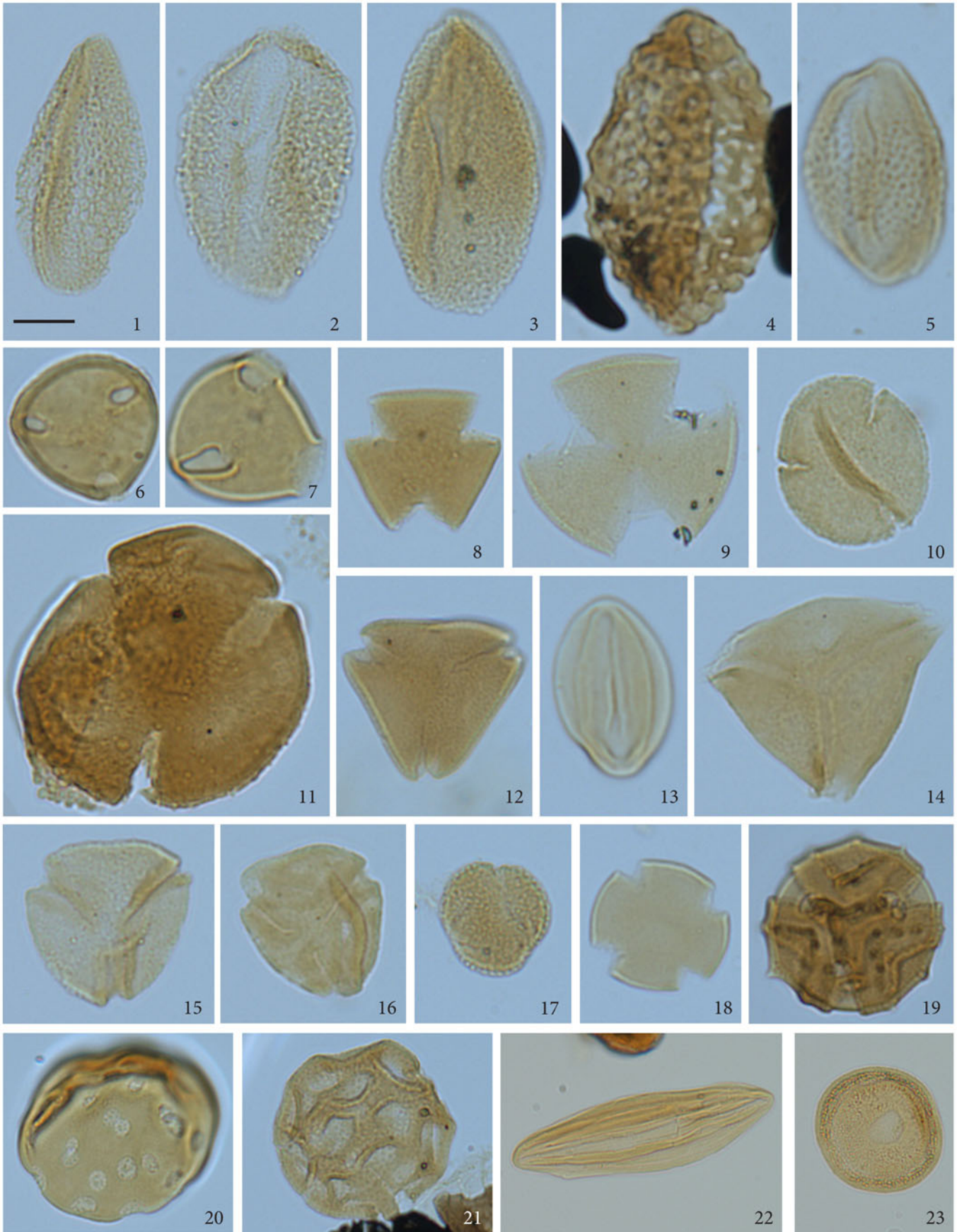
where cc = concentration per gram of dried sediment (gdw^{-1}), P_c = the number of palynomorphs counted, L_t = the number of *Lycopodium* spores per tablet, T = the total number of *Lycopodium* tablets added per sample, L_c = the number of *Lycopodium* spores counted, W = the weight of dried sediment.

A detailed and comprehensive account of all palynomorphs recovered from the cores is not the intent of nor is it within the scope of this paper. The following systematic section includes only the angiosperm pollen recovered and identified. They are classified here according to the system proposed by Potonié (1960). Each taxon is described as to its characteristic morphological features as determined via light microscopy. The sculpture description scheme follows Erdtman (1952). Each section is followed by remarks concerning the taxon and a discussion of suggested or known biological affinities.

4. Composition of the palynoflora

Table 1 provides the data summary for all samples analyzed at TDP Site 31 and TDP Site 36, per depth. The first section of the table provides the concentration of marine and terrestrial palynomorphs calculated for each sample. The second part of the table provides the relative abundance (% of total assemblage) for all the species recovered from the sites, organized by biological affinities (dinoflagellate cysts, acritarchs, spores, gymnosperms, and angiosperms). Detailed graphs of the relative abundance (%) between the marine and terrestrial fractions, along with the relative abundance (%) of all key palynomorphs, organized by biological affinity and depth, were previously published in Haynes et al. (2017) (see Figure 7 for TDP Site 31 and Figure 14 for TDP Site 36).

