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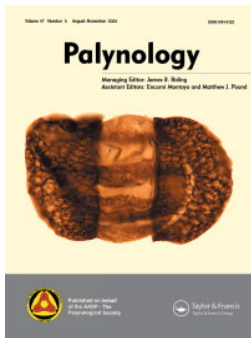
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Descriptive systematics of Upper Palaeocene–Lower Eocene pollen and spores from the northern Niger Delta, south-eastern Nigeria

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ABSTRACT

Fossil pollen and spores are a vital source of information on the geological history of tropical vegetation including reconstructions of vegetation diversity and composition. However, such work relies on a sound taxonomic framework, and this is challenging to achieve because of the large number of pollen and spore morphotypes that are encountered in palynological preparations from tropical sediments. In tropical West Africa, for example, extensive taxonomic work on Cretaceous–Paleogene pollen and spores was undertaken in the later part of the twentieth century, but more recent palynological work has focussed on stratigraphy and basin evolution, and there is a need for additional taxonomic work on the pollen and spores of this region. We have undertaken a descriptive systematic study of pollen and spores (sporomorphs) from 15 sediment samples spanning the Upper Palaeocene–Lower Eocene of south-eastern Nigeria. A palynoflora consisting of 29 spores, two gymnosperm pollen grains, and 138 angiosperm pollen grains is described. Two new spore species are proposed, and one new genus and 18 new species of angiosperm pollen are proposed. The general vegetation type represented by the palynoflora consists of palm-dominated swamps, perhaps with mangroves. The richness of each sample ranges from 29 to 76 sporomorph taxa, and rarefaction analysis suggests an increase in diversity from the Palaeocene to the Eocene in this region. Samples from the Palaeocene Upper Nsukka Formation are dominated by pollen with botanical affinities to the Arecaceae (palms) and Araceae (arums), and this assemblage is very similar to the Palaeocene in the Neotropics.

KEYWORDS



tropical rainforests; West Africa; vegetation evolution; palaeoecology; taxonomy; Paleogene


1. Introduction

Tropical rainforests are the most structurally complex and diverse land ecosystems on Earth, and they form the primary gene pool for the flowering plants (Morley 2000). Plant macrofossils from South America indicate that rainforests as we know them today – restricted to low-latitude areas with high annual rainfall and equable temperatures (Johnson and Ellis 2002) – have a history stretching back at least as far as the late Palaeocene, 58 million years ago (Wing et al. 2009). However, owing to dense vegetation cover and a lack of exploration in the modern tropics, macrofossil data on the origin and subsequent evolution of tropical rainforests is scarce (Wilf et al. 2005). In contrast to plant macrofossils, pollen and spores have high preservation potential, are deposited in a wide variety of sediments (Mander and Punyasena 2018), and consequently provide an abundant source of information on the evolution of tropical vegetation.

Early palynological work in tropical regions provided an overview of the fossil pollen and spores present in Cretaceous

to Paleogene strata, and focussed on the taxonomic description of the morphotypes present, the palynological correlation of sedimentary rocks, and the association between the floral changes recorded by fossil pollen and spores and palaeoclimatic change in this time interval (e.g. Van der Hammen 1954, 1956a, 1956b, 1957a, 1957b, 1958; Van der Hammen and Wymstra 1964; van Hoeken-Klinkenberg 1964, 1966; Belsky et al. 1965; Jardiné and Magloire 1965; Clarke 1966; Leidelmeyer 1966; Van der Hammen and Garcia 1966; Boltenhagen 1967; Clarke and Frederiksen 1968). This phase of tropical palynological work culminated in the establishment of a pantropical palynological zonation scheme with more detailed regional divisions (Germeraad et al. 1968). It was suggested that the boundaries of each palynological zone are marked by the first stratigraphical appearance of new pollen and spore morphotypes (thought to reflect the evolution of new plant groups), but that the extinction of morphotypes is diachronous across regions and is consequently of less biostratigraphical value at large geographical scales (Germeraad et al. 1968).

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Taxonomic practice during this early phase of tropical palynological work is marked by the widespread use of illegitimate names and the inadequate circumscription of fossil species. For example, as stated by Jaramillo and Dilcher (2001), many illegitimate generic names for fossil pollen and spores were proposed by Van der Hammen (1954, 1956a, 1956b), including *Psilamonoletes*, *Monoporites*, *Psilatricolpites*, *Psilatricolporites*, *Psilatriporites*, *Retitricolpites*, *Retitricolporites*, *Scabratricolpites*, *Scabratricolporites*, *Stephanocolpites* and *Striatricolpites* (Jansonius and Hills 1976), and these have been used in both the Neotropics and the Old World tropics. Other generic names such as *Brevitricolpites* González Guzmán 1967 encompass so much morphological variation – in the case of *Brevitricolpites*, pollen grains with gemmate, clavate, scabrate or verrucate surface ornamentation and either colpi or colpori (Jansonius and Hills 1976) – that they can contain a vast number of species, and it is unclear whether such large genera reflect evolutionary radiation or variable taxonomic practice among workers (e.g. Foote 2012; Sigwart et al. 2018). Such taxonomic problems are perhaps of less concern in a stratigraphical context because of the focus on a relatively small number of taxa. For example, while Germeraad et al. (1968) noted the high diversity of pollen and spore morphotypes encountered in palynological preparations from the tropical Cretaceous–Paleogene, their concern was with pruning this diversity down and focussing on taxa that have biostratigraphical utility:

TROPICAL TERTIARY POLLEN FLORAS ARE VERY RICH IN SPECIES AND THE AVERAGE TYPE COLLECTION MAY EASILY CONTAIN 800–1,000 DIFFERENT SPECIES. FOR STRATIGRAPHICAL PURPOSES GENERALLY LESS THAN 200 ARE OF IMPORTANCE PER AREA. FOR A COMPREHENSIVE REVIEW, SUCH AS THIS, A FURTHER REDUCTION IS DESIRABLE AND ONLY 49 SPECIES ARE DISCUSSED. THESE ARE, FIRSTLY, THE SPECIES USED TO ESTABLISH THE MAJOR ZONATION, AND SOME WHICH ARE OF IMPORTANCE FOR ELUCIDATING LOCAL CORRELATION PROBLEMS. (Germeraad et al. 1968, p. 191)

Recent palynological work in the tropics has involved confronting the large number of pollen and spore morphotypes present in order to reconstruct the diversity and composition of vegetation through time and space, and in this context the underlying taxonomy becomes critical. Coarse and overly 'lumped' classifications may underestimate diversity (e.g. Mander and Punyasena 2014), homogenising time periods and biogeographical regions, while very fine and 'over-split' classifications may overestimate diversity, and may lack repeatability and have limited applicability outside an individual stratigraphical succession. Consequently, workers have begun revising the taxonomy of tropical palynofloras to generate a stable taxonomic framework for fossil pollen and spores in low latitudes, which is challenging because of the high diversity encountered in tropical palynological preparations. Some of this work has been done monographically (e.g. Hoorn 1994; Jaramillo and Dilcher 2001; Silva-Caminha et al. 2010; D'Apolito et al. 2021), some as part of wider studies of the evolution and biogeography of tropical vegetation (e.g. Jaramillo et al. 2007; Hoorn and Bacon in Bacon et al. 2018), and synthesis of this work is ongoing in the Morphological Electronic Database of Cretaceous–Cenozoic and Extant Pollen, Spores and Dinoflagellates from Northern South America (Jaramillo and Rueda 2023). This systematic

work underpins macroevolutionary studies showing that Neotropical tropical plant diversity is sensitive to global temperature, which may govern the rise and fall of tropical plant diversity over geological time scales (Jaramillo et al. 2006), biogeographical observations that the latitudinal diversity gradient among plants was reduced in the Palaeocene compared to the Holocene (Jaramillo et al. 2007) and that higher temperatures and more seasonally dry climates during the Palaeocene–Eocene Thermal Maximum (PETM) led to the northward range expansion of tropical plants (Korassidis et al. 2023), and a demonstration that the end-Cretaceous mass extinction event reduced Neotropical plant diversity by 45% (Carvalho et al. 2021).

There were extensive taxonomic studies in the later part of the twentieth century on western African tropical palynology (e.g. Belsky et al. 1965; Jardiné and Magloire 1965; Boltenhagen 1967; Adegoke 1969; Jan du Chêne 1977; Legoux 1978; Salard-Chebaldaff 1979), while recent palynological studies in tropical West Africa have focussed on stratigraphy and basin evolution, often in the context of oil exploration (e.g. Ikegwuonu and Umeji 2016; Lucas 2017; Chiadikobi et al. 2018; Bolaji et al. 2020; Ikegwuonu et al. 2020; Agharanya et al. 2022). Nevertheless, to create a sound taxonomic framework for studies of ancient vegetation diversity and composition in tropical West Africa, the fossil pollen and spores of this region require additional taxonomic work as there are numerous species that have not been described. We have undertaken a descriptive systematic study of pollen and spores from 15 sediment samples spanning the Upper Palaeocene–Lower Eocene of south-eastern Nigeria. This interval of time was a period of major plant diversification in tropical West Africa (Morley 2000), and our aims are as follows: (i) describe the pollen and spores preserved in these samples and revise the systematics where necessary; and (ii) make some preliminary observations on the general character of the palynoflora – including recovery, diversity and composition – to guide future work.

2. Materials and methods

Fifteen sediment samples were examined from the Upper Palaeocene–Lower Eocene of the northern Niger Delta (formerly the Anambra Basin), Nigeria (Figure 1; Table 1). These samples were collected during fieldwork that is reported in Oboh-Ikuenobe et al. (2005) and were chosen to provide an overview of the pollen and spores preserved in the rock succession under investigation. Samples were digested in hydrochloric (10%) and hydrofluoric (70%) acids, oxidised with Schultze solution, sieved at 10 µm and stained with safranin. Microscope slides were mounted in epoxy resin and scanned in complete transects using a transmitted light microscope with brightfield illumination. Pollen and spores were inspected using a 40 × 0.85 na objective and a 63 × 1.4 na oil immersion objective. At least 300 grains per slide were counted, and reworked grains (identified by an extremely poor state of preservation) were omitted. Where recovery did not permit a count of 300 grains, then the entire slide was counted. In cases where a count of 300 was reached, the remainder of the slide

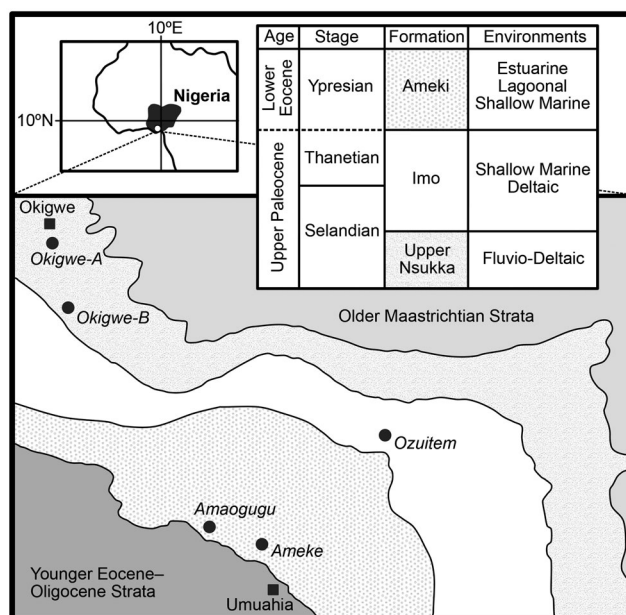


Figure 1. Map and stratigraphy of the rock succession under investigation (modified from Oboh-Ikuenobe et al. 2005). The towns Okigwe (Imo State) and Umuhia (Abia State) are labelled with closed squares. The five sections from which samples were studied are labelled with closed circles. General environments for the Imo Formation from Obi (2000; fluvio-deltaic); the Imo Formation from Reymont (1965; shallow marine) and Anyanwu and Arua (1990; deltaic); and the Ameki Formation from White (1926; estuarine), Nwajide (1979) and Arua (1986; both lagoonal), and Adegoke (1969) and Fayose and Ola (1990; both shallow marine). The Palaeocene–Eocene boundary is placed between the Imo and Ameki formations following Nwajide (1990) and Oboh-Ikuenobe et al. (2005) and shown as a dashed line to indicate uncertainty. See Table 1 for details of samples taken from each section.

was scanned for morphotypes that had not been encountered in the count and these were recorded as present but were not included in subsequent statistical analyses (performed in R version 4.2.2 (R Core Team 2022) with vegan (Oksanen et al. 2022)). Rarefaction analyses were performed on abundance data, and non-metric multidimensional scaling (NMDS) analyses were performed on relative abundance (percentage) data with a Bray-Curtis distance metric.

Classification of pollen and spores was undertaken using published descriptive work on the Upper Cretaceous and Paleogene fossil pollen and spores of tropical West Africa (van Hoeken-Klinkenberg 1964, 1966; Belsky et al. 1965; Jardiné and Magloire 1965; Clarke 1966; Boltenhagen 1967; Clarke and Frederiksen 1968; Germeraad et al. 1968; Boltenhagen 1976; Jan du Chêne 1977; Jan du Chêne et al. 1978; Legoux 1978; Salard-Chebouldaëff 1979; Doyle et al. 1982; Boltenhagen and Salard-Chebouldaëff 1987; Oboh and Salami 1989; Salami 1990; Salard-Chebouldaëff 1990), the Upper Cretaceous and Paleogene Neotropics (Van der Hammen and Wymstra 1964; Leidelmeyer 1966; Van der Hammen and Garcia 1966; Jaramillo and Dilcher 2001; Jaramillo et al. 2007), the Morphological Electronic Database of Cretaceous–Tertiary and Extant Pollen and Spores from Northern South America (Jaramillo and Rueda 2023), the Genera File of Fossil Spores and Pollen (Jansonius and Hills 1976 and supplements), and the examination of type material held in the collections of the Muséum National d'Histoire Naturelle in Paris.

If a morphotype could neither be assigned to an existing species nor satisfactorily compared (cf.) or given a firm affinity (aff.) to an existing species, then a new species is proposed if two or more specimens were observed and measured and the material is of sufficient quality. We made one exception to this in proposing *Syncolporites rostro* sp. nov., which is represented by a single specimen. However, this specimen is very well preserved and the morphology of the grain is highly distinctive.

If a morphotype was distinctive and could neither be assigned to an existing species nor satisfactorily compared (cf.) or given a firm affinity (aff.) to an existing species, but the material was insufficient to propose a new species, either because only one specimen was encountered or because of poor preservation in the population of specimens examined, then an informal species epithet is provided. Such informal species could be formalised in future work.

Table 1. Details of the samples examined together with palynofacies and depositional environment from Oboh-Ikuenobe et al. (2005), the number of specimens counted in each sample, the observed richness of each sample, and the number of expected species in each sample at different numbers of individuals following individual rarefaction.

Formation	Age	Section and sample number	Height in section (m)	Sample number (Oboh-Ikuenobe et al. 2005)	Palynofacies	Depositional environment	Lithology	Specimens	Sobs	S(100)	S(150)
Ameki	?Ypresian	Amaogugu 7.1	8.2	7	–	–	VF sandstone	223	57	40.42	48.68
Ameki	?Ypresian	Amaogugu 1.1	0.2	1	–	–	Shale	233	76	50.14	62.16
Ameki	?Ypresian	Ameke 11.1	30.7	11	C	Estuarine/proximal–distal lagoon	Shale	175	55	41.30	51.04
Ameki	?Ypresian	Ameke 1.1	3	1	D	Distal lagoon/foreshore	Siltstone	197	64	46.45	56.86
Imo	?Thanetian	Ozuitem 6.1	35	6	C	Estuarine/proximal–distal lagoon	Shale	301	58	36.63	43.94
Imo	?Thanetian	Ozuitem 3.1	28	3	D	Distal lagoon/foreshore	Shale	300	67	40.17	48.98
Upper Nsukka	Selandian	Okigwe B 7.1	38	7	B	Estuarine/proximal lagoon	Shale	267	50	32.30	39.05
Upper Nsukka	Selandian	Okigwe B 6.1	33	6	B	Estuarine/proximal lagoon	Mudstone	280	55	36.17	43.16
Upper Nsukka	Selandian	Okigwe B 4.1	28.5	4	D	Distal lagoon/foreshore	Mudstone	254	29	17.57	21.96
Upper Nsukka	Selandian	Okigwe B 3.1	11	3	C	Estuarine/proximal–distal lagoon	Mudstone	300	54	31.86	39.89
Upper Nsukka	Selandian	Okigwe B 2.1	6	2	D	Distal lagoon/foreshore	Black shale	302	44	27.71	33.18
Upper Nsukka	Selandian	Okigwe B 1.1	2.5	1	B	Estuarine/proximal lagoon	Black shale	300	40	28.31	32.74
Upper Nsukka	Selandian	Okigwe A 7.1	33	7	D	Distal lagoon/foreshore	Black shale	303	45	28.08	33.82
Upper Nsukka	Selandian	Okigwe A 5.1	18	5	B	Estuarine/proximal lagoon	Black shale	300	47	29.73	35.88
Upper Nsukka	Selandian	Okigwe A 1.1	2	1	B	Estuarine/proximal lagoon	Black shale	301	52	31.36	38.29

Sobs = number of species observed; S(100) number of species expected at 100 individuals; S(150) number of species expected at 150 individuals.