Both marine and terrestrial palynomorphs occur in all samples. Only minor differences between sites are observed in the composition of recovered palynomorph assemblages (Table 1). Although all samples have clearly been deposited under marine conditions (i.e. all samples except the lowermost sample in TDP Site 36 include dinoflagellate cysts), the concentration in terrestrial palynomorphs is much higher at both sites than the concentration in marine palynomorphs.



At TDP Site 31, the concentration of marine palynomorphs (*D*) (dinoflagellate cysts and acritarchs) ranges from 123 to 2,528 Dgdw⁻¹ while the concentration of terrestrial palynomorphs (*T*) (pollen and spores) ranges from 2,592 to 17,600 Tgdw⁻¹ (see Table 1 for details). Note that three samples (at 5.05 m, 15.12 m, and 77.10 m) were barren of palynomorphs, most likely due to local depositional or diagenetic factors that led to oxidation as evidenced by sulfur isotopes (Haynes et al. 2017) and microbial destruction of the palynomorphs.

All four samples from TDP Site 36 produced palynomorphs. Similar to patterns found at TDP Site 31, the concentration of the marine fraction is noticeably lower than the terrestrial component. Site 36 marine palynomorphs (*D*) range from 0 to 765 Dgdw⁻¹ while the concentration of terrestrial palynomorphs (*T*) (pollen and spores) ranges from 6,709 to an amazingly high value of 170,537 Tgdw⁻¹ (see Table 1). The very high abundance of pollen at 108.59 m at TDP Site 36 is represented by a mostly monospecific assemblage of the gymnosperm *Classopollis*. A monospecific forest of the parent plant of *Classopollis* was likely close to the site.

At both sites, the terrestrial assemblage is dominated by gymnosperms (23.6% of the assemblage on average, ranging from 47 to 100% of the assemblage), while angiosperms are present, but most often not abundant (6.9% of the assemblage on average, ranging from 0 to 50% of the assemblage). Bryophytes, pteridophytes, and fungal elements are rare (2.5% of the assemblage on average, ranging from 0 to 15% of the assemblage).

Gymnosperms are dominated by four taxa or pollen groups. *Classopollis* Pflug 1953, which is thought to represent extinct cheirolepid conifers, is the most abundant pollen taxon. Srivastava (1976) discussed at length the fossil genus *Classopollis*, noting that the name is valid for Mesozoic circular pollen, bearing subequatorial thinning, an equatorial thickened band, a polar distal pore, and proximal tetrad scar (Plate 1, image 23). The next most abundant gymnosperm group is Gnetophyte pollen, which includes *Ephedripites* Bolkhovitina 1953 ex Potonié 1956 (Plate 1, image 22) as well as other genera likely related to *Ephedra*-type plants, such as *Jugella* Mtchedlishvili & Shakhmundes 1973 and *Gnetaceaepollenites* Thiergart 1937. These taxa are grouped together here because of their common morphological features and their similar ecological significance. *Cycadopites* Wodehouse 1933 (Ginkgophyta, Cycadales, or Bennettitales) pollen are present but rare. The next most abundant genus is *Exesipollenites* Balme 1957, a plant thought to be related to the Cupressaceae or possibly the Taxodiaceae family, although this difference might now be obsolete as a recent taxonomic review of extant species considers Taxodiaceae a

junior synonym of Cupressaceae (Christenhusz et al. 2011). The last group, which is rare at both sites, are the bisaccate conifer pollen grains typical of Podocarpaceae (only found in one sample in each core).

Angiosperms are mostly present in low relative abundances and diversity. Their assemblages are dominated by two genera, *Hexaporotricolpites* Boltenhagen 1967 and a variety of periporate grains such as *Cretacaeiporites* Hengreen 1974. Not much is known about the likely botanical affinity of the first genus, but grains that are somewhat similar to *Cretacaeiporites* and other periporates are often produced today by extant families such as the Chenopodiaceae, Amaranthaceae and Caryophyllaceae.

All samples contain marine palynomorphs. Only four genera are recorded and all are in low abundances. Several species of *Spiniferites* Mantell 1850 and the acritarch *Veryhachium* Deunff 1954 occur throughout the samples at both sites, along with specimens of the genus *Dinogymnium* Evitt, Clarke & Verdier 1967 and what may be a new species of the genus *Florentinia* Davey and Verdier 1973. *Spiniferites* has a broad environmental range from littoral to open marine settings (Mertens et al. 2018). *Veryhachium*'s environmental significance was discussed by Vecoli (2000) in his study of the northern Sahara Platform in Algeria and Tunisia. At those sites, the species was the most abundant in a near-shore setting. *Dinogymnium* is mostly found in close proximity to land, in estuarine and/or inner shelf environments. For instance, they were abundant in Santonian–Maastrichtian strata sampled from the Upper Magdalena Valley basin in central Colombia, in what used to be at the time of deposition, a passive margin setting on inner-to-outer shelf (Garzon et al. 2012). In Colombia, they were often found associated with pteridophytes or bryophyte spores. *Dinogymnium* specimens were a common component of the marine palynomorphs in TDP Site 31, but only in samples from intervals at 25.89 and 29.01 m where spores are also dominant. They were not found at Site TDP 36.

5. Systematic palynology of angiosperms

Plate 1 illustrates specimens of each taxon discussed below (Plate 1, images 1–21) along with two predominant gymnosperm species (Plate 1, images 22–23).

Anteturma POLLENITES Potonié 1931
Turma PLICATES Naumova 1939 emend. Potonié 1960
Subturma MONOCOLPATES Iversen & Trols-Smith 1950
Genus *Liliacidites* Couper 1953
Type species *Liliacidites kaitangataensis* Couper 1953

Liliacidites sp. A

Plate 1: images 1–3

Plate 1. Scale bar: 10 μm (it applied to all images). Angiosperms: 1. *Liliacidites* sp. A. TDP Site 31, 3/COR, EFS L16/1. 2. *Liliacidites* sp. A. TDP Site 31, 3/COR, EFS R26/4. 3. *Tricolpites* sp. A. TDP Site 31, 4/COR, EFS H21/0 (note colpi indistinct). 4. *Liliacidites* sp. B. TDP Site 36, 24/COR, EFS R22/4. 5. *Tricolpites* sp. D. TDP Site 31, 24COR, EFS Q34/8. 6. *Triporopollenites* sp. A. TDP Site 31, 3/COR, EFS S11/2. 7. *Triporopollenites* sp. A. TDP Site 31, 3/COR, EFS V14/0. 8. *Tricolpites* sp. A. TDP Site 31, 3/COR, EFS W13/2. 9. *Tricolpites* sp. B. TDP Site 31, 6/COR, EFS R26/3. 10. *Tricolpites* sp. C. TDP Site 31, 3/COR, EFS P24/1. 11. *Tricolpites* sp. E. TDP Site 31, 3COR, EFS N44/4. 12. *Tricolpites* sp. F. TDP Site 31, 4/COR, EFS Q26/3. 13. *Tricolpites* sp. G. TDP Site 31, 3/COR, EFS K9/2. 14. *Syncolporites* sp. A. TDP Site 31, 3/COR, EFS O10/2. 15. *Tricolporites* sp. A. TDP Site 31, 3/COR, EFS R18/0. 16. *Tricolporites* sp. B. TDP Site 31, 3/COR, EFS L18/4. 17. *Tricolporites* sp. C. TDP Site 31, 4/COR, EFS U30/0. 18. *Tetracolpites* sp. A. TDP Site 31, 4/COR, EFS V25/0. 19. *Hexaporotricolpites* sp. A. TDP Site 31, 7COR, EFS W33/2. 20. *Periporopollenites* sp. A. TDP Site 31, 3/COR, EFS X14/1. 21. *Cretacaeiporites infrabaculatus* Boltenhagen 1975, TDP Site 31, 4/COR, EFS N34/1. Gymnosperms: 22. *Ephedripites* TDP Site 31, S3, EFS U9/2. 23. *Classopollis* TDP Site 31, S3, EFS L19/2. Note that 3/COR, 4/COR, 6/COR, and S3 refer to the sample numbers.

Description. Pollen grains single, elongate ellipsoidal, monosulcate, bilaterally symmetrical, isopolar; sulcus straight, narrow, extending nearly the full length of the grain, simple, not bordered, ends of sulcus somewhat gaping; surface reticulate, with lumen decreasing in size near the sulcus and toward each end of the long axis, lumen maximum diameter 2.0 to 2.5 μm , muri less than 1.0 μm thick; exine thin at $<1.0 \mu\text{m}$; longest dimension 33.6(39.5)43.0 μm (6 grains measured).

Affinity. See affinity discussion under *Liliacidites* sp. B below.

Liliacidites sp. B

Plate 1: image 4

Description. Pollen grain single, elongate, broad ellipsoidal, monosulcate, bilaterally symmetrical, isopolar; sulcus long extending nearly the full length of the grain, sulcus simple, not bordered; surface reticulate, reticulation consistent over entire surface of grain; longest dimension 55 μm (single specimen recovered). Note that this pollen grain is exhibiting a much darker wall, likely the result of more advanced thermal maturation. It is possible that this specimen is reworked from a somewhat older Cretaceous section.

Comparison. *Liliacidites* sp. B differs significantly from *Liliacidites* sp. A by its size and the thickness of its wall.