If a morphotype was either insufficiently distinctive or encompassed a large degree of morphological variation and could neither be satisfactorily provided with a single formal or informal species epithet nor be split into two or more formal or informal species, then the species abbreviation 'sp.' is used. If more than one such morphotype was encountered within a genus, then morphotypes are given successive abbreviations – sp. 1, sp. 2 and so on. Such morphotypes that encompass a relatively wide range of morphological variation could be split and formally named in future work. Morphotypes that could not be adequately characterised owing to poor orientation within the slide, obstruction by palynological debris, or poor preservation are not included in this paper.

3. Systematic palaeontology

One hundred and sixty-nine pollen and spores are described. The descriptions are arranged into morphological groups and then alphabetically within each group. The descriptions include 29 spores, two gymnosperm pollen grains, and 138 angiosperm pollen grains. Two new spore species are proposed, and one new genus and 18 new species of angiosperm pollen are proposed. The new genus contains two new species and these, together with two other new angiosperm pollen species and one spore species, are taxa that had been given informal names in previous work and are formalised here. Informal species names are given in italic typeface within quotation marks.

The descriptive terminology used here follows Punt et al. (2007). Specimens were located using England Finder co-ordinates, and the microscope slides used in this work are deposited in the palynology collection of the Smithsonian Tropical Research Institute, Panama. Numbers of specimens measured and observed are reported for all species described. A botanical affinity to the order or family level is reported for pollen grains and spores where possible, but clade-level affinities such as monocot or eudicot are omitted.

Abbreviations:

nm = number of specimens measured

no = number of specimens observed

Pteridophyte and Bryophyte spores

Alete spores

Genus *Rugaletes* Foster 1979

Type. *Rugaletes playfordii* Foster 1979

Rugaletes playfordii Foster 1979

Plate 1, figure 1

Diagnosis. Alete, sub-circular-oval, length 46 µm, width 38 µm, rugulate, muri 3–10 µm long, 1 µm wide, grooves 0.5 µm wide.

Description. Monad, amb sub-circular-oval; alete, sporoderm 1-layered, exospore 2 µm thick; surface ornamentation

rugulate over entire body, muri 3–10 µm in length, 1 µm in width, grooves 0.5 µm in width.

Dimensions. Smallest dimension 38 µm, largest dimension 46 µm; nm: 1; no: 7.

Material. Amaogugu 1.1 (P58,1), specimen slightly damaged.

Monolete spores

Genus *Cicatricosporites* Pflug & Thomson in Thomson & Pflug 1953

Type. *Cicatricosporites eocenicus* (Selling 1944) Jansonius & Hills 1976

Cicatricosporites eocenicus (Selling 1944) Jansonius & Hills 1976

Plate 1, figures 2–3

Synonymy. *Cicatricosporites norrisii* Srivastava 1971.

Diagnosis. Monolete, equatorial diameter 45 µm, oval and plano-convex, cicatricose, muri arranged parallel to laesura.

Description. Monad, lateral shape oval and plano-convex, monolete, margo 2 µm wide, margo distinct and formed of a single ridge either side of the commissure, commissure 33 µm in length; sporoderm 1-layered, exospore 1.5 µm; surface ornamentation striate (cicatricose), muri 1.5 µm wide and spaced 0.5 µm apart, arranged parallel to laesura.

Dimensions. Equatorial diameter 45 µm, polar axis 31 µm; nm: 1; no: 2.

Material. Ozuitem 6.1 (Q42,1), equatorial view.

Botanical affinity. Schizaeaceae (Jaramillo and Rueda 2023).

Genus *Laevigatosporites* Ibrahim 1933

Type. *Laevigatosporites thiessenii* Kosanke 1943

Laevigatosporites aff. *catanejensis* Muller et al. 1987

Plate 1, figure 4

Diagnosis. Monolete, equatorial diameter 60 µm, sub-circular, laesura straight and reaching equator, 2-layered sporoderm, granulate-gemmate.

Description. Monad, lateral shape sub-circular, slightly plano-convex; monolete, commissure distinct, laesura straight, reaches equator (39 µm); sporoderm 2-layered, exospore 1.5 µm, inner exospore 0.5 µm thick, outer exospore 1 µm thick; surface ornamentation granulate-gemmate, granulae distributed densely over the spore surface, isolated gemmae distributed randomly over the spore surface.

Dimensions. Equatorial diameter 60 µm; nm: 1; no: 6.

Comparisons. *Laevigatosporites catanejensis* Muller et al. 1987 is very similar but has granulae sparsely distributed over the spore surface.

Material. Amaogugu 1.1 (X68,3), equatorial view.

Botanical affinity. Marattiaceae (Balme 1995; Wang et al. 2001).

Laevigatosporites ovatus Wilson & Webster 1946

Plate 1, figure 5

Diagnosis. Monolete, equatorial diameter 34 µm, oval and plano-convex, laesura straight, laevigate.

Description. Monad, amb oval; monolete, laesura straight, approximately half the equatorial diameter of the spore; sporoderm 1-layered, exospore 1–1.5 µm thick; surface ornamentation laevigate.

Dimensions. Equatorial diameter 29–(34)–39 µm; nm: 5; no: 76.

Material. Okigwe B4.1 (D44), polar view.

Botanical affinity. Marattiaceae (Balme 1995; Wang et al. 2001).

Genus *Polypodiisporites* Potonié 1931 in Potonié & Gelletich 1933 ex Potonié 1956, emend. Khan & Martin 1972

Type. *Polypodiisporites favus* (Potonié 1931) Potonié 1956

Polypodiisporites specious Sah 1967

Plate 1, figure 6

Synonymy. *Polypodiisporites* aff. *specious* Jaramillo & Dilcher 2001.

Diagnosis. Monolete, equatorial diameter 40 µm, reniform, proximal face psilate, verrucate elsewhere, verrucae denser on distal face than elsewhere.

Description. Monad, lateral shape oval and plano-convex, reniform; monolete, laesura 20 µm; sporoderm 1-layered, exospore 0.5–1 µm thick; surface ornamentation psilate on proximal face, rest of spore verrucate, verrucae 1–3.5 µm in diameter, 0.5–1 µm high and spaced up to 1.5 µm apart, verrucae irregularly shaped, some verrucae rounded, others polygonal with up to six distinct faces, verrucae denser on the distal face (spaced <0.5 µm apart) than elsewhere on the spore.

Dimensions. Equatorial diameter 34.5–(40)–45 µm; nm: 9; no: 106.

Comparisons. Specimens assigned to this species conform to *Polypodiisporites* aff. *specious* Jaramillo & Dilcher 2001.

Material. Ozuitem 3.1 (W62, 3), equatorial view.

Botanical affinity. Polypodiaceae (D'Apolito et al. 2021).

Polypodiisporites sp.

Plate 1, figure 7

Diagnosis. Monolete, equatorial diameter 28 µm, oval, granulate-verrucate, granulae denser on proximal face than elsewhere, verrucae scarce and isolated.

Description. Monad, amb oval, slightly plano-convex; monolete, laesura straight, does not reach equator (20 µm); sporoderm 1-layered, exospore 1 µm thick; surface ornamentation granulate-verrucate, verrucae scarce and isolated, 0.5 µm high and irregularly shaped, granulae faint and distributed densely over the spore surface, granulae denser on the proximal face.

Dimensions. Equatorial diameter 28 µm; nm: 1; no: 8.

Comparisons. *Scabramonoletes microreticuloides* Ramanujam 1966 lacks verrucae and has granulae that fuse into a microreticulum.

Material. Okigwe B4.1 (S42,1), polar view.

Trilete spores

Genus *Apiculatasporites* Ibrahim 1933

Type. *Apiculatasporites spinulistriatus* Potonié & Kremp 1955

Apiculatasporites sp. 1

Plate 1, figure 8

Diagnosis. Trilete, sub-circular, 16 µm, echinate, spines 2 µm high, expanded at base and evenly distributed.

Description. Monad, amb sub-circular; trilete; sporoderm 1-layered, exospore <0.5 µm thick; surface ornamentation echinate, spines 2 µm in height and 1 µm in diameter, spines taper sharply from a relatively wide base to a narrow tip, spines distributed evenly over the spore surface at 1–2 µm intervals.

Dimensions. Equatorial diameter 16 µm; nm: 1; no: 26.

Material. Amaogugu 1.1 (W54,1), polar view, specimen slightly folded.

Apiculatasporites sp. 2

Plate 1, figure 9

Diagnosis. Trilete, kyrtomate, triangular and slightly convex, 18 µm, echinate, spines 4 µm in height and 2 µm in diameter.

Description. Monad, amb triangular and slightly convex; trilete, kyrtomate, kyrtome surrounds trilete mark, 1.5 µm wide; sporoderm 1-layered, exospore 1.5 µm thick; surface ornamentation echinate, spines 4 µm in height and 2 µm in diameter, spines taper sharply from a relatively wide base to a narrow tip, spines distributed over the spore surface at 1–5 µm intervals.

Dimensions. Equatorial diameter 18 µm; nm: 1; no: 11.

Material. Okigwe B4.1 (X33), polar view.

Genus *Deltoidospora* Miner 1935

Type. *Deltoidospora hallii* (Miner 1935) Potonié 1956

Deltoidospora sp. 1

Plate 1, figures 10–11

Diagnosis. Trilete, equatorial diameter 35 µm, sub-triangular, laesurae long, psilate.

Description. Monad, amb sub-triangular; trilete, laesurae straight and long, do not reach equator (11–15 µm), thin margo present, margo 0.5 µm wide and formed by slight thickening of the sporoderm; sporoderm 1-layered, exospore 0.5–1.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 27–(35)–42.5 µm; nm: 26; no: 293.

Material. Okigwe B3.1 (M53,2), polar view, Ameke 11.1 (J58), polar view.

Botanical affinity. Cyathaceae, Dicksoniaceae, Dipteridaceae, Matoniaceae (Balme 1995; Mander 2011).

Deltoidospora sp. 2

Plate 1, figure 12

Diagnosis. Trilete, equatorial diameter 31 µm, sub-triangular, laesurae long, kyrtomate, psilate.

Description. Monad, amb sub-triangular; trilete, laesurae straight and long, do not reach equator (9–12 µm), kyrtome present; sporoderm 1-layered, exospore 0.5–1.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 26.3–(31)–36.1 µm; nm: 14; no: 36.

Material. Okigwe A5.1 (Q43,4), polar view.

Botanical affinity. Cyathaceae, Dicksoniaceae, Dipteridaceae, Matoniaceae (Balme 1995; Mander 2011).

Genus *Densoisporites* Weyland & Krieger 1953 emend.
Dettman 1963

Type. *Densoisporites velatus* (Weyland & Krieger 1953) Potonié 1956

Densoisporites sp.

Plate 1, figures 13–14

Diagnosis. Trilete, equatorial diameter 33 µm, sub-circular, cingulate, laesurae straight, proximal face psilate, distal face foveolate.

Description. Monad, amb sub-circular; trilete, laesurae reach equator, cingulum 4 µm thick, psilate and with prominent internal radial structures; sporoderm 2-layered, exospore 1 µm; surface ornamentation on the distal face foveolate, with scattered irregularly shaped verrucae 2–4 µm wide and 0.5 µm high, proximal face psilate.

Dimensions. Equatorial diameter 33 µm; nm: 1; no: 1.

Comparisons. This morphotype is assigned to *Densoisporites* Weyland & Krieger 1953 emend. Dettman 1963 on the basis of its cingulum with internal radial structure. *Polypodiaceoisporites* Potonié 1951 ex Potonié 1956 has a triangular amb; *Pteridacidites* Sah 1967 and *Cyatheacidites* Cookson 1947 ex Potonié 1956 lack prominent internal radial structure in the cingulum.

Material. Okigwe B4.1 (X57,1), polar view, specimen slightly fragmented.

Genus *Dictyophyllidites* Couper 1958 emend. Dettman 1963

Type. *Dictyophyllidites harrisii* Couper 1958

Dictyophyllidites cf. *equiexinus* (Couper 1958) Dettmann 1963

Plate 1, figure 15

Diagnosis. Trilete, equatorial diameter 65 µm, sub-circular, laesurae straight, 1/3 the radius of the amb and slightly unequal in length, psilate.

Description. Monad, amb sub-circular; trilete, laesurae straight, 1/3 the radius of the amb, do not reach equator; sporoderm 1-layered, exospore 3–4.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 62–(65)–68 µm; nm: 2; no: 11.

Comparisons. *Dictyophyllidites equiexinus* (Couper 1958) Dettmann 1963 has longer laesurae and a triangular amb. *Psilatriteles* Van der Hammen 1954 ex Potonié 1956 has laesurae that extend between 3/4 and 4/4 of the amb radius. *Calamospora* Schopf Wilson & Bentall 1944 has a thin sporoderm, less than 2 µm in spores less than 100 µm in diameter.

Material. Okigwe A1.1 (D48,3), polar view.

Genus *Distaverrusporites* Muller 1968

Type. *Distaverrusporites simplex* Muller 1968

Distaverrusporites margaritatus Muller 1968

Plate 1, figures 16–17

Diagnosis. Trilete, equatorial diameter 25 µm, sub-circular, cingulate, proximal face psilate, distal face verrucate.

Description. Monad, amb sub-circular; cingulum 1–2 µm thick with prominent dense verrucae 1–3 µm wide and 1 µm high, cingulum distinguished from the spore body by a prominent band of exospore 0.5 µm wide; trilete mark faint; sporoderm 1-layered, exospore 1 µm; surface ornamentation on the proximal face psilate, surface ornamentation on the distal face verrucate, verrucae 1–3 µm wide and 0.5 µm high.

Dimensions. Equatorial diameter 20–(25)–30 µm; nm: 3; no: 3.

Comparisons. *Pteridacidites* Sah 1967 lacks ornamentation on the cingulum.

Material. Okigwe B4.1 (V56), polar view.

Distaverrusporites? sp.

Plate 1, figure 18

Diagnosis. Trilete, equatorial diameter 32 µm, sub-circular, laesurae crenulate and reaching equator, large and prominent verrucae at equator, proximal and distal faces scabrate.

Description. Monad, amb sub-circular; trilete, laesurae crenulate, reaching equator (9 µm); sporoderm 1-layered, exospore 1 µm thick; surface ornamentation at the equator verrucate, verrucae 1–5 µm wide and 1–4 µm high, surface ornamentation on proximal and distal faces scabrate.

Dimensions. Equatorial diameter 32 µm; nm: 1; no: 1.

Comparisons. This specimen does not fit into any established genera but is tentatively placed in *Distaverrusporites* Muller 1968. *Leptolepidites* Couper 1953 emend. Schulz 1967 only includes species with verrucate ornamentation on the distal face. *Distaverrusporites margaritatus* Muller 1968 has two size classes of verrucae: *Distaverrusporites simplex* Muller 1968 is verrucate at the equator and on the distal face, *Ischyosporites granulosus* Tralau 1968 has fewer and much larger verrucae.

Material. Okigwe A7.1 (P48,1), polar view.

Genus *Foveotriteles* Potonié 1956

Type. *Foveotriteles scrobiculatus* (Ross ex Weyland & Krieger 1953) Potonié 1956

Foveotriteles margaritae (Van der Hammen 1954) Germeraad et al. 1968

Plate 1, figure 19

Diagnosis. Trilete, equatorial diameter 53 µm, laesurae straight and unequal in length, foveo-reticulate, lumina 0.5–2 µm, muri 0.5 µm.

Description. Monad, amb sub-circular; trilete, laesurae straight and slightly indistinct, do not reach equator, unequal length (5–17 µm); sporoderm 1-layered, exospore 2 µm thick;

surface ornamentation of exospore foveo-reticulate, lumina 0.5–2 µm, muri 0.5 µm anastomosing across the spore.

Dimensions. Equatorial diameter 53 µm; nm: 1; no: 1.

Material. Amaogugu 7.1 (K51,4), polar view.

Foveotriletes sp.

Plate 1, figure 20

Diagnosis. Trilete, sub-triangular, equatorial diameter 43.5 µm, laesurae straight and long, foveolate.

Description. Monad, amb sub-triangular and slightly convex; trilete, laesurae straight and long, laesurae reach equator; sporoderm 1-layered, exospore 1 µm; surface ornamentation foveolate, lumina polygonal and densely distributed over the entire spore surface.

Dimensions. Equatorial diameter 38.5–(43.5)–48 µm; nm: 3; no: 3.

Comparisons. *Foveotriletes parviretus* (Balme) Dettman 1963 has an amb that is triangular and concave.

Material. Okigwe B1.1 (L45,4), polar view.

Genus *Matonisporites* Couper 1958

Type. *Matonisporites phleboteroides* Couper 1958

Matonisporites sp.

Plate 1, figures 21–22

Diagnosis. Trilete, triangular, equatorial diameter 33 µm, valvate, marginate, verrucate.