Affinity. Several monocotyledon taxa produce pollen with a simple, single sulcus, and many of the features comparable to the fossil form. Some extant Liliaceae taxa produce pollen that is similar to *Liliacidites* sp. B, however pollen with a similar morphology (one sulcus and a reticulate surface) may be found in the Liliaceae, Iridaceae, Amaryllidaceae, Arecaceae and perhaps other monocotyledon families.

Subturma TRIPTYCHA Naumova 1939 emend.

Potonié 1960

Genus *Tricolpites* Cookson ex Couper 1953

emend. Jarzen & Dettmann 1989

Type species *Tricolpites reticulatus* Cookson 1947 ex

Couper 1953

Tricolpites sp. A

Plate 1: image 8

Description. Pollen grains tricolpate, anguloaperturate, isopolar, amb triangular with straight sides; colpi meridionally aligned, incised about half the distance to the poles, with margins not thickened, colpi gaping at the equator; exine thin, layers not discernible, about 1.0 μm thick; exine surface granulate to scabrate, ornament evenly distributed over surface of grain; equatorial diameter 21.6(23.5)33.0 μm (10 specimens measured).

Affinity. Angiosperm, dicotyledon.

Tricolpites sp. B

Plate 1: image 9

Description. Pollen grains tricolpate, anguloaperturate, isopolar, amb rounded triangular, with slightly convex sides; colpi meridionally aligned, incised about half the distance to the poles, with margins not thickened, colpi gaping at the equator; exine thin, layers not discernible, about 1.0 μm thick; exine surface granulate to scabrate, ornament evenly distributed over surface of grain; equatorial diameter 35(36)37 μm (2 specimens measured).

Comparison. *Tricolpites* sp. B differs from *Tricolpites* sp. A by its rounded-triangular amb, very different from the straight triangular amb of *Tricolpites* sp. A, and by its larger size. Salard-Chebouldaef (1990) illustrated a specimen of *Psilatricolpites hammenii* recovered from some Senonian sections in West Africa. This species seems identical to our *Tricolpites* sp. B, but the author lists a range limited to the Senonian only. If the species has an earlier FAD, it could be conspecific.

Affinity. Angiosperm, dicotyledon.

Tricolpites sp. C

Plate 1: image 10

Description. Pollen grains tricolpate, anguloaperturate, isopolar, amb perfectly rounded to slightly triangular, with convex sides; colpi meridionally aligned, incised about one-third the distance to the poles, with margins slightly thickened, colpi gaping at the equator; exine thin, about 1.0 μm thick; exine surface granulate to scabrate, ornament evenly distributed over surface of grain; equatorial diameter 22.0(25.7)31.2 μm (10 specimens measured).

Affinity. Angiosperm, dicotyledon. Based on the overall pollen morphology, it is possible that this species could be assigned to the genus *Pseudobombax* or some of the related species from the subfamily Bombacoideae.

Tricolpites sp. D

Plate 1: image 5

Description. Pollen grains tricolpate, grain prolate, colpi extending nearly to the poles, narrow, not bordered; surface finely reticulate, reticulation finer to absent near poles, muri and lumen widths both less than 1.0 μm ; exine thin, layers not discernible, $<1.0 \mu\text{m}$ thick, overall dimensions: polar axis 26.5(34.8)48.0 μm , equatorial diameter 24.0(24.3)48.0 μm , $p/e = 1.43$ (7 specimens measured).

Affinity. Angiosperm, dicotyledon.

Tricolpites sp. E

Plate 1: image 11

Description. Pollen grains tricolpate, amb rounded triangular to nearly circular, apertures situated in the interapical areas; colpi meridionally situated, short (brevicolpate), 7.3 to 12.0 μm long, extending one-third or less the distance to the poles; surface very finely regulate to nearly psilate; exine apparently not layered, about 3.0 μm thick, slightly thicker at apertures; equatorial diameter 48(51.5)55 μm (2 specimens measured). Note that these pollen grains also exhibit a much darker wall, likely the result of more advanced thermal maturation. It is possible that these specimens are reworked from a somewhat older Cretaceous section.

Affinity. Angiosperm, dicotyledon. The grains bear some resemblance to extant *Gunnera* pollen (although it is quite large for an affinity to *Gunnera*) or with some species of Bombacaceae.

Tricolpites sp. F

Plate 1: image 12

Description. Pollen grains tricolpate, triangular, isopolar, amb sharply triangular, apertures at apices of triangle; colpi narrow, not bordered, extending one-half to two-thirds the distance to the poles; surface finely scabrate, scabrae evenly

distributed over the surface of the grain; equatorial diameter 26.5(28.8)31.2 μm (2 specimens measured).

Affinity. Angiosperm, dicotyledon.

Tricolpites sp. G

Plate 1: image 13

Description. Pollen grains tricolpate, grain prolate, colpi extending nearly to the poles, narrow, not bordered; surface psilate; exine thin, layers not discernable, ≤ 1.0 μm thick, overall dimensions: polar axis 26.0(27.0)28.8 μm , equatorial axis 16.8(18.4)19.2 μm p/e = 1.47 (3 specimens measured).

Affinity. Angiosperm, dicotyledon.