Description. Monad, amb triangular and slightly convex, exine differentially thickened from <0.5 µm in the interradian regions to 2.5 µm at the apices of the outline where it extends to form valvae, valvae psilate, 13 µm wide and extending 2.5 µm; trilete, laesurae do not reach equator, margo 1.5 µm wide, margo distinct; sporoderm 1-layered, exospore 0.5 µm thick; surface ornamentation verrucate, verrucae on proximal face 0.5 µm high, 1 µm wide and spaced regularly over the proximal face at 1 µm intervals, distal face psilate, margo granulate.

Dimensions. Equatorial diameter 33 µm; nm: 1; no: 1.

Comparisons. *Matonisporites phleboteroides* Couper 1958 is wholly psilate, smaller, has a more continuous and pronounced thickening of the exine in the interradian regions, and has smaller valvae.

Material. Ameke 11.1 (O44,2), polar view.

Genus *Microreticulatisporites* Knox 1950

Type. *Microreticulatisporites lacunosus* (Ibrahim 1933) Knox 1950
Microreticulatisporites cf. *uniformis* Singh 1964

Plate 1, figures 23–24

Diagnosis. Trilete, equatorial diameter 30 µm, laesurae straight and unequal in length, reticulate, heterobrochate, lumina 0.5–1 µm, muri 0.5 µm.

Description. Monad, amb sub-circular; trilete, laesurae straight and long; sporoderm 1-layered, exospore 1 µm thick; surface ornamentation of exospore reticulate, heterobrochate, lumina 0.5–1.5 µm, muri 0.5 µm.

Dimensions. Equatorial diameter 30 µm; nm: 1; no: 3.

Comparisons. *Microreticulatisporites uniformis* Singh 1964 has a coarser reticulum (lumina 2–3 µm wide).

Material. Okigwe B1.1 (Y63,1), polar view.

Genus *Osmundacidites* Couper 1953 emend. Norris 1986

Type. *Osmundacidites wellmanii* Couper 1953

Osmundacidites minor Jaramillo & Dilcher 2001

Plate 1, figures 25–26

Diagnosis. Trilete, circular, equatorial diameter 31 µm, laesurae straight and long, marginate, scabrate.

Description. Monad, amb circular; trilete, margo <0.5 µm, laesurae straight and long (12 µm), almost reaching equator; sporoderm 1-layered, exospore 0.5 µm; surface ornamentation scabrate in proximal and distal face, sculptural elements distributed densely and evenly over the spore surface.

Dimensions. Equatorial diameter 30–(31)–32 µm; nm: 3; no: 8.

Material. Okigwe A1.1 (P41), polar view.

Botanical affinity. Osmundaceae (Mander 2011).

Genus *Polypodiaceoisporites* Potonié 1951 ex Potonié 1956

Type. *Polypodiaceoisporites speciosus* Potonié 1951 ex Potonié 1956

Polypodiaceoisporites? fossulatus Jaramillo & Dilcher 2001

Plate 1, figures 27–28

Diagnosis. Trilete, equatorial diameter 47 µm, sub-triangular, cingulate, cingulum 4.5 µm in the interradian regions and at the apices of the outline, kyrtomate, proximal face verrucate, distal face fossulate.

Description. Monad, amb sub-triangular, cingulum uniform in thickness, 4.5 µm in the interradian regions and at the apices of the outline; trilete, commissure distinct, laesurae do not extend into cingulum, kyrtome present and formed of fused verrucae; sporoderm 1-layered, exospore 1.5 µm thick; surface ornamentation verrucate on proximal face, fossulate on distal face, fossulae 1–2 µm wide and occasionally joined together to form a negative reticulum, cingulum psilate.

Dimensions. Equatorial diameter 44–(47.4)–51 µm; nm: 2; no: 12.

Comparisons. Spores within *Polypodiaceoisporites* Potonié 1951 ex Potonié 1956 have a reticulate distal face. These specimens conform in every respect to *Polypodiaceoisporites? fossulatus* Jaramillo & Dilcher 2001 except for the measurements of the cingulum, which is thickened in the interradian region in *Polypodiaceoisporites? fossulatus* Jaramillo & Dilcher 2001.

Material. Ameke 11.1 (V57,2), polar view.

Botanical affinity. Pteridaceae (Jaramillo et al. 2014).

Polypodiaceoisporites 'striatus'

Plate 1, figures 29–30

Diagnosis. Trilete, equatorial diameter 32 µm, sub-triangular, rounded at the apices, cingulate, cingulum 1 µm thick in the

interradial regions and 0.5 µm thick at the apices of the outline, proximal face striate (cicatricose), distal face rugulate.

Description. Monad, amb sub-triangular, rounded at the apices, cingulum 1 µm thick in the interradian regions and 0.5 µm thick at the apices of the outline; trilete, commissure distinct, laesurae do not reach equator; sporoderm 1-layered, exospore 0.5 µm thick; surface ornamentation striate (cicatricose) on proximal face, muri 1–2 µm wide and spaced 1–1.5 µm apart, arranged concentrically, rugulate on distal face, muri 1.5–2 µm wide, grooves 0.5–1 µm wide.

Dimensions. Equatorial diameter 27.5–(31.5)–35 µm; nm: 2; no: 2.

Comparisons. *Polypodiaceoisorites pseudopsilatus* Lorente 1986 is rugulate on the distal face but psilate on the proximal face.

Material. Amaogugu 7.1 (T44), polar view.

Genus *Psilatriletes* Van der Hammen 1954 ex Potonié 1956

Type. *Psilatriletes detortus* (Weyland & Krieger 1953) Potonié 1956

Psilatriletes brevilaesuratus sp. nov.

Plate 2, figure 1

Synonymy. *Psilatriletes 'brevilaesuratus'* Jaramillo et al. 2014.

Diagnosis. Trilete, equatorial diameter 79 µm, sub-circular, laesurae crenulate, marginate, granulate in interradian areas, psilate elsewhere.

Etymology. After the short laesurae.

Description. Monad, amb sub-circular; trilete, laesurae slightly crenulate, do not reach equator (26 µm), margo thin (0.5 µm), interradian areas characterised by granular surface ornamentation, granules distributed unevenly across the interradian areas and spaced <0.5–3 µm apart; sporoderm 1-layered, exospore 1 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 75–(79)–83 µm; nm: 2; no: 2.

Comparisons. This species conforms to the informal species *Psilatriletes 'brevilaesuratus'* Jaramillo et al. (2014) (see Jaramillo and Rueda 2023) and is formalised here.

Material. Holotype Amaogugu 1.1 (V42,3), polar view, Plate 2, figure 1.

Botanical affinity. *Antrophyum* (Pteridaceae) (Jaramillo et al. 2014).

Genus *Pteridacidites* Sah 1967

Type. *Pteridacidites africanus* Sah 1967

Pteridacidites sp. 1

Plate 2, figures 2–3

Diagnosis. Trilete, equatorial diameter 36 µm, triangular and rounded at apices, marginate, laesurae straight, proximal face granulate–verrucate, distal face verrucate.

Description. Monad, amb triangular, rounded at the apices; trilete, commissure distinct, margo psilate 1.5 µm wide, laesurae straight and long, do not extend into cingulum (12 µm), cingulum 4 µm thick and psilate; sporoderm 1-layered, exospore 1 µm; surface ornamentation on the distal face verrucate, verrucae 3–5 µm wide and 1–4 µm high,

distributed 1–3 µm over the spore surface, surface ornamentation on the proximal face granulate–verrucate, granules distributed sparsely over the spore surface, verrucae 1 µm high and 0.5 µm wide, distributed sparsely over the spore surface.

Dimensions. Equatorial diameter 36 µm; nm: 1; no: 6.

Comparisons. *Pteridacidites* sp. 1 Jaramillo & Dilcher 2001 has larger and fewer verrucae (Jaramillo and Dilcher 2001). *Pteridacidites africanus* Sah 1961 is larger (60–80 µm).

Material. Ameke 1.1 (V48,2), polar view.

Pteridacidites sp. 2

Plate 2, figures 4–5

Diagnosis. Trilete, equatorial diameter 31 µm, triangular and slightly convex, laesurae straight and long, cingulate, proximal face densely verrucate, distal face rugulate.

Description. Monad, amb triangular, slightly convex; trilete, laesurae straight and long, and extend 1 µm short of the cingulum (13 µm), cingulum 3 µm thick and psilate; sporoderm 1-layered, exospore 1 µm; surface ornamentation on the distal face rugulate, surface ornamentation on the proximal face verrucate, verrucae 1 µm high and <0.5 µm wide, distributed densely over the spore surface.

Dimensions. Equatorial diameter 31 µm; nm: 1; no: 6.

Comparisons. *Pteridacidites* sp. 1 Jaramillo & Dilcher 2001 has a psilate proximal face. *Pteridacidites africanus* Sah 1961 is larger (60–80 µm).

Material. Ameke 1.1 (T46), polar view, distal face slightly fragmented.

Genus *Punctatisporites* Ibrahim 1933

Type. *Punctatisporites punctatus* Ibrahim 1933

Punctatisporites interfoveolatus sp. nov.

Plate 2, figures 6–9

Diagnosis. Trilete, equatorial diameter 39 µm, sub-circular, laesurae short, foveolate ornamentation in interradian area, psilate elsewhere.

Etymology. After the foveolate interradian area.

Description. Monad, amb sub-circular; trilete, laesurae slightly curved and short, do not reach equator (13 µm), interradian areas characterised by foveolate–reticulate surface ornamentation, reticulum heterobrochate, muri 0.5 µm wide, lumina 0.5–1.5 µm, generally increasing in size towards laesurae; sporoderm 1-layered, exospore 0.5 µm thick; surface ornamentation psilate elsewhere.

Dimensions. Equatorial diameter 34–(39)–43.5 µm; nm: 11; no: 68.

Comparisons. *Psilatriletes* Van der Hammen 1954 ex Potonié 1956 is strictly psilate. *Punctatisporites punctatus* Ibrahim 1933 Krutzsch 1959, has uniformly punctate surface ornamentation (the 'sandpaper' of Ibrahim (1933); see Jansonius and Hills 1976 card 2286).

Material. Holotype Okigwe B1.1 (R33,4) Plate 2, figures 6–7, polar view; paratypes Okigwe B1.1 (E43, Plate 2, figure 8, polar view; X50, Plate 2, figure 9, polar view).

Genus *Verrucosisporites* Ibrahim 1933 emend. Potonié & Kremp 1954

Type. *Verrucosisporites verrucosus* Ibrahim 1933

Verrucosisporites major (Couper 1958) Burden & Hills 1989
Plate 2, figures 10–11

Synonymy. *Leptolepidites major* Couper 1958.

Converrucosisporites saskatchewanensis Pocock 1962.

Verrucosisporites rarus Burger 1966.

Diagnosis. Trilete, sub-circular, equatorial diameter 32 µm, laesurae straight and long, granulate around laesurae, verrucate elsewhere, verrucae at equator rounded, verrucae polygonal elsewhere and forming rugulae on distal face.

Description. Monad, amb sub-circular; trilete, laesurae straight, almost reaching equator (13 µm); sporoderm 1-layered, exospore 1 µm thick; surface ornamentation verrucate, verrucae at the equator rounded (1–1.5 µm high), verrucae elsewhere polygonal 1–3 µm wide, and coalescing into rugulae on the distal face, surface ornamentation around the laesurae granulate.

Dimensions. Equatorial diameter 31–(31.75)–32.5 µm; nm: 2; no: 5.

Comparisons. *Tuberositriletes montuosus* Doring 1964 is triangular and larger (60–78 µm), *Tuberositriletes verrucatus* Jaramillo & Dilcher 2001 is triangular and has larger verrucae, the verrucae of *Leptolepidites verrucatus* Couper 1953 are equally developed on proximal and distal faces.

Material. Ameke 1.1 (N49), polar view.

Verrucosisporites cf. *verrucosus* Ibrahim 1933

Plate 2, figure 12

Diagnosis. Trilete, circular, equatorial diameter 23 µm, laesurae straight and long, marginate, verrucate.

Description. Monad, amb circular; trilete, margo <0.5 µm, margo psilate, laesurae straight and long (9 µm) almost reaching equator; sporoderm 1-layered, exospore 1 µm; surface ornamentation verrucate on proximal and distal face, verrucae distributed densely and evenly over the spore surface.

Dimensions. Equatorial diameter 20.5–(23)–25 µm; nm: 2; no: 4.

Comparisons. *Verrucosisporites verrucosus* Ibrahim 1933 has slightly shorter laesurae, lacks a margo and is larger.

Material. Okigwe B3.1 (R37,4), polar view.

Genus *Verrutrites* Pierce 1961

Type. *Verrutrites verus* Pierce 1961

Verrutrites virueloides Jaramillo et al. 2007

Plate 2, figure 13

Synonymy. *Verrutrites 'viruelensis'* Instituto Colombiano del Petróleo (Colombian Petroleum Institute).

Diagnosis. Trilete, equatorial diameter 44 µm, sub-triangular, broad and rounded at the apices, laesurae do not reach equator, scabrate, sculptural elements sparsely distributed.

Description. Monad, amb sub-triangular, broad and rounded at the apices; trilete, laesurae straight, not reaching equator (10 µm); sporoderm 1-layered, exospore 1 µm thick; surface ornamentation scabrate, scabrae distributed sparseley over the spore surface (spaced 1–2 µm apart).

Dimensions. Equatorial diameter 44 µm; nm: 1; no: 7.

Material. Okigwe A1.1 (E45), polar view.

Genus *Zlivisporis* Pacltová 1961

Type. *Zlivisporis blanensis* Pacltová 1961

Zlivisporis blanensis Pacltová 1961

Plate 2, figure 14

Synonymy. *Triporoletes blanensis* (Pacltová) Srivastava 1975.

Diagnosis. Trilete, equatorial diameter 48 µm, sporoderm 2-layered, exospore reticulate, heterobrochate, perispore granulate.

Description. Monad, amb circular; trilete, laesurae straight, not reaching equator (17 µm); sporoderm 2-layered, exospore 0.5 µm thick, perispore 3.5 µm thick; surface ornamentation of exospore reticulate, heterobrochate, lumina 1.5–4 µm, muri 0.5 µm, surface ornamentation of perispore granulate.

Dimensions. Equatorial diameter 48 µm; nm: 1; no: 4.

Material. Amaogugu 1.1 (U44), polar view.

Botanical affinity. Marchantiaceae (Eisawi & Schrank 2008).

Gymnosperm pollen

Genus *Cycadopites* Wodehouse 1933 emend. Herbst 1965

Type. *Cycadopites follicularis* Wilson & Webster 1946

Cycadopites deterius (Balme 1957) Pocock 1970

Plate 2, figure 15

Synonymy. *Entylissa deterius* Balme 1957.

Diagnosis. Monocolpate, elliptic, atectate, psilate, length 49 µm, width 22 µm.

Description. Monad, bilateral, heteropolar, amb elliptic; monocolpate, colpus long, borders curved, ends flared; exine atectate, 0.5 µm thick; surface ornamentation psilate.

Dimensions. Length 49 µm, width 22 µm; nm: 1; no: 18.

Material. Okigwe B1.1 (V55), polar view.

Botanical affinity. Cycadales/Ginkgoales (Mander 2011).

Genus *Cyclusphaera* Elisk 1966

Type. *Cyclusphaera euribei* Elisk 1966

Cyclusphaera scabrata Jaramillo & Dilcher 2001

Plate 2, figure 16

Synonymy. *Cyclusphaera* cf. *euribei* Schuler & Doubinger 1970.

Diagnosis. Diporate, sub-circular, intectate, scabrate, largest dimension 35 µm, smallest dimension 31 µm.

Description. Monad, radial, amb sub-circular; diporate, pori slightly elliptic (22 µm long, 17 µm wide), margin of pori irregular; exine intectate, 2 µm thick; surface ornamentation scabrate.

Dimensions. Largest dimension 35 µm, smallest dimension 31 µm; nm: 1; no: 11.

Material. Okigwe B4.1 (L46,2).

Botanical affinity. Araucariaceae (Jaramillo et al. 2013).

Angiosperm pollen

Inaperturate pollen

Genus *Inaperturopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type. *Inaperturopollenites dubius* (Potonié & Venitz 1934) Pflug & Thomson in Thomson & Pflug 1953

Inaperturopollenites fossulatus sp. nov.

Plate 2, figures 17–18

Diagnosis. Inaperturate, sub-triangular, intectate, fossulate, largest dimension 27 µm.

Etymology. After the fossulate surface ornamentation.

Description. Monad, amb sub-triangular; inaperturate; exine intectate, <0.5 µm thick; surface ornamentation fossulate, grooves 0.5 µm wide.

Dimensions. Largest dimension 24.5–(27)–29 µm; nm: 2; no: 8.

Comparisons. *Inaperturopollenites microclavatus* Regali et al. 1974 has clavate surface ornamentation. *Inaperturopollenites cursus* Sarmiento 1992 has reticulate surface ornamentation.

Material. Holotype Ozuitem 3.1 (W34,2), Plate 2, figures 17–18.

Inaperturopollenites? sp. 1

Plate 2, figure 19

Diagnosis. Inaperturate?, sub-circular, intectate, gemmate with scattered clavae, largest dimension 50 µm.