Subturma POLYTYCHES Naumova 1939

Genus *Tetracolpites* Vimal ex Srivastava 1966

Type species *Tetracolpites reticulatus* Srivastava 1966

Tetracolpites sp. A

Plate 1: image 18

Description. Pollen grain tetracolpate, isopolar, amb rounded square; colpi meridionally situated, incised about half the distance to the poles; surface finely scabrate to nearly psilate; exine thin, < 1.0 μm thick; equatorial diameter 21 μm (single specimen measured).

Comparisons. *Tetracolpites* sp. A differs from *Stephanocolpites* sp. A (Jarzen 1981) in not having the granular mound present at one of the poles, and lacking the finely pitted surface. The species described here differs from Srivastava's (Srivastava 1966) type species (*Tetracolpites reticulatus*) in lacking the reticulate exine structure. Salard-Cheboldaeff (1990) illustrated a specimen of *Retitetracolpites gabonensis* from West Africa that has similar apertures and amb, but the species from West Africa has a noticeably reticulated wall structure and was found only in Senonian sections.

Affinity. Angiosperm, dicotyledon. Vimal (1952) compared *Tetracolpites* to the extant taxon *Fraxinus americana* L. Several modern angiosperm families have tetracolpate pollen. For instance, *Nicotiana* (Solanaceae), *Asarum* (Asaroideae) or *Stachys* (Lamiaceae) are examples of plants producing tetracolpate pollen, and all can be found today in Africa, but these pollen wall structures are very different. With only a single specimen recovered, there is insufficient data to reliably compare this taxon to any extant taxa.

Subturma PTYCHOTRIPORINES Naumova 1939

Genus *Tricolporites* Erdtman 1947

Type species *Tricolporites protrudens* Erdtman 1949

Tricolporites sp. A

Plate 1: image 15

Description. Pollen grains single, tricolporate, amb rounded triangular, apertures situated at the apices; each colpus has a pore, thickened margins, extending about one half the distance to the poles; surface psilate to very finely scabrate; exine < 1.0 μm thick, slightly thicker at colpus margins; equatorial diameter: 19.2(22.3)28.8 μm (10 specimens measured).

Comparisons. *Retitricolporites pristinus* Singh 1983 is similar to the form described here, but differs in having a finely reticulate surface.

Affinity. Angiosperm, dicotyledon.

Tricolporites sp. B

Plate 1: image 16

Description. Similar to *Tricolporites* sp. A except with longer colpi, colpi almost extending to the poles, giving the grains a syncolporate appearance; surface finely granulate to psilate; exine thin about 1.0 μm thick; equatorial diameter: 21.6(23.4)26.4 μm (7 specimens measured).

Affinity. Angiosperm, dicotyledon.

Tricolporites sp. C

Plate 1: image 17

Description. Pollen grains single, tricolporate, amb rounded triangular, apertures situated at the apices of the triangle; colpi each with a pore, colpi margins not thickened, extending about one-third to one-half the distance to the poles; surface reticulate, gradually diminishing toward colpi margins; exine < 1.0 μm thick, thicker at colpi margins; dimensions, equatorial diameter: 19.0(24.9)33.5 μm (5 specimens measured).

Affinity. Angiosperm, dicotyledon.

Class SYNCOLPORATAE Iversen & Troels-Smith 1950

Genus *Syncolporites* van der Hammen 1954

Type species *Syncolporites lisamae* van der Hammen 1954

Syncolporites sp. A

Plate 1: image 14

Description. Pollen grain single, amb more or less triangular, apertures located at the apices of the triangle; apertures are colpi with pores, colpi meeting at the poles, narrow; surface psilate to finely scabrate; exine thin, about 1.0 μm thick but thickened at colpi; equatorial diameter 31 μm (single specimen measured).

Comparisons. With only a single specimen recovered, comparison with other described forms is difficult, however this form differs significantly from the type species *S. lisamae* by its triangular amb, lack of thickening at the pores and much smoother wall structure.

Affinity. Angiosperm, dicotyledon.

Subturma PTYCHOPOLYPORINES Naumova 1939

emend. Potonié 1960

Genus *Hexaporo-tricolpites* Boltenhagen 1967

Type species *Hexaporo-tricolpites emelianovii* Boltenhagen 1967

Hexaporo-tricolpites sp. A

Plate 1: image 19

Description. Pollen grains single, prolate to spheroidal, hexaporo-tricolpate, with two pores at the polar ends of each colpus, colpi extending about one-half or more the distance to poles; surface finely granulate with low spinules, measuring less than 1.0 μm in height; exine 2.5 to 3.0 μm thick, sexine up to 2.5 μm thick, nexine up to 1.0 μm thick, columellae clearly visible in cross section; equatorial diameter: 25(28)30 μm (4 specimens measured).

Comparisons. *Hexaporotricolpites* appears in the upper Albian to lower Cenomanian in Brazil (Herngreen 1973), and has a range from the upper Albian to Cenomanian in West Africa (Jardiné et al. 1972). *Hexaporotricolpites lamellaferus* Jardiné et al. 1972, was recovered from the upper Albian of Gabon, Congo, Angola, and in the upper Albian to lower Cenomanian of Brazil, but it was not found in the Albian to Cenomanian of Senegal and Ivory Coast (Kotova 1978).

Affinity. Angiosperm, dicotyledon. Boltenhagen (1969) suggested comparison of *Hexaporotricolpites* with the pollen of Didymelaceae (= Buxaceae according to the Angiosperm Phylogeny Group 2009). Pollen of *Didymeles madagascarensis* Willdenow 1806 also has three colpi with each colpus bearing two pores. The surface is distinctly reticulate. Erdtman (1952) illustrates line drawings of *D. madagascarensis*. Erdtman further compares the pollen of *Didymeles* with *Breynia* J.R. Forst. & G. Forst. 1776 and *Breyniopsis* Beille 1925 in the Euphorbiaceae. Inspection of the pollen of the Euphorbiaceae subtribe Flueggeinae reveals that pollen bearing similar diporate apertures include the genera *Breynia*, *Phyllanthus* L. 1753 (in part), and *Sauropus* Blume 1826 (Sagun and van der Ham 2003).

Turma POROSES Naumova emend. Potonié 1960

Subturma TRIPORINES Naumova 1939

Genus *Triporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type species *Triporopollenites coryloides* Pflug in Thomson & Pflug 1953

Triporopollenites sp. A

Plate 1: images 6–7

Description. Pollen grains single, triporate, subtriangular, peroblate; heteropolar with 2 to 3 of the pores situated slightly off the equator, circular, pore diameter 5 to 7 μm , pores simple; surface psilate to very finely granulate; exine 2.5 to 4.0 μm thick; equatorial diameter 22.0(25.5)31.0 μm (7 specimens measured).

Comparisons. The specimen of *Triorites africaensis* Jardiné and Maglorie 1963 as illustrated by Schrank (1994, figures 8i–j) is similar to the specimens described here except for the position of the pores positioned slightly off the equatorial position. Salard-Chebouldaef (1990) illustrates a specimen of *Loranthacites nataliae* that also displays a triporate aperture system situated off the equator, and a similar amb shape. But that author found that species in much younger (Oligocene–Miocene) West African sections, and the wall structure of that *Loranthacites* is far from psilate, unlike our specimens.

Affinity. Angiosperm, dicotyledon. Ward and Doyle (1994) have suggested affinity of *Triorites africaensis* with the Proteaceae, based on detailed LM, SEM, and TEM work. The position of the pores of the species illustrated here proscribes it to be assigned to the Proteaceae. Further investigations are needed to assign an affinity to this species.

Subturma PERIPORITI van der Hammen 1956

Genus *Periporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type species *Periporopollenites stigmatosus* (Potonié) Thomson & Pflug 1953

Periporopollenites sp. A

Plate 1: image 20

Description. Pollen grain single, spheroidal to rounded polygonal, periporate, pores large, evenly distributed over the surface of the grain, pore number 15–25, generally 4 to 8 μm diameter, circular to elliptical, with granulate membrane covering each pore; surface psilate to finely granulate; exine ≤ 1.0 μm thick; diameter of grain 28.8(33.2)38.4 μm (10 specimens measured).

Affinity. Angiosperm, dicotyledon. Several families display pollen with a periporate aperture condition with pore membranes. Some Juglandaceae (e.g. *Juglans nigra* L. 1753) have similar pollen, showing perforated membrane for each pore. The pores in *Juglans nigra*, however, are aspidate, and occur only in one hemisphere of the grain. In other genera of the Juglandaceae, the pores are fewer and arranged equatorially (Wodehouse 1935). *Liquidambar styraciflua* L. 1753 (Hammamelidaceae) bears pollen with 12 to 20 pores, each pore showing granulate to verrucate pore membrane. In many respects the grains described here resemble those of *Liquidambar styraciflua*, but the pores in *Periporopollenites* sp. A are smaller than those of *Liquidambar* and too large to be assigned to most genera of the Chenopodiaceae family.

Subturma PERIPORITI van der Hammen 1956

Genus *Cretacaeiporites* Herngreen 1974

Type species *Cretacaeiporites polygonalis* (Jardiné & Magaloire) Herngreen 1974

Cretacaeiporites infrabaculatus Boltenhagen 1975

Plate 1: image 21

Description. Pollen grain single, spheroidal, polyforate, pores large, generally 7.0 to 10.0 μm in diameter, circular to elliptical; surface psilate to finely granulate, with small bacula interspersed between pores; exine 1.5 μm thick; diameter of grain 30(34.5)39 μm (2 specimens measured).

Comparisons. Species of *Cretacaeiporites* have been recovered from several localities in Africa spanning Turonian to Maastrichtian deposits.