Description. Monad, amb sub-circular; inaperturate?; exine intectate, 1 µm thick; surface ornamentation gemmate, gemmae 1–5 µm wide, 1–4 µm high, spaced 1–5 µm apart and distributed irregularly over the grain surface, scattered clavae.

Dimensions. Largest dimension 50 µm; nm: 1; no: 1.

Comparisons. *Inaperturopollenites microclavatus* Regali et al. 1974 has clavate surface ornamentation. *Inaperturopollenites cursus* Sarmiento 1992 has reticulate surface ornamentation. Specimen differs from other *Inaperturopollenites* species in having an intectate exine and mixed gemmate–clavate surface ornamentation but the material is insufficient to erect a new species. *Gemmamonocolpites galeanoana* Hoorn and Bacon 2018 lacks clavae.

Material. Ameke 1.1 (K51), specimen fragmented.

Inaperturopollenites? sp. 2

Plate 2, figure 20

Diagnosis. Inaperturate?, oval, tectate, clavate with scattered gemmae, largest dimension 95 µm.

Description. Monad, amb oval; inaperturate?; exine tectate, columellae indistinct, nexine 0.5 µm thick, tectum 1 µm thick; surface ornamentation clavate, clavae 1 µm wide, 2 µm high, densely distributed over the grain surface, scattered gemmae, 8 µm wide, 7 µm high.

Dimensions. Largest dimension 95 µm; nm: 1; no: 3.

Comparisons. *Inaperturopollenites microclavatus* Regali et al. 1974 has clavate surface ornamentation. *Inaperturopollenites cursus* Sarmiento 1992 has reticulate surface ornamentation. Specimen differs from other *Inaperturopollenites* species in having a tectate exine, mixed clavate–gemmate surface ornamentation and large size (95 µm), but the material is insufficient to erect a new species.

Material. Ozuitem 3.1 (X42,1), specimen fragmented.

Genus *Praedapollis* Boltenhagen & Salard 1973

Type. *Praedapollis africanus* Boltenhagen & Salard 1973

Praedapollis africanus Boltenhagen & Salard 1973

Plate 2, figures 21–22

Diagnosis. Sub-circular, endoapertures absent, tectate, echinae distributed densely and unevenly across a free inner body, reticulate, inner body largest dimension 35 µm wide, outer body largest dimension 46 µm.

Description. Monad, radial, amb sub-circular; endoapertures absent; tectate, columellae distinct, nexine 1 µm thick, columellae 1.5 µm thick, 1 µm wide, positioned on the surface of a free inner body separated from the enclosing tectum, columellae formed of echinae distributed densely and unevenly across the surface of the nexine, tectum 1–1.5 µm thick; surface ornamentation reticulate, lumina 3–7 µm wide, muri 1 µm wide.

Dimensions. Inner body smallest dimension 28 µm, largest dimension 35 µm wide, outer body smallest dimension 42 µm, largest dimension 46 µm; nm: 1; no: 12.

Comparisons. *Spirosyncolpites spiralis* González Guzmán 1967 has a wider muri (2 µm) and wider (2–3 µm) and thicker (5–6 µm) columellae. *Periretitricolpites anambraensis* Jan du Chêne et al. 1978 is tricolpate. *Praedapollis africanus* Boltenhagen & Salard 1973 is described as triporate (Jansonius and Hills 1976, card 2140) but the specimens examined here lack endoapertures. The holotype specimen of *P. africanus* Boltenhagen & Salard 1973 was examined and found to lack endoapertures, but one paratype specimen examined consists of an inner body that lacks an enclosing reticulum and is apparently triporate. In the type material examined there is no specimen of *P. africanus* Boltenhagen & Salard 1973 that consists of an inner body with apertures together with an enclosing reticulum. On specimens of *P. africanus* Boltenhagen & Salard 1973 recovered from the Neogene Niger Delta, Legoux (1978, p. 280) commented:

‘Dans certains cas, on devine des ‘encoches’ sur la nexine qui correspondent peut-être aux pores (Pl. 13, fig. 2–3); dans d’autres cas, aucun pore n’est visible (Pl. 12, fig. 6 et Pl. 13 fig. 1). Sur l’un des exemplaires, le reticule déchire laisse entrevoir une grande partie de la nexine: aucun pore n’est visible’.

[In some cases, we can guess there are 'notches' on the nexine which perhaps correspond to pores; in other cases, no pore is visible. On one of the specimens, the torn reticulum reveals a large part of the nexine: no pore is visible.]

The diagnosis of *P. africanus* Boltenhagen & Salard 1973 highlights this situation: 'pores can only be seen in specimens that have lost the reticulum' (Jansonius and Hills 1976, card 2140). Boltenhagen and Salard (1973) have apparently defined a taxon using specimens with certain morphological features (endoapertures) that are not found together in whole intact specimens. It is unclear whether such a synthetic taxon concept is satisfactory. On the one hand, specimens that have a free inner body with an enclosing reticulum and are lacking endoapertures could represent a different ontogenetic stage to specimens that are apparently triporate but lack an enclosing reticulum. On the other hand, these two morphological types may represent two separate taxa.

Material. Ameke 1.1 (S47).

Botanical affinity. Morley (2000, p. 136–137) compares *P. africanus* Boltenhagen & Salard 1973 to *Arapatiella* (Fabaceae). However, in *Arapatiella* the reticulum is attached to the inner body whereas in *P. africanus* Boltenhagen & Salard 1973 the inner body is free.

Monocolpate pollen

Genus *Longapertites* van Hoeken-Klinkenberg 1964

Type. *Longapertites marginatus* van Hoeken-Klinkenberg 1964

Longapertites microfoveolatus Adegoke & Jan du Chêne 1975

Plate 3, figure 1

Diagnosis. Monocolpate (longaperturate), oblate, tectate, surface ornamentation micropitted, equatorial diameter 48 µm.

Description. Monad, bilateral, oblate, proximal face flat, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the flat proximal face; tectate, columellae distinct, exine 1 µm thick; surface ornamentation micropitted, coarsening slightly to form rugulae in proximal area of the grain, muri 1.5 µm wide, extent of rugulae slightly variable, sometimes covering up to half the grain.

Dimensions. Equatorial diameter 43–(48)–53 µm; nm: 6; no: 135.

Comparisons. *Longapertites rugulatus* Beilstein 1994 has rugulae covering the entire surface of the grain.

Material. Okigwe B1.1 (X38,3), equatorial view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Longapertites proxapertitoides var. *proxapertoides* Van der Hammen & Garcia 1966

Plate 3, figure 2

Diagnosis. Monocolpate (longaperturate), oblate, tectate, surface ornamentation foveolate, equatorial diameter 54 µm.

Description. Monad, bilateral, oblate, proximal face slightly convex, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the slightly convex proximal face; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation foveolate, lumina 0.5–1 µm densely and evenly distributed, some lumina coalesce to form irregular grooves.

Dimensions. Equatorial diameter width 42 µm, equatorial diameter length 49.2–(54)–58 µm; nm: 8; no: 176.

Material. Okigwe A5.1 (X44,2), equatorial view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Longapertites proxapertitoides var. *reticuloides* Van der Hammen & Garcia 1966

Plate 3, figures 3–4

Synonymy. *Longapertites proxapertitoides* var. *reticuloides* González Guzmán 1967.

Diagnosis. Monocolpate (longaperturate), oblate, tectate, surface ornamentation reticulate, heterobrochate, equatorial diameter 35 µm.

Description. Monad, bilateral, oblate proximal face convex, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the convex proximal face; tectate, columellae distinct, simplicolumellate, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, lumina 1–3 µm wide, muri 1 µm wide, lumina gradually increase in size from the distal to the proximal face.

Dimensions. Equatorial diameter 34.6–(35)–36 µm; nm: 2; no: 12.

Material. Amaogugu 1.1 (T38), equatorial view, Ozuitem 3.1 (V65,1), polar view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Longapertites vaneendenburgi Germeraad et al. 1968

Plate 3, figure 5

Diagnosis. Monocolpate (longaperturate), oblate, tectate, surface ornamentation micropitted, equatorial diameter 70 µm.

Description. Monad, bilateral, oblate, proximal face flat, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the flat proximal face; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation micropitted, lumina 0.4 µm densely and evenly distributed.

Dimensions. Equatorial diameter 60.5–(70)–78.5 µm; nm: 5; no: 121.

Material. Okigwe B2.1 (L39,2), equatorial view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Longapertites cf. *marginatus* van Hoeken-Klinkenberg 1964

Plate 3, figure 6

Diagnosis. Monocolpate (longaperturate), oblate, tectate, surface ornamentation micropitted, equatorial diameter 32 µm.

Description. Monad, bilateral, oblate, proximal face flat, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the flat proximal face; tectate, columellae distinct, simplicolumellate, exine 1 µm thick; surface ornamentation micropitted in distal area of the grain, ornamentation progressively coarsens towards the proximal area of the grain, which is characterised by reticulate surface ornamentation, lumina 1 µm, muri 1 µm, in some specimens the variation in lumina size is not prominent and the lumina are mostly 1 µm with a very subtle coarsening towards the proximal area of the grain.

Dimensions. Equatorial diameter 30.5–(31.5)–33 µm; nm: 8; no: 42.

Comparisons. This species conforms in every respect to *Longapertites marginatus* van Hoeken-Klinkenberg 1964 except for the equatorial diameter, which is approximately half in this species, and the exine thickness, which is 1 µm thick in this species. A small variety of *L. marginatus* van Hoeken-Klinkenberg 1964 conforming to the description of the grains encountered here has been reported from the Palaeocene of Sudan (Assemblage Zone IV of Eisawi and Schrank (2008)). *Longapertites marginatus* var. *parvus* Schrank 1994 has uniformly fine foveolate surface ornamentation.

Material. Amaogugu 1.1 (S58,3), equatorial view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Longapertites crassireticuloides sp. nov.

Plate 3, figures 7–8

Synonymy. *Longapertites* sp. 1 Jaramillo & Dilcher 2001.

Diagnosis. Monocolpate (longaperturate), suboblate, tectate, surface ornamentation reticulate curvilinear, heterobrochate, equatorial diameter 42 µm.

Etymology. After the coarse reticulum.

Description. Monad, bilateral, suboblate, proximal face convex, distal face convex; monocolpate, colpus extends around the convex face of the grain, terminating sharply with the junction of the convex proximal face; tectate, columellae distinct, simplicolumellate, columellae 0.5 µm in diameter spaced 0.5 µm apart, exine 2 µm thick, nexine 0.5 µm, sexine 1.5 µm; surface ornamentation reticulate, curvilinear, heterobrochate, lumina 1–5 µm, muri 1 µm wide.

Dimensions. Equatorial diameter 39.2–(41.5)–44 µm; nm: 2; no: 3.

Comparisons. The reticulum of *Longapertites proapertoides* var. *reticuloides* Van der Hammen & Garcia 1966 has narrower lumina (1–3 µm), *Longapertites chlonovae* Boltenhagen 1976 is smaller (29 µm).

Material. Holotype Okigwe A5.1 (M33,4), Plate 3, figure 7, paratype Okigwe A5.1 (G33,3), Plate 3, figure 8, both equatorial view.

Botanical affinity. Arecaceae (Germeraad et al. 1968; Morley 2000).

Genus *Mauritiidites* van Hoeken-Klinkenberg 1964

Type. *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964

Mauritiidites crassibaculatus van Hoeken-Klinkenberg 1964

Plate 3, figures 9–10

Diagnosis. Monocolpate, oval, intectate, surface ornamentation baculate, equatorial diameter 44 µm.

Description. Monad, bilateral, amb oval; monocolpate, colpus 38–42 µm long, 3–4 µm wide, borders slightly irregular; intectate, exine 1–1.5 µm thick; surface ornamentation baculate, baculae spaced 3–10 µm apart, 3–4 µm high, 2.5–3 µm wide.

Dimensions. Polar view length 42–(43.5)–45 µm, polar view width 29–(30)–31.5 µm; nm: 8; no: 50.

Comparisons. *Mauritiidites franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 is echinate–baculate with finer sculptural elements (1–2.5 µm wide). *Mauritiidites franciscoi* var. *minutus* Van der Hammen & Garcia 1966 is smaller and has finer sculptural elements (0.5–2 µm wide, 1–3 µm high). *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964 is larger and has longer baculae (6 µm high) but the size range of the specimens assigned here to *M. crassibaculatus* van Hoeken-Klinkenberg 1964 is similar to the size range of Somalian specimens assigned to *M. crassibaculatus* van Hoeken-Klinkenberg 1964 by Schrank (1994) (32–55 µm).

Material. Okigwe A1.1 (D53,4), polar view.

Botanical affinity. Arecaceae (Morley (2000) and by comparison to *Mauritia*).

Mauritiidites franciscoi var. *franciscoi* van Hoeken-Klinkenberg 1964

Plate 3, figures 11–13

Diagnosis. Monocolpate, oval, intectate, surface ornamentation echinate–baculate, equatorial diameter 41 µm.

Description. Monad, bilateral, amb oval; monocolpate, colpus long, slightly rounded at the ends, borders slightly irregular; intectate, exine 1–2 µm thick, surface ornamentation echinate–baculate, sculptural elements deeply rooted in the exine with pronounced bases, sculptural elements 1–2.5 µm wide at base and 3–5 µm high.

Dimensions. Polar view length 35.3–(41)–48.3 µm, polar view width 33.1–(35.5)–38 µm; nm: 12; no: 216.

Comparisons. *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964 has thicker (3 µm) baculae. *Mauritiidites franciscoi* var. *minutus* Van der Hammen & Garcia 1966 is smaller, has smaller sculptural elements and a slightly thinner exine. There seems to be intergradation between *M. franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 and *M. franciscoi* var. *minutus* Van der Hammen & Garcia 1966 in the material studied here, particularly in surface ornamentation, but specimens assigned to *M. franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 have been separated from *M. franciscoi* var. *minutus* Van der Hammen & Garcia 1966 primarily on the basis of their large size (polar view length >35 µm) and longer sculptural elements (>3 µm).

Material. Okigwe B3.1 (M33,2), polar view.

Botanical affinity. Arecaceae (Morley (2000), D'Apolito et al. (2021) and by comparison to *Mauritia*).

Mauritiidites franciscoi var. *minutus* Van der Hammen & Garcia 1966

Plate 3, figures 14–16

Diagnosis. Monocolpate, oval, intectate, surface ornamentation echinate–baculate, equatorial diameter 31 μm .

Description. Monad, bilateral, amb oval; monocolpate, colpus long, slightly rounded at the ends, borders slightly irregular; intectate, exine 0.5–1 μm thick, surface ornamentation echinate–baculate, sculptural elements deeply rooted in the exine with pronounced bases, sculptural elements 0.5–2 μm wide at base and 1–3 μm high.

Dimensions. Polar view length 26.3–(30.5)–34.8 μm , polar view width 24.4–(25.5)–27.5; nm: 10; no: 55.

Comparisons. *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964 is larger and has longer (6 μm) and thicker (3 μm) baculae. *Mauritiidites franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 is larger and has longer sculptural elements and a thicker exine. There seems to be intergradation between *M. franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 and *M. franciscoi* var. *minutus* Van der Hammen & Garcia 1966 in the material studied here, particularly in surface ornamentation, but specimens assigned to *M. franciscoi* var. *minutus* Van der Hammen & Garcia 1966 have been separated from *M. franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964 primarily on the basis of their smaller size (polar view length <35 μm) and shorter sculptural elements (<3 μm).

Material. Okigwe B6.1 (R46), polar view.

Botanical affinity. Arecaceae (D’Apolito et al. 2021 and by comparison to *Mauritia*).

Genus *Monocolpopollenites* Pflug in Thomson & Pflug 1953 emend. Nichols et al. 1973

Type. *Monocolpopollenites tranquillus* (Potonié 1934) Jansonius & Hills 1976

Monocolpopollenites ovatus Jaramillo & Dilcher 2001

Plate 3, figure 17

Diagnosis. Monocolpate, elliptic, tectate, micropitted, faintly verrucate at equator, equatorial diameter 36 μm .

Description. Monad, bilateral, heteropolar, amb elliptic; monocolpate, colpus long, extending to the poles, borders slightly curved; exine tectate, collumellae indistinct, <1 μm thick; surface ornamentation micropitted, lumina <0.5 μm spaced 0.5 μm apart, surface ornamentation occasionally faintly verrucate at the equator, verrucae 1–3 μm wide and 1–2 μm high.

Dimensions. Equatorial diameter 30–(36)–42 μm ; nm: 6; no: 65.

Comparisons. *Arecipites regio* Jaramillo & Dilcher 2001 has a slightly narrower width and hence a more oval (less rounded) outline and lacks verrucae at the equator.

Material. Okigwe B1.1 (Y57,4), polar view.

Botanical affinity. Arecaceae (Morley 2000).

Monocolpopollenites tranquillus (Potonié 1934) Jansonius & Hills 1976

Plate 3, figure 18

Synonymy. *Pollenites tranquillus* Potonié 1934.

Diagnosis. Monocolpate, oval, tectate, scabrate, equatorial diameter 30 μm .

Description. Monad, bilateral, heteropolar, amb oval; monocolpate, colpus long (23 μm), borders straight, ends rounded; exine tectate, columellae indistinct, 1 μm thick; surface ornamentation scabrate.

Dimensions. Polar view length 30 μm , polar view width 23 μm ; nm: 1; no: 27.

Comparisons. *Psilamonolpites medius* (Van der Hammen 1956) Van der Hammen & Garcia 1966 is intectate.

Material. Ameke 1.1 (V52,1), polar view.

Botanical affinity. Arecaceae (Morley 2000).

Genus *Psilamonolpites* Van der Hammen & Garcia 1966

Type. *Psilamonolpites medius* (Van der Hammen 1954) Van der Hammen & Garcia 1966

Psilamonolpites grandis Van der Hammen & Garcia 1966

Plate 3, figure 19

Diagnosis. Monocolpate, oval, colpus marginate, atectate, psilate, equatorial diameter 42 μm .

Description. Monad, bilateral, amb oval; monocolpate, colpus long (36 μm), ends rounded and slightly flared, borders curved, marginate, margo 0.5 μm wide, margo formed by 0.5 μm thickening of exine; atectate, exine 1 μm thick; surface ornamentation psilate.

Dimensions. Polar view length 42 μm , polar view width 30 μm ; nm: 1; no: 22.

Comparisons. *Psilamonolpites medius* (Van der Hammen 1956) Van der Hammen & Garcia 1966 is smaller and has a thinner exine (0.5 μm thick).

Material. Ozuitem 6.1 (V55,4), polar view.

Botanical affinity. Arecaceae (by comparison with *Psilamonolpites medius* (Van der Hammen 1956) Van der Hammen & Garcia 1965).

Psilamonolpites medius (Van der Hammen 1954) Van der Hammen & Garcia 1966

Plate 3, figure 20

Synonymy. *Monolpites medius* Van der Hammen 1954.

Diagnosis. Monocolpate, oval, colpus margins invaginated, atectate, psilate, equatorial diameter 28 μm .

Description. Monad, bilateral, amb oval; monocolpate, colpus long (25 μm), ends rounded and flared, borders curved, margins invaginated; atectate, exine <0.5 μm thick; surface ornamentation psilate.

Dimensions. Polar view length 28 μm , polar view width 20 μm ; nm: 1; no: 21.

Comparisons. *Psilamonolpites grandis* Van der Hammen & Garcia 1966 is larger and has a thicker exine (1 μm thick).

Material. Amaogugu 7.1 (T56,3), polar view.

Botanical affinity. Arecaceae (Morley 2000; D’Apolito et al. 2021).

Genus *Retimonolpites* Pierce 1961

Type. *Retimonolpites dividius* Pierce 1961

Retimonocolpites aff. *nigeriensis* van-Hoeken-Klinkenberg 1966

Plate 3, figures 21–23

Diagnosis. Monocolpate, elliptic, intectate, reticulate, heterobrochate, equatorial diameter 34 µm.

Description. Monad, bilateral, amb elliptic; monocolpate, colpus long, borders regular, rounded at the ends; intectate, exine 1 µm thick; surface ornamentation, heterobrochate, muri 0.5 µm, lumina 1.5 µm, decreasing to 1 µm at the extremities of the grain.

Dimensions. Polar view length 32.5–(34)–35 µm, polar view width 20–(21.5)–23 µm; nm: 3; no: 25.

Comparisons. *Retimonocolpites nigeriensis* van-Hoeken-Klinkenberg 1966 is larger (equatorial diameter 46 µm) and has lumina that decrease from 2.5 µm to 1 µm at the extremities of the grain. *Retimonocolpites abeokutaensis* Jan du Chêne 1977 is slightly larger (equatorial diameter 40 µm) and is homobrochate.

Material. Okigwe B7.1 (N56,3), polar view.

Botanical affinity. Arecaceae (Morley 2000).

Trichotomocolpate pollen

Genus *Luminidites* Pocknall & Mildenhall 1984

Type. *Luminidites reticulatus* (Couper 1960) Pocknall & Mildenhall 1984

Luminidites microreticulatus sp. nov.

Plate 3, figures 24–29

Diagnosis. Trichotomocolpate, triangular, tectate, columellae distinct, surface ornamentation micropitted–reticulate homobrochate occasionally fossulate, equatorial diameter 29 µm.

Etymology. After the fine reticulate surface ornamentation.

Description. Monad, radial, amb triangular, rounded at the apices; trichotomocolpate, 3 µm wide at centre, each arm 11 µm long, margo 0.5–1 µm wide formed by a thickening of the sexine; tectate, columellae distinct, 0.5 µm wide and spaced 0.5 µm apart exine 1 µm thick, nexine 0.5 µm thick, sexine 0.5 µm thick; surface ornamentation micropitted–reticulate homobrochate, lumina 0.5 µm, lumina increase in size slightly towards the equator, lumina occasionally coalesce to form fossulae 0.5–1 µm wide and 2–5 µm long.

Dimensions. Equatorial diameter 25–(28.5)–32 µm; nm: 16; no: 88.

Comparisons. *Luminidites reticulatus* (Couper 1960) Pocknall & Mildenhall 1984 is reticulate with lumina varying in size from 1 to 9 µm. *Luminidites colombianensis* Jaramillo & Dilcher 2001 is larger (35–46 µm) and is heterobrochate with lumina varying from >0.5 µm to 1 µm. *Luminidites amazonicus* D'Apolito et al. 2021 lacks a margo and has a coarser reticulum.

Material. Holotype Okigwe B4.1 (H53,3), Plate 3, figures 24–25, polar view; paratypes Okigwe B4.1 (F48, Plate 3, figures 26–27; P52,2, Plate 3, figures 28–29) polar view.

Botanical affinity. Arecaceae (by comparison with *Luminidites amazonicus* D'Apolito et al. 2021 and *Bactris*).

Zona-aperturate pollen

Genus *Proxapertites* Van der Hammen 1956 emend. Singh 1975

Type. *Proxapertites operculatus* (Van der Hammen 1954) Van der Hammen 1956

Proxapertites cursus van Hoeken-Klinkenberg 1966

Plate 3, figures 30–31

Diagnosis. Zonasulculate, sub-circular, tectate, reticulate, heterobrochate, equatorial diameter 37 µm.

Description. Monad, amb sub-circular; zonasulculate; tectate, nexine 0.5 µm thick, columellae 1 µm thick, tectum 0.5 mm thick; surface ornamentation reticulate, heterobrochate, lumina 1–2.5 µm in size, spaced 1.5 µm apart, rounded-oval in shape, muri 1–1.5 µm wide.

Dimensions. Equatorial diameter 34–(37)–40.5 µm; nm: 8; no: 136.

Material. Okigwe B6.1 (T35), polar view.

Botanical affinity. Araceae (Zetter et al. 2001).

Proxapertites humbertoides (Van der Hammen 1954) Sarmiento 1992

Plate 3, figure 32

Synonymy. *Monocolpites humbertoides* Van der Hammen 1954.

Foveomorphomonocolpites humbertoides (Van der Hammen 1954)

Sole de Porta 1971.

Proxapertites maracaiboensis Muller et al. 1987.

Diagnosis. Zonasulculate, oval, tectate, foveolate, equatorial diameter 124 µm.

Description. Monad, amb oval; zonasulculate; tectate, nexine not observed, sexine 2 µm thick, collumellae 1–2 µm wide and spaced 2–4 µm apart, columellae coalesce to form an infratectal ridge 1–2 µm wide beneath the muri; surface ornamentation foveolate, lumina variable in size (1–13 µm in diameter) and shape (circular to irregular), muri 2–8 µm.

Dimensions. Equatorial diameter 122.3–(124)–126 µm; nm: 2; no: 24.

Material. Okigwe B2.1 (P62), specimen fragmented; only the sexine is preserved.

Proxapertites magnus Muller et al. 1987

Plate 3, figure 33

Diagnosis. Zonasulculate, oval, tectate, foveolate, equatorial diameter 71 µm.

Description. Monad, amb oval; zonasulculate; tectate, nexine 0.5–1 µm thick, columellae 1–1.5 µm thick, tectum 0.5–1 µm thick, exine 2–3 µm thick; surface ornamentation foveolate, lumina 0.5–1 µm in diameter, circular, spread densely and evenly over the grain surface.

Dimensions. Equatorial diameter 67.3–(71)–75.5 µm; nm: 4; no: 17.

Material. Okigwe B6.1 (U54,2), polar view.

Proxapertites operculatus (Van der Hammen 1954) Van der Hammen 1956

Plate 3, figures 34–35

Synonymy. *Monocolpites operculatus* Van der Hammen 1954.

Diagnosis. Zonasulcate, sub-circular, tectate, reticulate, homobrochate, equatorial diameter 35 µm.

Description. Monad, amb sub-circular; zonasulcate, sulculus extending around the circumference of the outline, margin of the sulculus irregular; tectate, nexine 0.5 µm thick, columellae 0.5 µm thick, tectum 0.5 µm thick; surface ornamentation reticulate, homobrochate, lumina 0.5–1 µm and sub-circular, muri 0.5 µm.

Dimensions. Equatorial diameter 30.3–(35)–40 µm; nm: 12; no: 372.

Material. Okigwe B2.1 (U51,2), polar view.

Botanical affinity. Araceae (Zetter et al. 2001).

Proxapertites psilatus Sarmiento 1992

Plate 3, figures 36–37

Diagnosis. Zonasulcate, oval, tectate, columellae indistinct, psilate, equatorial diameter 29 µm.

Description. Monad, amb circular; zonasulcate, sulculus extending around the circumference of the outline, margin of the sulculus irregular; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation psilate, occasionally micropitted to faintly scabrate with sculptural elements densely and evenly distributed over the surface of the grain.

Dimensions. Equatorial diameter 26–(29)–32 µm; nm: 10; no: 166.

Material. Ozuitem 6.1 (Q34), polar view.

Botanical affinity. Magnoliales (by comparison with psilate zona-aperturate pollen grains produced by *Guatteria* (Annonaceae) and *Eupomtia* (Eupomatiaceae) (Zetter et al. 2001)), Nymphaeaceae (D'Apolito et al. 2021).

Genus *Spinizonocolpites* Muller 1968 emend. Muller et al. 1987

Type. *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973

Spinizonocolpites prominatus (McIntyre 1965) Stover & Evans 1973

Plate 4, figures 1–3

Synonymy. *Spinizonocolpites echinatus* Muller 1968.

Diagnosis. Zonasulcate, tectate, columellae distinct, echinate, equatorial diameter 45 µm.

Description. Monad, radial, amb sub-circular; zonasulcate, borders of sulculus irregular; tectate, columellae distinct, exine 1 µm thick; surface ornamentation echinate, echinae 5–9 µm high with blunt rounded apices and expanded bases, echinae spaced 3–11 µm apart, surface ornamentation elsewhere reticulate, muri 0.5–1 µm wide, lumina 0.5–1 µm wide.

Dimensions. Equatorial diameter 42–(44.5)–47 µm; nm: 3; no: 18.

Comparisons. *Spinizonocolpites echinatus* Muller 1968 is a junior synonym of *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973 (Pocknall et al. 2022).

Material. Ameke 1.1 (Q30), polar view; Amaogugu 7.1 (Q45), polar view.

Botanical affinity. Arecaceae (Germeraad et al. 1968 and by comparison with *Nypa fruticans*).

Spinizonocolpites cf. *Spinizonocolpites* aff. *baculatus* Muller 1968

Plate 4, figure 4

Diagnosis. Zonasulcate, tectate, columellae indistinct, baculate, equatorial diameter 63 µm.

Description. Monad, amb sub-circular; zonasulcate; tectate, columellae indistinct, exine 2 µm thick; surface ornamentation baculate, baculae 11 µm long, 3 µm wide with blunt rounded apices and expanded bases, exine psilate elsewhere.

Dimensions. Equatorial diameter 63 µm; nm: 1; no: 8.

Comparisons. This species conforms to *Spinizonocolpites* aff. *baculatus* Muller 1968 but has a psilate rather than reticulate exine in areas not covered by echinae, which may be due to poor preservation.

Material. Okigwe B7.1 (J40,1), polar view.

Botanical affinity. Arecaceae (by comparison with *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973 and *Nypa fruticans*).

Genus *Saturna* Salard-Chebaldaeff 1978

Type. *Saturna enigmaticus* Salard-Chebaldaeff 1978

Saturna enigmaticus Salard-Chebaldaeff 1978

Plate 4, figure 5

Diagnosis. Circular, aperture indistinct, tectate, reticulate, heterobrochate, largest dimension 29 µm.

Description. Monad, radial, amb circular; aperture indistinct, a possible sub-equatorial furrow may divide the grain into two uneven parts; tectate, columellae distinct, spaced 1 µm apart, nexine <0.5 µm thick, columellae 1 µm thick, tectum 1 µm thick; surface ornamentation reticulate, heterobrochate, simplicolumellate, lumina 3 µm wide at equator, 0.5 µm towards centre of outline, muri 1 µm wide.

Dimensions. Largest dimension 29 µm; nm: 1; no: 2.

Comparisons. *Spirosyncolpites bruni* Legoux 1978 is homobrochate and has considerably larger lumina. The description of the type species *Saturna enigmaticus* Salard-Chebaldaeff 1978 begins 'Spores or pollen?' (Jansonius and Hills 1976, Card 3611). *Saturna enigmaticus* Salard-Chebaldaeff 1978 is included among angiosperm pollen here on the basis of the possible sub-equatorial furrow, which may represent a zona-sulculus, and the presence of columellae.

Material. Okigwe B1.1 (H32,2).

Monoporate pollen

Genus *Milfordia* Erdtman 1960 emend. Partridge in Stover & Partridge 1973

Type. *Milfordia hypolaenoides* Erdtman 1960*Milfordia confossus* (Fairchild in Stover et al. 1966) comb. nov.

Basonym = *Monulcipollenites confossus* Fairchild in Stover et al. 1966

Plate 4, figure 6

Diagnosis. Monoporate, circular, pore annulate, intectate, foveolate, equatorial diameter 34 µm.

Description. Monad, radial, amb circular; monoporate, pore circular, margins regular, 5 µm wide, annulate, annulus 1.5 µm wide; intectate, exine 0.5 µm thick; surface ornamentation foveolate, foveolae <1–0.5 µm wide decreasing slightly towards the pore, and spaced 1–3 µm apart.

Dimensions. Equatorial diameter 34 µm; nm: 1; no: 1.

Comparisons. This species conforms to *Monulcipollenites confossus* Fairchild 1966 but the emendation of *Milfordia* Erdtman 1960 emend. Krutzsch 1970 emend. Partridge in Stover & Partridge 1973 means that *Monulcipollenites* Fairchild in Stover et al. (1966) is a junior synonym of *Milfordia* Erdtman 1960 emend. Partridge in Stover & Partridge 1973 (Jansonius & Hills 1976).

Material. Okigwe B1.1 (S48), polar view.

Botanical affinity. Restionaceae (by comparison with *Restio bifidus* in Linder and Ferguson (1985), see also Morley (2000)).

Milfordia homeopunctata (McIntyre 1965) Partridge in Stover & Partridge 1973

Plate 4, figure 7

Synonymy. *Monoporopollenites homeopunctatus* McIntyre 1965.

Diagnosis. Monoporate, circular, pore margins irregular and jagged, intectate, foveolate, equatorial diameter 28 µm.

Description. Monad, radial, amb circular; monoporate, pore sub-circular, margins irregular and jagged, 6 µm wide; intectate, exine 0.5 µm thick; surface ornamentation foveolate, foveolae 0.5 µm wide and spaced 1–3 µm apart, in some areas these foveolae coalesce to form grooves.

Dimensions. Equatorial diameter 28 µm; nm: 1; no: 7.

Comparisons. *Milfordia hypolaenoides* Erdtman 1960 has an elongate pore interpreted as a colpus.

Material. Ozuitem 3.1 (W65,2), polar view.

Botanical affinity. Restionaceae (by comparison with *Lepyrodia scariosa* in Linder and Ferguson (1985), see also Morley (2000)).

Genus *Monoporopollenites* Meyer 1956

Type. *Monoporopollenites graminoides* Meyer 1956

Monoporopollenites annulatus (Van der Hammen 1954) Jaramillo & Dilcher, 2001

Synonymy. *Monoporites annulatus* Van der Hammen 1954.

Monoporites annulatus (Van der Hammen 1954) Germeraad et al. 1968.

Monoporites annulatus (Van der Hammen 1954) Regali et al. 1974.

Monoporites annuloides González Guzmán 1967

Plate 4, figure 8

Diagnosis. Monoporate, sub-circular, pore annulate, tectate, scabrate, equatorial diameter 30 µm.

Description. Monad, radial, amb sub-circular; monoporate, pore circular, margins regular, 2 µm wide, annulate, annulus 2 µm wide; tectate, collumellae sometimes indistinct, exine 1 µm thick; surface ornamentation scabrate.

Dimensions. Equatorial diameter 26–(30)–34 µm; nm: 10; no: 187.

Comparisons. Monoporate pollen types with foveolate surface ornamentation are included within *Milfordia* Erdtman 1960 emend. Partridge in Stover & Partridge 1973. *Monoporopollenites graminoides* Meyer 1956 is intectate.

Material. Okigwe B4.1 (V56,1), polar view.