Cretacaeiporites polygonalis Herngreen 1974 occurs in Senegal in the upper Albian to lower Cenomanian; in Brazil, it appears from the lower Albian and in high abundance in the Albian to Cenomanian. Rare specimens of this species were recognized in Cenomanian assemblages from Deep Sea Drilling Project (DSDP) Sites 370 and 367 in the Eastern Atlantic. Single specimens of *Cretacaeiporites mulleri* Herngreen 1973 and *C. scabratus* Herngreen 1974 were observed in upper Albian to Cenomanian assemblages from DSDP Sites 370 and 367, but these species are common in upper Albian to lower Cenomanian sediments of Brazil. These species were recognized in Senegal only in the upper Cenomanian and Turonian (Kotova 1978).

Affinity. Angiosperm, dicotyledon. Polyforate (periporate) pollen forms are produced by extant families such as the Chenopodiaceae, Amaranthaceae, and Caryophyllaceae. Ward and Doyle (1994), using LM, SEM, and TEM, have compared several ultrastructural features of *Cretacaeiporites scabratus* Herngreen 1974 from northern Gondwana with the Ranunculaceae, and suggest that some species of the genus derive from probable tricolpate ancestors.

6. Discussion and environmental affinity

As far as we know, the present palynological study, briefly discussed in Haynes et al. (2017), is the first palynological study of a Tanzanian (East African) section of Turonian age. Herngreen and Chlonova (1981) described a West Africa Turonian palynomorph complex characterized by periporate grains belonging to *Cretacaeiporites* (up to 17%), *Ephedripites* group (from 1 to 28%), and tricolpate grains (30 to 65%). These authors also noted that both in South American and African sequences, polyplcate types decrease steadily in abundance in post-Turonian sequences. The dominance of the *Ephedripites* group (Plate 1, image 22) in our samples tends to support the trend previously described for Turonian-aged deposits elsewhere. Overall, the assemblage found here is also very similar to older Cenomanian pollen and spore assemblages from Africa, except for the absence of elater-bearing species, which are abundant in most Albian-Cenomanian African (Herngreen and Chlonova 1981) and South American (Dino et al. 1999) sections.

The prevalence in our study of polyplcate species of the *Ephedripites* group, with a variety of wall ridges, is very interesting as the modern analogue of these plants today, extant *Ephedra*, is mostly well adapted to arid climates. Schrank (2010), who studied a Lower Cretaceous southeastern Tanzanian section, also noted that ephedroid pollen are indicative of dry regions (arid to semi-arid conditions) and noted that previous studies did not find this pollen type in temperate humid paleoenvironments.

The *Ephedripites* group in our samples is associated with two main angiosperm types, the polyporate genus *Cretacaeiporites* (and other grains of similar morphology) and the hexaporo-tricolpate genus *Hexaporo-tricolpites*. Both genera have their first appearance datum (FAD) in the Albian, and the latter taxon is known to be endemic to African and South American provinces (Herngreen and Chlonova 1981). These regions are known to lack or have rare conifer pollen grains of bisaccate and trisaccate morphology similar to patterns present in our TDP samples.

Understanding the environmental significance of *Classopollis* (Plate 1, image 23) is necessary for this study as this conifer genus is frequently the most dominant palynomorph type recovered in the two sections studied. Srivastava (1976) analyzed *Classopollis* in detail and indicated that this genus had a global distribution in Upper Triassic to Turonian strata and he proposed that the most likely affinity for this extinct genus is with the araucarian and/or gnetalean conifers. He noted that the parent plant required well-drained soils of upland slopes and lowlands near coastal areas, in warm climatic conditions. A fairly strong consensus for a Cheirolepidiaceae affinity for *Classopollis* has been established for quite a while (Balme 1995 and references therein). Schrank (2010) follows that consensus and agrees with Srivastava (1976) that *Classopollis* is a xerophytic, drought-resistant, thermophilic genus. In his 2010 paper, Schrank provided additional data that agrees with Srivastava's (1976) theory that the *Classopollis*-producing plants grew in low-lying coastal environments close to lagoon-like depositional sites. Schrank further confirmed that these plants were sometimes associated with evaporitic deposits providing even more support that this group is tolerant of an arid environment. Kürschner et al. (2013) support a Cheirolepidiaceae

affinity as well. Here we follow the recommendation of these authors (Srivastava 1976; Balme 1995; Schrank 2010; Kürschner et al. 2013) that *Classopollis* pollen should be considered as related to the Cheirolepidiaceae family and that it was likely produced by an extinct conifer growing in coastal regions, and indicative of warm arid environments.

Mejia-Velasquez et al. (2012) discussed the climatic implications of a palynological assemblage recovered similar to the TDP assemblages. Mejia-Velasquez et al. (2012) considered *Classopollis* and ephedroid pollen grains to be indicators of arid climates, while fern spores were used as indicators of humid climates. The abundant *Classopollis* and ephedroid pollen have been associated with sediments deposited during dry phases, with paleotemperatures estimated to be as high as 31 °C, a mean annual temperature based on geochemical proxies derived from lipids of archaeal membrane (Schouten et al. 2003). Similar temperatures (30–33 °C) were reported for the TDP sites based on oxygen isotopic results of planktic foraminifera (MacLeod et al. 2013).