Botanical affinity. Poaceae (by comparison with extant Poaceae).

Genus *Retimonoporites* Brenner & Bickoff 1992

Type. *Retimonoporites operculatus* Brenner & Bickoff 1992

Retimonoporites heterobrochatus sp. nov.

Plate 4, figures 9–12

Diagnosis. Monoporate, circular, tectate, reticulate, heterobrochate, equatorial diameter 33 µm.

Etymology. After the heterobrochate reticulum.

Description. Monad, radial, amb circular; monoporate, pore oval, simple, pore margins slightly irregular, pore 3–4 µm wide, 4–6 µm long; tectate, collumellae distinct, exine 1.5 µm thick, nexine 0.5 µm thick, sexine 1 µm thick; surface ornamentation reticulate, heterobrochate, lumina 2–4 µm wide, lumina vary in size randomly over the surface of the grain, muri 1 µm wide and simplicolumellate.

Dimensions. Equatorial diameter 27.5–(32.5)–37.8 µm; nm: 5; no: 8.

Comparisons. *Retimonoporites operculatus* Brenner & Bickoff 1992 is smaller (13 µm) and homobrochate.

Material. Holotype Okigwe B3.1 (G33), Plate 4, figures 9–10; paratype Okigwe B3.1 (F40,2), Plate 4, figures 11–12.

Diporate pollen

Genus *Retidiporites* Varma & Rawat 1963

Type. *Retidiporites bengalensis* Varma & Rawat 1963

Retidiporites magdalenensis Van der Hammen & Garcia 1966

Plate 4, figure 13

Diagnosis. Diporate, elliptic, tectate, reticulate, homobrochate, largest dimension 31 µm, smallest dimension 20 µm.

Description. Monad, bilateral, amb elliptic; diporate, pori 8 µm wide; tectate, columellae distinct, exine 1 µm thick; surface ornamentation reticulate, homobrochate, lumina 0.5 µm wide, muri 0.5–1 µm wide, lumina distributed densely and evenly over the pollen surface.

Dimensions. Largest dimension 31 µm, smallest dimension 20 µm; nm: 1; no: 9.

Material. Okigwe B1.1 (T30,2), polar view.

Botanical affinity. Proteaceae (Germeraad et al. 1968).

Tricolpate pollen

Genus *Bacubrevitricolpites* Rao & Ramanujam 1982

Type. *Bacubrevitricolpites rotundus* Rao & Ramanujam 1982

Bacubrevitricolpites sp.

Plate 4, figures 14–15

Diagnosis. Tricolpate, triangular, colpi short and costate, tectate, baculate, baculae spaced 2–4 µm apart, equatorial diameter 38 µm.

Description. Monad, radial, amb triangular obtuse-convex; tricolpate, colpi short (9 µm), costate (costae 2 µm wide); exine tectate, columellae indistinct, 1 µm thick; surface ornamentation baculate, baculae 1–2 µm high, spaced 2–4 µm and distributed irregularly, pollen surface elsewhere densely covered with microechinae.

Dimensions. Equatorial diameter 38 µm; nm: 1; no: 1.

Comparisons. *Bacubrevitricolpites rotundus* Rao & Ramanujam 1982 has a rounded amb and a dense covering of baculae.

Material. Amaogugu 1.1 (P56,4), oblique view.

Genus *Crototricolpites* Leidekmeyer 1966

Type. *Crototricolpites annemariae* Leidekmeyer 1966

Crototricolpites densus Salard-Chaeboldaef 1978

Plate 4, figure 16

Diagnosis. Tricolpate, circular, tectate with indistinct columellae, clavate, clavae arranged in *Croton* pattern, 28 µm.

Description. Monad, radial, amb circular; tricolpate, colpi 6–10 µm wide, margins irregular; tectate, columellae indistinct; surface ornamentation clavate, clavae 1.5 µm high, 0.5–1 µm wide, triangular–rounded in plan view, arranged in a *Croton* pattern.

Dimensions. Equatorial diameter 28 µm; nm 1; no: 2.

Comparisons. The colpi of *Crototricolpites crotonisculptus* van Hoeken-Klinkenberg 1966 are constricted at the equator.

Material. Okigwe B2.1 (M35), polar view.

Botanical affinity. Euphorbiaceae (Salard-Chaeboldaef 1978).

Crototricolpites aff. *finitus* Silva-Caminha et al. 2010

Plate 4, figure 17

Diagnosis. Tricolpate, sub-triangular obtuse-convex, intectate, clavate, equatorial diameter 30 µm.

Description. Monad, radial, amb sub-triangular obtuse-convex; tricolpate, colpi simple, some specimens with a faint margo formed by a slight thinning of the exine; exine intectate, 1–2 µm thick; surface ornamentation clavate, clavae 1 µm high, 0.5 µm wide, spaced 1–1.5 µm apart, densely and evenly distributed, and arranged in a *Croton*-like pattern in some areas of the exine.

Dimensions. Equatorial diameter 24–(29.5)–35 µm; nm: 5; no: 57.

Comparisons. *Crototricolpites finitus* Silva-Caminha et al. 2010 is very similar but it has an inner body. *Clavatricolpites densiclavatus* Jaramillo & Dilcher 2001 is slightly larger (26–42 µm in polar view) and has larger sculptural elements (clavae 1–1.5 µm high and 0.7–1 µm wide). *Clavatricolpites daemonei* has taller clavae (2 µm) and a very thin exine.

Material. Okigwe B1.1 (H40,1), oblique view.

Botanical affinity. Euphorbiaceae (Jaramillo & Rueda 2023).

Crototricolpites 'superatus'

Plate 4, figure 18

Diagnosis. Tricolpate, colpi costate, circular, tectate, clavate, clavae arranged in *Croton* pattern and situated on top of a reticulum, 29 µm.

Description. Monad, radial, amb circular; tricolpate; exine tectate, 1 µm thick; surface ornamentation reticulate homobrochate, muri 1 µm, lumina 2 µm, clavae 1 µm high and triangular in plan view are positioned on top of the muri and are arranged in a *Croton* pattern.

Dimensions. Equatorial diameter 29 µm; nm 1; no: 1.

Comparisons. *Crototricolpites americanus* Wijmstra 1971 has a narrower lumina and digitate columellae.

Material. Okigwe A7.1 (W37,3), specimen partially obscured, oblique view.

Genus *Echitricolpites* Regali et al. 1974

Type. *Echitricolpites communis* Regali et al. 1974

Echitricolpites serratus sp. nov.

Plate 4, figures 19–21

Synonymy. *Echitricolpites* sp. 1 Jaramillo & Dilcher 2001.

Echitricolpites 'guaneorum' Jaramillo & Rueda 2023.

Diagnosis. Tricolpate, prolate, tectate, columellae distinct, echinate and micropitted, equatorial diameter 30 µm.

Etymology. After the saw-like appearance of the echinae arranged in longitudinal rows.

Description. Monad, radial, prolate; tricolpate, colpi narrow (<0.5 µm) and 30 µm long; tectate, columellae distinct, exine 0.5 µm thick; surface ornamentation echinate, echinae spaced 1–2 µm and distributed in longitudinal rows over the surface of the grain, echinae 1 µm at base and 1.5 µm high, exine between echinae micropitted.

Dimensions. Equatorial diameter 25–(29.5)–33.5 µm, nm: 3; no: 5.

Comparisons. *Echitricolpites communis* Regali et al. 1974 has larger echinae that are distributed more evenly over the pollen surface. This species conforms to the informal species *Echitricolpites 'guaneorum'* (see Jaramillo and Rueda 2023) and is formalised here.

Material. Holotype Okigwe B1.1 (H64,4), Plate 4, figure 19, equatorial view; paratype Okigwe A1.1 (S40,4), Plate 4, figures 20–21, equatorial view.

Echitricolpites aff. *communis* Regali et al. 1974

Plate 4, figure 22

Diagnosis. Tricolpate, sub-circular, tectate, columellae indistinct, micropitted and echinate, equatorial diameter 42 µm.

Description. Monad, radial, amb sub-circular; tricolpate, colpi wide (6–24 µm) and long (23 µm); exine tectate, columellae indistinct, 1 µm thick; surface ornamentation micropitted and echinate, echinae spaced 4–6 µm, 2 µm wide at base and 2 µm high, some sculptural elements more rounded (verrucae) although this could be due to preservation.

Dimensions. Equatorial diameter 23.5–(42)–60.5 µm; nm 5; no 6.

Comparisons. *Echitricolpites communis* Regali et al. 1974 has a smaller size range (38–53 µm), is brevicolpate, and has smaller echinae, a thinner exine (0.5 µm) and distinct columellae.

Material. Okigwe B3.1 (G54,2), polar view.

Genus *Foveotricolpites* Pierce 1961

Type. *Foveotricolpites sphaeroides* Pierce 1961

Foveotricolpites simplex (González Guzmán 1967) D'Apolito et al. 2021

Plate 4, figures 23–24

Synonymy. *Retitricolpites simplex* González Guzmán 1967.

Diagnosis. Tricolpate, oval, colpi invaginated, tectate, columellae indistinct, micropitted, equatorial diameter 27 µm.

Description. Monad, radial, prolate; tricolpate, colpi 26 µm long, 1 µm wide, colpi invaginated, invagination 1 µm wide; tectate, columellae distinct, exine 1 µm thick; surface ornamentation micropitted, lumina <0.5 µm spread densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 23–(26.5)–30.2 µm; nm 9; no: 67.

Material. Ozuitem 6.1 (Y31,2), equatorial view.

Botanical affinity. Euphorbiaceae (Jaramillo et al. 2014).

Genus *Ladakhipollenites* Mathur & Jain 1980

Type. *Ladakhipollenites levis* (Sah & Dutta 1966) Mathur & Jain 1980

Ladakhipollenites colpiconstrictus (van Hoeken-Klinkenberg 1966) D'Apolito et al. 2021

Plate 4, figures 25–26

Synonymy. *Psilatricolpites colpiconstrictus* van Hoeken-Klinkenberg 1966.

Diagnosis. Tricolpate, prolate, colpi marginate, margo discontinuous, colpi constricted at equator, psilate, equatorial diameter 27 µm.

Description. Monad, radial, prolate; tricolpate, colpi 26 µm long, 3 µm wide, constricted at equator, marginate, margo 1 µm wide but not continuous around colpi; tectate, columellae distinct, spaced 0.5 µm apart and visible through the tectum, nexine 0.5 µm, sexine 0.5 µm; surface ornamentation psilate.

Dimensions. Equatorial diameter 27 µm; nm: 1; no: 4.

Comparisons. This species was included in *Psilatricolpites* by van Hoeken-Klinkenberg (1966) and was transferred to *Ladakhipollenites* by D'Apolito et al. (2021).

Material. Ozuitem 6.1 (M53), equatorial view.

Botanical affinity. Fabaceae (by comparison with *Ladakhipollenites? pseudocolpiconstrictus* D'Apolito et al. 2021).

Ladakhipollenites simplex (González Guzmán 1967) Jaramillo & Dilcher 2001

Plate 4, figures 27–28

Synonymy. *Psilatricolpites simplex* González Guzmán 1967.

Diagnosis. Tricolpate, prolate to sub-prolate, colpi marginate, tectate, columellae indistinct, scabrate, equatorial diameter 26 µm.

Description. Monad, radial, prolate to sub-prolate; tricolpate, colpi 17 µm long, 2 µm wide, ends rounded, marginate, margo 1 µm wide; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation scabrate, sculptural elements spaced 0.5 µm apart, distributed densely over the surface of the pollen grain.

Dimensions. Equatorial diameter 25–(26)–27 µm; nm: 2; no: 30.

Material. Amaogugu 7.1 (U38,2), equatorial view; Okigwe B2.1 (O54,3), equatorial view.

Ladakhipollenites hammenii (Boltenhagen 1976) comb. nov.

Basonym = *Psilatricolpites hammenii* Boltenhagen 1976

Plate 4, figure 29

Diagnosis. Tricolpate, triangular obtuse-convex, colpi marginate, intectate, psilate at equator, micropitted elsewhere, equatorial diameter 31 µm.

Description. Monad, radial, amb triangular obtuse-convex; tricolpate, colpi 9 µm long, 7 µm wide, margins of colpi slightly irregular and rounded in apocolpium, marginate, margo 1 µm wide and formed by thinning of the exine; intectate, exine 1 µm thick; surface ornamentation psilate at equator, micropitted elsewhere.

Dimensions. Equatorial diameter 23–(31)–38.5 µm; nm: 10; no: 59.

Comparisons. *Tricolpites protoclarensis* Jaramillo & Dilcher 2001 is tectate; *Tricolpites microreticulatus* Belsky, Boltenhagen & Potonié 1965 has pseudocostate colpi. *Psilatricolpites* (Van der Hammen) Pierce 1961 is an illegitimate genus (Jansonius and Hills 1976, card 2233). *Ladakhipollenites* Mathur & Jain, 1980 accommodates tricolpate psilate pollen grains.

Material. Amaogugu 7.1 (R55,1), polar view.

Ladakhipollenites sp. 1

Plate 4, figures 30–31

Diagnosis. Tricolpate, sub-circular, tectate, columellae indistinct, psilate, equatorial diameter 25 µm.

Description. Monad, radial, amb sub-circular; tricolpate, colpi 7 µm long, 3 µm wide, margins of colpi straight and pointed-sub-rounded in apocolpium; tectate, columellae indistinct,

exine 1 µm thick at the centre of the mesocolpia, thickens gradually to 1.5 µm close to the colpi and thins gradually to 1 µm thick adjacent to the colpi; surface ornamentation psilate.

Dimensions. Equatorial diameter 23–(24.5)–26 µm; nm: 4; no: 19.

Comparisons. *Ladakhipollenites hammenii* (Boltenhagen 1976) comb. nov. is intectate and has longer colpi.

Material. Amaogugu 1.1 (V34,2), polar view.

Ladakhipollenites sp. 2

Plate 4, figure 32

Diagnosis. Tricolpate, sub-triangular, colpi marginate, tectate, scabrate, equatorial diameter 28 µm.

Description. Monad, radial, amb sub-triangular; tricolpate, colpi very long, almost reaching apocolpia, 12 µm long, colpi 2 µm wide near apocolpium and flare to 7–12 µm near equator, margins irregular, colpi marginate, margo 3 µm wide joining in apocolpial region, margo formed by exine thickening by 0.5 µm; tectate, collumellae indistinct, exine 0.5 µm thick; surface ornamentation scabrate.

Dimensions. Equatorial diameter 28 µm; nm: 1; no: 3.

Comparisons. *Scabratricolpites thomasi* Sarmiento 1992 has simple colpi.

Material. Okigwe A5.1 (U40,3), polar view.

Ladakhipollenites? *thomasi* (Sarmiento 1992) comb. nov.

Basonym = *Scabratricolpites thomasi* Sarmiento 1992

Plate 4, figures 33–34

Diagnosis. Tricolpate, sub-circular; colpi long, sub-circular, tectate, scabrate, equatorial diameter 24.5 µm.

Description. Monad, radial, amb sub-circular; tricolpate, colpi long and margins slightly irregular; tectate, collumellae distinct, exine 1.5 µm thick; surface ornamentation scabrate, scabrae distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 24.5 µm; nm: 1; no: 1.

Comparisons. *Scabratricolpites* (Van der Hammen 1956) González Guzmán 1967 is a junior synonym of *Batrachium* L. and therefore an illegitimate genus (Jansonius and Hills 1976, card 2519). *Ladakhipollenites* Mathur & Jain 1980 accommodates tricolpate psilate pollen grains. D'Apolito et al. (2021) provisionally placed the psilate to micropitted pollen grain *Ladakhipollenites?* *sphaericus* D'Apolito et al. 2021 in *Ladakhipollenites*, thereby expanding the circumscription of the genus. *Scabratricolpites thomasi* Sarmiento 1992 is provisionally placed in *Ladakhipollenites* here as it cannot be satisfactorily placed in any other genus, noting that if *Ladakhipollenites?* *sphaericus* D'Apolito et al. 2021 is also accepted then this would increase the circumscription of *Ladakhipollenites* Mathur & Jain 1980 to accommodate tricolpate psilate, scabrate and micropitted pollen grains.

Material. Amaogugu 7.1 (L47,3), polar view.

Genus *Retibrevitricolpites* van Hoeken-Klinkenberg 1966

Type. *Retibrevitricolpites triangulatus* van Hoeken-Klinkenberg 1966

Retibrevitricolpites 'reciprocus'

Plate 5, figures 1–2

Diagnosis. Brevitricolpate, triangular and slightly rounded, tectate, reticulate, heterobrochate, on one pole lumina decrease in size from equator to pole, on the opposite pole lumina increase in size from equator to pole, equatorial diameter 27 µm.

Description. Monad, radial, amb triangular and slightly rounded; brevitrilcolpate, colpi 4 µm wide, borders distinct; tectate, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, simplicolumellate, muri 0.5 µm wide, lumina 0.5–2 µm wide, on one pole lumina decrease in size from equator to pole, on the opposite pole lumina increase in size from equator to pole.

Dimensions. Equatorial diameter 27 µm; nm: 1; no: 1.