Along the climatic implications derived from the abundance of cheirolepids and gnetaleans, we should consider the fact that their abundance could partially be an artifact of distribution and production bias. Anemophilous plants (wind-pollinated) like gymnosperm pollen of bisaccate morphology, are known to be over-represented in the pollen record in coastal regions (Warny et al. 2003). It is thus possible that the cheirolepids and gnetaleans can be over represented because of higher production and wider dispersal by wind.

The other common pollen type found in TDP samples is the genus *Exesipollenites*. This genus was first described by Balme (1957) from Jurassic sediments of the Perth Basin in Western Australia. The type description includes pollen forms that are circular to oval in outline, and bearing a thinned pore-like (?leptoma) depression near the pole of one face. The type species size range varies from 25 to 33 microns. The pollen forms recovered here fall within the generic description of Balme (1957) and later modified by Pocock (1970). Recently, Peñalver et al. (2015) have identified *Exesipollenites* pollen on the bodies of long-proboscid flies, preserved in Cretaceous amber, from Spain and Myanmar, suggesting that the parent plant (gymnosperm) was probably pollinated by insects. *Exesipollenites* pollen has been recovered *in situ* from male cones of *Elatides curvifolia* (Dunker) Nathorst 1897 (Balme 1995), indicating a probable Taxodiaceae affinity. Li et al. (2015) proposed that *Exesipollenites* was produced by an extinct conifer associated with arid climates.

Bryophyte and pteridophyte spores are rare in our samples, mostly found in the top of the section at TDP 31. These plants require high soil humidity during their reproductive cycle. The paucity of these plants is further indication that drier climatic conditions prevailed throughout the period of deposition.

Seventeen angiosperm pollen forms were also identified from the two cores studied. As noted earlier, the angiosperm component is never abundant, with some taxa represented by single grain occurrences. Because of the low frequency of angiosperms, and the scarcity of some taxa, identification at the species level was not attempted for most taxa. As noted earlier, two forms, *Cretacaeiporites* and *Hexaporo-tricolpites*, were the only abundant angiosperms recovered. Not much is

known of *Hexaporotricolpites* spp., but grains that are somewhat similar to *Cretacaeiporites* and other periporates are often produced today by wildflowers of families such as Chenopodiaceae, Amaranthaceae, and Caryophyllaceae and are often abundant in coastal environments.

In summary, the rarity of spore-producing plants, and the dominance of *Ephedripites* and *Classopollis* pollen indicates that the environment on the nearby land was mostly covered by *Ephedra*-type plants and *Classopollis*-producing gymnosperms. Nevertheless, some of this abundance might partially be a result of their means of dispersal, as anemophilous pollen are often over-represented in comparison to zoophylous pollen types (as are most Cheirolepidiaceae and most Gnetales). Indeed, the Turonian flora represent a small number of angiosperms. Hu et al. (2008) postulated that many of the Early and early Late Cretaceous angiosperms were likely already zoophilous and this could partially explain their under-representation. Rare cycads and, for part of the interval, the parent tree of *Exesipollenites* complete the assemblage recovered. The rarity of bryophytes and pteridophytes, along with the abundance of *Ephedripites* and *Classopollis* are indicative of warm arid climates. This conclusion is consistent with results of a study of Cretaceous palynofloral provinces by Herngreen et al. (1996). They noted that many provinces saw an increase in abundance and diversity of angiospermous grains, which indicate more humid conditions, only after mid-Turonian time. Such an increase in both abundance and diversity of angiosperms was not observed at our site. Dispersal consideration and production bias aside, this scarcity is most likely because conditions remained quite dry throughout the time interval sampled.

7. Conclusions

A Turonian marine sequence in southeast Tanzania has yielded a rich pollen assemblage providing a clear picture about the type of vegetation that grew on the coastal area studied. All species with known or assumed biological affinities indicate an adjacent land with abundant coastal vegetation dominated by three types of gymnosperms - *Ephedripites* (analogue to *Ephedra*), *Classopollis* (Cheirolepidiaceae), and *Exesipollenites* (with a likely affinity to Taxodiaceae). The assemblage indicates a warm (tropical or sub-tropical) climate with plants growing on a well-drained soil for the entirety of the interval sampled. The scarcity of spores suggests a lack of moisture in an arid to semi-arid environment. This inference, in turn, provides preliminary constraints on the basic environmental requirements for the fifteen new angiosperm species described (two additional species show signs of thermal maturation and could be reworked from somewhat older Cretaceous sections). The low abundance in angiosperm taxa may be a result of dispersal mechanisms as the sediments studied were deposited in marine settings, where zoophylous species are often underrepresented. Overall, the assemblage shows a homogenous distribution and the minor changes in relative abundance among the taxa are likely due to minor climatic changes, minor sea-level fluctuations, and/or taphonomic variation during an otherwise very stable climatic interval.

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