Comparisons. The reticulum of *Retibrevitricolpites distinctus* van Hoeken-Klinkenberg 1966 is coarse on the mesocolpium and fine on the apocolpium. *Retibrevitricolporites speciosus* Jaramillo & Dilcher 2001 is tricolporate and heterobrochate and has a spherical inner body.

Material. Ozuitem 6.1 (X32,2), polar view.

Genus *Retitrescolpites* Sah 1967

Type. *Retitrescolpites typicus* Sah 1967

Retitrescolpites cecryphalium (Leidelmeyer 1966) comb. nov.

Basonym = *Retitricolpites cecryphalium* Leidelmeyer 1966

Plate 5, figures 3–6

Diagnosis. Tricolpate, sub-circular, tectate, reticulate, heterobrochate, equatorial diameter 39 µm.

Description. Monad, radial, amb sub-circular; tricolpate, colpi 10 µm long, simple, margins irregular, ends slightly pointed; tectate, exine 4.5 µm thick, nexine 2 µm thick, columellae 0.5 µm thick, tectum 2 µm thick, columellae 0.5 µm wide, spaced 0.5–2 µm apart, free collumellae tips visible beneath the tectum; surface ornamentation reticulate, heterobrochate, muri 0.5–1 µm wide, lumina 2–5 µm wide, lumina width varies randomly across the surface of the grain.

Dimensions. Equatorial diameter 36–(38.5)–41.1 µm; nm: 10; no: 60.

Comparisons. *Retitricolpites cecryphalium* Leidelmeyer 1966 is larger (48–50 µm) and has a thinner exine (3 µm) but otherwise is very similar. *Retitricolporites?* *irregularis* (Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001 is tricolporate. *Retitrescolpites definidus* Jaramillo et al. 2007 has a thinner exine (2.5 µm) and costate colpi. *Retitricolpites* (Van der Hammen 1956) Van der Hammen & Wymstra 1964 is an illegitimate genus (Jansonius and Hills 1976, card 2401). *Retitrescolpites* Sah 1967 accommodates tricolpate grains with reticulate surface ornamentation.

Material. Ozuitem 6.1 (T32,4), polar view; Ozuitem 3.1 (N42,3), polar view.

Retitrescolpites aff. *magnus* (González Guzmán 1967) Jaramillo & Dilcher 2001

Plate 5, figures 7–8

Diagnosis. Tricolpate, prolate, tectate, reticulate, heterobrochate, equatorial diameter 23 μm .

Description. Monad, radial, prolate; tricolpate, colpi long (29 μm), margins regular; tectate, nexine 0.5 μm thick, columellae 1 μm thick, tectum 1 μm thick; surface ornamentation reticulate, heterobrochate, muri 0.5 μm wide, lumina 0.7–1.5 μm wide, lumina decrease in size towards colpi, simplicolumellate.

Dimensions. Equatorial diameter 23 μm ; nm: 1; no: 3.

Comparisons. *Retitrescolpites magnus* (González Guzmán 1967) Jaramillo & Dilcher 2001 is very similar but homobrochate.

Material. Ozuitem 6.1 (W35,2), equatorial view.

Retitrescolpites cf. '*opitaeorum*'

Plate 5, figures 9–10

Diagnosis. Tricolpate, sub-triangular, tectate, reticulate, heterobrochate, equatorial diameter 23 μm .

Description. Monad, radial, amb sub-triangular obtuse–concave; tricolpate, colpi 6 μm long, margins regular, ends slightly pointed; tectate, nexine 0.5 μm thick, columellae 0.5 μm thick, tectum 0.5 μm thick, columellae 0.5 μm wide, spaced 1 μm apart; surface ornamentation reticulate, heterobrochate, muri 0.5 μm wide, simplicolumellate, lumina 0.5–1.5 μm wide.

Dimensions. Equatorial diameter 21–(23)–25.2 μm ; nm: 4; no: 20.

Comparisons. The reticulum of the informal species *Retitrescolpites 'opitaeorum'* (see Jaramillo and Rueda 2023) reduces slightly to form a margo.

Material. Okigwe B4.1 (K58,1), polar view.

Retitrescolpites mirabilis sp. nov.

Plate 5, figures 11–12

Diagnosis. Tricolpate, sub-circular, tectate, reticulate, curvilinear, heterobrochate, lumina size bimodal, equatorial diameter 55 μm .

Etymology. After the striking morphology.

Description. Monad, radial, amb sub-circular; tricolpate, colpi 30 μm long, 14 μm wide, borders slightly curved, ends pointed, apocolpium small (4 μm); tectate, exine 3 μm thick; surface ornamentation reticulate, heterobrochate, curvilinear, size of lumina markedly bimodal, larger lumina 3–9 μm wide, muri 2 μm wide, smaller lumina on muri 0.5–1 μm .

Dimensions. Equatorial diameter 54–(54.6)–55.2 μm ; nm: 2; no: 3.

Comparisons. *Albertipollenites limai* Dino 1994 has a narrower lumina, narrower muri and shorter colpi.

Material. Holotype Amaogugu 7.1 (M57,3), Plate 5, figure 11, polar view; paratype Amaogugu 7.1 (L64,3), Plate 5, figure 12, polar view.

Retitrescolpites sp. 1

Plate 5, figure 13

Diagnosis. Tricolpate, circular, colpi marginate, tectate, duplicolumellate, reticulate, heterobrochate, equatorial diameter 35 μm .

Description. Monad, radial, amb circular; tricolpate, colpi 10 μm long, 8 μm wide, borders straight, ends pointed, marginate, margo 1.5 μm wide, defined by marked decrease in size of lumina of reticulum; tectate, columellae distinct, exine 1.5 μm thick; surface ornamentation reticulate, heterobrochate, muri 1 μm wide, duplicolumellate, lumina decrease in size from 3–4 μm at the equator to 1.5 μm at the pole, ornamentation of margo reticulate, muri 0.5 μm wide, duplicolumellate, lumina 0.5–1 μm .

Dimensions. Equatorial diameter 35 μm ; nm: 1; no: 1.

Comparisons. *Retitrescolpites baculatus* Jaramillo & Dilcher 2001 has distinctive very tall columellae with some ending in a rounded, constricted tip.

Material. Ozuitem 6.1 (K60,3), polar view.

Retitrescolpites sp. 2

Plate 5, figures 14–15

Diagnosis. Tricolpate, circular, colpi marginate, tectate, reticulate, heterobrochate, thickening at apocolpia, equatorial diameter 40 μm .

Description. Monad, radial, amb circular; tricolpate, colpi 17 μm long, 14 μm wide, borders straight, ends pointed, marginate, margo 1 μm wide, defined by psilate surface ornamentation; tectate, columellae distinct, exine 1.5 μm thick; surface ornamentation reticulate, heterobrochate, simplicolumellate, muri 1 μm wide, lumina 1–1.5 μm , apocolpia characterised by thicker nexine and foveo-reticulate surface ornamentation, muri in polar region 1 μm wide, lumina 0.5 μm .

Dimensions. Equatorial diameter 40 μm ; nm: 1; no: 1.

Comparisons. *Retitricolpites microreticulatus* (Van der Hammen 1954) Van der Hammen & Wymstra 1964 is smaller (20–30 μm), *Retitricolpites* sp. 2 Jan du Chêne et al. 1978 lacks apocolpial thickening.

Material. Ozuitem 6.1 (J42,4), polar view.

Retitrescolpites sp. 3

Plate 5, figure 16

Diagnosis. Tricolpate, triangular, colpi located at pole, colpi marginate, tectate, reticulate, heterobrochate, equatorial diameter 43 μm .

Description. Monad, radial, amb triangular, apices rounded; tricolpate, 20 μm long, 1 μm wide at centre, ends rounded and slightly flared (2.5 μm wide), marginate, margo 1 μm wide, defined by finer surface ornamentation; tectate, columellae distinct, nexine 0.5 μm thick, columellae 0.5 μm thick and 0.5 μm in diameter, tectum 0.5 μm thick, and spaced 1–2 μm apart; surface ornamentation reticulate, heterobrochate, curvilinear, simplicolumellate, muri 0.5–1 μm wide, lumina 2–3 μm wide, in places the reticulum appears free and detached from the nexine.

Dimensions. Equatorial diameter 43 μm ; nm: 1; no: 2.

Material. Ameke 1.1 (W38), polar view, specimen slightly fragmented.

Retitrescolpites sp. 4

Plate 5, figure 17

Diagnosis. Tricolpate, circular, colpi costate, tectate, reticulate, heterobrochate, equatorial diameter 35 µm.

Description. Monad, radial, amb circular; tricolpate, colpi 10 µm long, ends slightly pointed, costate, costae 1 µm wide; tectate, nexine 1 µm thick, columellae 1 µm thick, tectum 0.5 µm thick, columellae 0.5 µm wide, spaced 1 µm apart; surface ornamentation reticulate, heterobrochate, muri 0.5 µm wide, lumina polygonal 1–3 µm wide.

Dimensions. Equatorial diameter 35 µm; nm: 1; no: 3.

Comparisons. *Retitrescolpites definidus* Jaramillo et al. 2007 has well-defined costae.

Material. Ozuitem 3.1 (Q35,2). polar view.

Genus *Rousea* Srivastava 1969

Type. *Rousea subtilis* Srivastava 1969

Rousea florentina (González Guzmán 1967) Jaramillo & Dilcher 2001

Plate 5, figures 18–19

Synonymy. *Retitricolpites florentinus* González Guzmán 1967.

Diagnosis. Tricolpate, prolate, tectate, reticulate, lumina decrease in size smoothly from mesocolpia to apocolpia, equatorial diameter 29.8 µm.

Description. Monad, radial, prolate; tricolpate, colpi long and simple; tectate, columellae distinct, nexine 0.5 µm thick, sexine 1 µm thick; surface ornamentation reticulate, heterobrochate, muri 1.5 µm wide, lumina irregular, 1.5 µm wide at equator and decrease smoothly to 0.5 µm wide at poles.

Dimensions. Equatorial diameter 29.8 µm; nm: 1; no: 3.

Comparisons. *Rousea georgensis* (Brenner 1963) Dettman 1973 is smaller (equatorial diameter 20 µm) with a reticulum formed by closely spaced pila with capita touching. *Rousea heteroreticulatus* (Boltenhagen 1976) comb. nov. is smaller. *Retitricolporites ogowensis* Boltenhagen 1976 is tricolporate.

Material. Amaogugu 1.1 (P60,4), equatorial view.

Rousea heteroreticulatus (Boltenhagen 1976) comb. nov.

Basonym = *Retitricolpites heteroreticulatus* Boltenhagen 1976

Plate 5, figures 20–21

Diagnosis. Tricolpate, prolate, colpi ends rounded and slightly flared, tectate, reticulate, heterobrochate, equatorial diameter 22 µm.

Description. Monad, radial, prolate; tricolpate, colpi 19 µm, simple, 1–2 µm wide, ends rounded and slightly flared; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, muri 0.5–1 µm wide, lumina polygonal, 1–1.5 µm wide at equator and decrease smoothly to <0.5 µm wide in at poles.

Dimensions. Equatorial diameter 21–(22)–23.4 µm; nm: 2; no: 22.

Comparisons. *Tricolpites vulgaris* (Pierce 1961) Srivastava 1969 has lumina that increase towards apocolpia. *Rousea georgensis* (Brenner 1963) Dettman 1973 has a reticulum formed by closely spaced pila with capita touching. *Rousea florentina* (González Guzmán 1967) Jaramillo & Dilcher 2001 is larger and has distinct columellae. *Retitricolpites* Van der

Hammen is an illegitimate genus (Jansonius and Hills 1976, card 2401). *Rousea* Srivastava 1969 accommodates reticulate pollen grains with lumina that decrease in size from the mesocolpia to the apocolpia.

Material. Ameke 1.1 (S55,4), equatorial view.

Genus *Striatopollis* Krutzsch 1959

Type. *Striatopollis sarstedtensis* Krutzsch 1959

Striatopollis catatumbus (González Guzmán 1967) Takahashi & Jux 1989

Plate 5, figures 22–23

Synonymy. *Striatricolpites catatumbus* González Guzmán 1967.

Striatricolpites catatumbus Germeraad et al. 1968.

Diagnosis. Tricolpate, prolate, tectate, striate, equatorial diameter 29 µm.

Description. Monad, radial, prolate; tricolpate, colpi long, extending almost to the poles; tectate, columellae distinct and arranged regularly under the muri, exine 1.5 µm thick; surface ornamentation striate, muri 1.2 µm wide, striae 0.5–1 µm wide, striae anastomosing and orientated sub-parallel to colpi.

Dimensions. Equatorial diameter 22.8–(29)–35.5 µm; nm: 8; no: 61.

Comparisons. No tricolporate specimens of *Striatopollis catatumbus* Takahashi & Jux 1989 were observed in the material studied.

Material. Amaogugu 7.1 (P37,4), equatorial view.

Botanical affinity. Fabaceae (Romero et al. 2020 and comparison with *Crudia*, *Macrolobium* and relatives).

Striatopollis sp.

Plate 5, figures 24–25

Diagnosis. Tricolpate, triangular, colpi marginate, tectate, striate, equatorial diameter 28 µm.

Description. Monad, radial, amb triangular; tricolpate, colpi 14 µm long, 2.5 µm wide at equator, narrowing to 1 µm at pole, very long, almost reaching apocolpia, ends rounded, marginate, margo <0.5 µm wide, margo produced by thinning of the exine; tectate, columellae distinct, exine 0.5 µm thick; surface ornamentation striate, muri 0.5 µm wide, striae 0.5 µm wide, arranged in a random fingerprint-like pattern.

Dimensions. Equatorial diameter 28 µm; nm: 1; no: 2.

Comparisons. *Psilatricolpites papilioniformis* Regali et al. 1974 has much fainter striations; *Tricolpites microstriatus* Jardiné and Magloire 1965 has a thicker exine. *Syncolporites subtilis* Boltenhagen 1976 is syncolporate.

Material. Okigwe B1.1 (V52,2), polar view.

Genus *Tricolpites* Cookson ex Couper 1953 emend. Belsky et al. 1965

Type. *Tricolpites reticulata* Cookson ex Couper 1953

Tricolpites clarensis (González Guzmán 1967) Jaramillo & Dilcher 2001

Plate 5, figures 26–27

Synonymy. *Retitricolpites clarensis* González Guzmán 1967.

Retitricolpites clarensis (González Guzmán 1967) van Hoeken-Klinkenberg 1966.

Retitricolpites clarensis (González Guzmán 1967) Wijmstra 1971.

Diagnosis. Tricolpate, sub-circular, colpi simple, tectate, reticulate, homobrochate equatorial diameter 32 µm.

Description. Monad, radial, amb sub-circular; tricolpate, colpi long, borders slightly irregular, ends pointed; tectate, columellae distinct, nexine <0.5 µm thick, columellae 0.5 µm thick, tectum <0.5 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5–1 µm wide, lumina sub-circular and distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 28–(31.5)–35 µm, nm: 6; no: 58.

Material. Amaogugu 7.1 (S56,1), polar view.

Tricolpites gageonnetii (Boltenhagen 1976) comb. nov.

Basonym = *Retitricolpites gageonnetii* Boltenhagen 1976

Plate 5, figures 28–29

Diagnosis. Tricolpate, circular, colpi marginate, tectate, reticulate, homobrochate equatorial diameter 30 µm.

Description. Monad, radial, amb circular; tricolpate, colpi 9 µm long, 7 µm wide, marginate, margo 2 µm wide, formed by thinning of the exine, ends pointed; tectate, columellae distinct, nexine <0.5 µm thick, columellae 0.5 µm thick, tectum <0.5 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm wide, lumina sub-circular and distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 28–(30)–34.5 µm; nm: 5; no: 33.

Comparisons. *Retitricolpites caquetanus* Hoorn 1994 has shorter colpi; *Tricolpites microreticulatus* Belsky, Boltenhagen & Potonié 1965 has costate colpi; *Tricolpites clarensis* (González Guzmán 1967) Jaramillo & Dilcher 2001 has a simple colpi. *Retitricolpites* Van der Hammen is an illegitimate genus (Jansonius and Hills 1976, card 2401).

Material. Okigwe B1.1 (W42), polar view.

Tricolpites multiornamentus sp. nov.

Plate 5, figures 30–33

Diagnosis. Tricolpate, sub-circular, semitectate, columellae distinct, reticulate homobrochate, borders of colpi clavate-baculate, equatorial diameter 26 µm.

Etymology. After the multiple types of surface ornamentation.

Description. Monad, radial, amb sub-circular; tricolpate, colpi 10 µm long, 12 µm wide, ends rounded, borders of the colpi characterised by prominent clavae and baculae 0.5–1 µm wide, 1–3 µm high; semitectate, columellae distinct, without capita occasionally free with no reticulum present, nexine 0.5 µm, columellae layer 0.5 µm, tectum 0.5 µm; surface

ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm wide.

Dimensions. Equatorial diameter 24.4–(26)–28 µm; nm: 2; no: 3.

Comparisons. *Rhoipites? basicus* D'Apolito et al. 2019 has simple colpi that lack clavae and baculae at the borders. *Tricolpites 'marginobaculatus'* Jaramillo & Rueda 2023 has a thinner exine and indistinct columellae.

Material. Holotype Okigwe B1.1 (N41,4), Plate 5, figures 30–31, polar view; paratype Okigwe B1.1 (M46), Plate 5, figures 32–33, polar view; an air bubble rests over this specimen.

Tricolpites brevicolpatus sp. nov.

Plate 5, figures 34–36

Diagnosis. Tricolpate, sub-circular, colpi short and marginate, tectate, columellae indistinct, reticulate, homobrochate, equatorial diameter 26 µm.

Etymology. After the short colpi.

Description. Monad, radial, amb sub-circular; tricolpate, colpi 5 µm long, 3 µm wide, colpi marginate, margo 0.5 µm wide and psilate, formed by a reduction of the reticulum and slight thickening of the exine; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation reticulate homobrochate, lumina 0.5–1 µm in diameter, distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 22.5–(25.5)–28 µm; nm: 7; no: 10.

Comparisons. *Tricolpites clarensis* (González Guzmán 1967) Jaramillo & Dilcher 2001 has long and simple colpi. *Psilatricolpites brevis* González Guzmán 1967 is psilate. *Retibrevitricolpites retibolus* Leidelmeyer 1966 has shorter colpi that lack margins. *Retitricolpites brevicolpatus* Sarmiento 1992 has coarser heterobrochate surface ornamentation with polygonal lumina that decrease from 1.5 µm in the mesocolpia to 1 µm at the apocolpia.

Material. Holotype Okigwe B1.1 (W56), Plate 5, figures 34–35, polar view; paratype Okigwe B1.1 (N42,3), Plate 5, figure 36, polar view.

Tricolpites sp. 1

Plate 5, figures 37–38

Diagnosis. Tricolpate, circular, tectate, reticulate, homobrochate, equatorial diameter 27 µm.

Description. Monad, radial, amb circular; tricolpate, colpi 8 µm long, 5 µm wide, ends pointed; tectate, columellae distinct, nexine 0.5 µm thick, columellae 1.5 µm thick, tectum 0.5 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm in diameter and rounded, lumina distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 24–(26.5)–29 µm; nm: 2; no: 2.

Comparisons. *Lanagiopollis crassa* (Van der Hammen & Wymstra 1964) Frederiksen 1988 is tricolporate. *Retitrescolpites* sp. 2 has longer colpi and is heterobrochate. *Tricolpites brevicolpatus* sp. nov. is brevicolpate and has marginate colpi.

Material. Ameke 11.1 (V39), polar view.

Tricolpites sp. 2

Plate 5, figure 39

Diagnosis. Tricolpate, sub-triangular, colpi marginate, tectate, reticulate, homobrochate, equatorial diameter 26 µm.

Description. Monad, radial, amb sub-triangular; tricolpate, colpi 11 µm long, 3 µm wide, marginate, margo 1 µm wide, produced by a thickening of the sexine and by a reduction of the surface ornamentation; tectate, columellae distinct, 0.5 µm wide, spaced 1 µm apart, exine 1 µm thick, nexine thickens slightly at the apocolpia, boundary of the thickened area diffuse; surface ornamentation reticulate, homobrochate, muri 1 µm wide, lumina 0.5–1 µm in diameter, lumina spread densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 26 µm; nm: 1; no: 3.

Comparisons. *Tricolpites clarensis* (González Guzmán 1967) Jaramillo & Dilcher 2001 has simple colpi. *Bombacacidites brevis* Muller et al. 1987 is tricolporate.

Material. Ozuitem 3.1 (P37,2), polar view.

Tricolpites sp. 3

Plate 5, figures 40–41

Diagnosis. Tricolpate, sub-prolate, tectate, reticulate, homobrochate, equatorial diameter 17 µm.

Description. Monad, radial, sub-prolate; tricolpate, colpi 8–14 µm long, 1–2 µm wide; tectate, columellae distinct, nexine 0.5 µm thick, sexine 1–1.5 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina sub-circular, 0.5–1 µm in diameter and distributed evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 13.4–(17)–21.5 µm; nm: 12; no: 54.

Comparisons. *Tricolpites* sp. 4 is heterobrochate.

Material. Amaogugu 7.1 (S40,4), equatorial view.

Tricolpites sp. 4

Plate 5, figures 42–43

Diagnosis. Tricolpate, circular-oval, tectate, reticulate, heterobrochate, simplicolumellate, curvimurate, equatorial diameter 18 µm.

Description. Monad, radial, amb circular-oval; tricolpate, colpi 6–12 µm long, 1–2 µm wide; tectate, columellae distinct, nexine <0.5 µm thick, sexine 1–2 µm thick; surface ornamentation reticulate, heterobrochate, simplicolumellate, curvimurate, muri 0.5 µm wide, lumina sub-circular, 0.5–1.5 µm in diameter and distributed evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 14.2–(17.5)–20.5 µm; nm: 7; no: 13.

Comparisons. *Tricolpites* sp. 3 is homobrochate.

Material. Ozuitem 6.1 (T32,2), polar view.

Tricolporate pollen

Genus *Bombacacidites* Couper 1960 emend. Krutzsch 1970

Type. *Bombacacidites bombaxoides* Couper 1960

Bombacacidites aff. *brevis* Muller et al. 1987

Plate 6, figure 1

Diagnosis. Tricolporate, planaperturate, sub-triangular obtuse-convex, colpi long (10–12 µm) and marginate, micropitted, equatorial diameter 32 µm.

Description. Monad, radial, amb sub-triangular obtuse-convex; tricolporate, colpi marginate, boundaries of margo irregular and extending into apocolpium, colpi long (10–12 µm), apocolpium small (4 µm wide), pore distinct, 5 µm wide; exine tectate, 1.5 µm thick, columellae indistinct, nexine 0.5 µm thick, columellae and tectum 1.5 µm thick; surface ornamentation micropitted.

Dimensions. Equatorial diameter 32 µm; nm: 1; no: 2.

Comparisons. *Bombacacidites brevis* (Dueñas 1980) Muller et al. 1987 has shorter colpi.

Material. Ozuitem 3.1 (X40), polar view.

Botanical affinity. Malvaceae (D'Apolito et al. 2021).

Bombacacidites 'pluricolumellatus'

Plate 6, figure 2

Diagnosis. Tricolporate, planaperturate, sub-triangular obtuse-convex, colpi costate, tectate, pluricolumellate, reticulate, heterobrochate, lumina slightly coarser at apocolpium, equatorial diameter 33 µm.

Description. Monad, radial, amb sub-triangular obtuse-convex; tricolporate, colpi costate (costae 2 µm wide), colpi 3 µm wide, pori indistinct; exine tectate, nexine 0.5 µm thick, columellae 2 µm thick, tectum <0.5 µm thick, columellae distinct, each columella 0.5–1 µm wide, columellae spaced <1 µm apart and only present under muri of reticulum; surface ornamentation reticulate, heterobrochate, muri 1 µm wide, slightly coarser at apocolpium, some muri simplicolumellate, others duplicolumellate, lumina 2–3 µm wide.

Dimensions. Equatorial diameter 33 µm; nm: 1; no: 1.

Comparisons. *Bombacacidites* sp. 1 of Jaramillo and Dilcher (2001) is larger (45 µm). *Bombacacidites* sp. 5 of Jaramillo & Dilcher (2001) is simplicolumellate. *Bombacacidites araracuarensis* Hoorn 1994 has coarser reticulum (lumina 4.5 µm wide) and is larger (50–55 µm).

Material. Okigwe B4.1 (H45,2), polar view. One of us (CJ) has observed specimens conforming to this description in the Oligocene of Colombia (unpublished data).

Genus *Fillaeopsidites* Salard-Chaeboldaëff 1979

Type. *Fillaeopsidites reticulatus* (Guinet & Salard-Chaeboldaëff 1975) Salard-Chaeboldaëff 1979

Fillaeopsidites cf. *reticulatus* (Guinet & Salard-Chaeboldaëff 1975) Salard-Chaeboldaëff 1978

Plate 6, figures 3–4

Diagnosis. Tetrahedral tetrad, monads tricolporate, colpi long and simple, tectate, micropitted, tetrad 47 µm in diameter, monads 24 µm in diameter.

Description. Tetrahedral tetrad, monad amb sub-triangular; monads tricolporate, colpi simple, and 10–12 µm long, pori

indistinct; tectate, exine 2 µm thick, nexine 0.5–1 µm, sexine 1 µm; surface ornamentation micropitted.

Dimensions. Tetrad 44–(46.5)–49 µm in diameter, monads 22–(23.5)–25 µm in diameter; nm: 3; no: 12.

Comparisons. *Fillaeopsidites reticulatus* (Guinet & Salard-Chaeboldaëff 1975) Salard-Chaeboldaëff 1978 is reticulate with lumina 1 µm wide that decrease in size towards the distal pole. *Psilatricolporites tetradus* Brenner 1968 is tricolpate and psilate.

Material. Okigwe A5.1 (E45,4), oblique view.

Genus *Foveotricolporites* Pierce 1961

Type. *Foveotricolporites rhombohedralis* Pierce 1961

Foveotricolporites cf. *crassiexinus* van Hoeken-Klinkenberg 1966

Plate 6, figures 5–10

Diagnosis. Tricolporate, prolate–perprolate, tectate, foveolate, equatorial diameter 19 µm.

Description. Monad, radial, prolate–perprolate; tricolporate, colpi long, almost reaching the equator, polar area small, colpi invaginated, pori 3 µm wide, pori costate, costae 2 µm wide; tectate, collumellae distinct, exine 3 µm thick, nexine 1 µm, collumellae 1 µm, sexine 1 µm; surface ornamentation foveolate, foveolae 1 µm wide distributed densely and evenly over the surface of the pollen grain, muri 1.5–3 µm wide.

Dimensions. Equatorial diameter 18.5–(19)–20 µm; nm: 2; no: 5.

Comparisons. *Foveotricolporites crassiexinus* van Hoeken-Klinkenberg 1966 is subprolate and has larger foveolae (1.5 µm).

Material. Ameke 1.1 (H31,3), equatorial view; Ameke 11.1 (R36,1), equatorial view.

Genus *Lanagiopollis* Morley 1982

Type. *Lanagiopollis regularis* Morley 1982

Lanagiopollis crassa (Van der Hammen & Wymstra 1964) Frederiksen 1988

Plate 6, figures 11–14

Synonymy. *Psilatricolporites crassus* Van der Hammen & Wymstra 1964.

Psilatricolporites crassus (Van der Hammen & Wymstra 1964) Gemeraad et al. 1968.

Diagnosis. Tricolporate, sub-circular, pori lalongate, tectate, psilate, tectum degraded to expose the columellae, equatorial diameter 52 µm.

Description. Monad, radial, amb sub-circular; tricolporate, occasionally tetracolporate (one specimen), colpi 27 µm long, 1 µm wide, margins well defined, ends pointed, pori lalongate, 7 µm wide; tectate, exine 2.5 µm thick, nexine 1 µm thick, columellae 0.5 µm thick, each columella 0.5 µm wide, columellae spaced 1 µm apart, tectum 1 µm thick; surface ornamentation psilate, over the majority of the grain surface the tectum has degraded to expose the columellae.

Dimensions. Equatorial diameter 49.2–(51.6)–54 µm; nm: 4; no: 12.

Material. Ozuitem 6.1 (S35,2), polar view, tetracolporate specimen; Ozuitem 3.1 (W59,3), oblique view.

Botanical affinity. Euphorbiaceae (by comparison with *Hura* (Germeraad et al. 1968)), Tetrameristaceae (by comparison with *Pelliciera rhizophorae* (Germeraad et al. 1968)).

Genus *Margocolporites* Ramanujam 1966 ex Srivastava 1969, emend. Pocknall & Mildenhall 1984

Type. *Margocolporites tsukadai* Ramanujam 1966 ex Srivastava 1969

Margocolporites cf. *mandjicus* Boltenhagen 1976

Plate 6, figure 15

Diagnosis. Tricolporate, circular, colpi marginate, tectate, reticulate, heterobrochate, equatorial diameter 26 µm.

Description. Monad, radial, amb circular; tricolporate, marginate, margo 2 µm wide and psilate, pori 3.5 µm wide; tectate, columellae distinct, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, lumina 0.5–1 µm, muri 0.5–1 µm, reticulum coarsens progressively from the apocolpia to the mesocolpia.

Dimensions. Equatorial diameter 26 µm; nm: 1; no: 3.

Comparisons. The margins of *Margocolporites mandjicus* Boltenhagen 1976 are more conspicuous and the reticulum is slightly coarser in the mesocolpium (1–3 µm). The colpi of *Margocolporites rauvolfi* Salard-Cheboldaëff 1979 are larger (35 µm) and have margins characterised by pronounced thinning of the exine that are rounded at the apocolpium.

Material. Okigwe B6.1 (M46,2), polar view.

Margocolporites cf. *rauvolfi* Salard-Cheboldaëff 1979

Plate 6, figure 16

Diagnosis. Tricolporate, sub-circular, colpi marginate, pori costate, tectate, reticulate homobrochate, equatorial diameter 37 µm.

Description. Monad, radial, amb sub-circular; tricolporate, colpi 13 µm long, borders straight, end pointed, marginate, margo 4 µm wide and formed by a thinning of the sexine, pori 5 µm wide and costate, costae 1 µm wide; tectate, nexine 1 µm thick, columellae 0.5 µm thick, columellae indistinct in certain areas, tectum 0.5 µm thick, exine thickens slightly in mesocolpia, formed by thickening of the nexine and sexine; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm wide.

Dimensions. Equatorial diameter 37 µm; nm: 1; no: 3.

Comparisons. *Margocolporites* sp. 1 Jaramillo & Dilcher 2001 has two distinctive rings around each pore formed by thickening and thinning of the nexine. The colpi of *Margocolporites rauvolfi* Salard-Cheboldaëff 1979 are shorter and have margins that are rounded at the apocolpium.

Material. Ameke 1.1 (H43,2), polar view.

Botanical affinity. Apocynaceae (Morley 2000).

Genus *Paripollis* Partridge in Stover & Partridge 1973

Type. *Paripollis ochesis* Partridge in Stover & Partridge 1973

Paripollis? ‘*dubius*’

Plate 6, figures 17–18

Diagnosis. Tricolporate, tetrahedral tetrad, colpi marginate, tectate, scabrate, tetrad 34 µm in diameter, monads 24 µm in diameter.

Description. Tetrahedral tetrad, radial, monad amb sub-circular; tricolporate, apertures arranged according to Fisher's rule (Punt et al. 2007), colpi short (6.5 µm long) and narrow (0.5–1 µm wide), colpi marginate, margo 1.5 µm wide, pori sub-circular (4.5 µm in diameter); tectate, columellae distinct, spaced 0.5 µm apart, exine 1 µm thick; surface ornamentation scabrate, sculptural elements spaced 1 µm apart and distributed densely and evenly over the surface of the pollen grain.

Dimensions. Tetrad 32–(33.5)–35 µm in diameter, equatorial diameter of monads 22.5–(24)–25.1 µm; nm: 3; no: 9.

Comparisons. *Fillaeopsidites reticulatus* Salard-Cheboldaëff 1978 has long colpi that lack margins, is larger (tetrad 50 µm) and has reticulate or foveolate surface ornamentation. *Kiellmeyerapollenites eocenicus* Sah & Kar 1974 has long funnel-shaped colpi with well-developed pori, is larger (tetrad 65–72 µm) and has pilate surface ornamentation that forms a reticulum. The colpi of *Ericipites longisulcus* (Wodehouse 1933) Krutzsch 1970 are narrow slits lacking margins. *Dicotetradites clavatus* (Couper 1953) Crosbie & Clowes 1980 is triporate. *Paripollis ochesis* Partridge in Stover & Partridge 1973 has faint colpi that lack margins and is verrucate with interspersed granulae. Specimens encountered here are tentatively assigned to *Paripollis* Partridge in Stover & Partridge 1973 on the basis of aperture arrangement and short colpi.

Material. Okigwe B1.1 (W32).

Genus *Psilabrevitricolporites* Van der Kaars 1983

Type. *Psilabrevitricolporites simpliformis* Van der Kaars 1983

Psilabrevitricolporites simpliformis Van der Kaars 1983

Plate 6, figure 19

Diagnosis. Tricolporate, triangular, colpi short, atectate, psilate, equatorial diameter 27 µm.

Description. Monad, radial, amb triangular slightly convex; tricolporate, colpi short (4 µm), margins regular and slightly curved, ends pointed, pori costate, costae 1–1.5 µm wide, exine slightly thicker in apocolpium, which is distinguished by a prominent region with the same outline as the outline; atectate, exine <0.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 27 µm; nm: 1; no: 11.

Material. Okigwe B3.1 (P44,4), polar view.

Psilabrevitricolporites porolatus sp. nov.

Plate 6, figures 20–23

Diagnosis. Tricolporate, sub-triangular and convex, colpi short, pori 10 µm wide, tectate, psilate-micropitted, equatorial diameter 28 µm.

Etymology. After the wide pori.

Description. Monad, radial, amb sub-triangular and convex; tricolporate, colpi 5 µm long, simple, borders regular and straight, ends pointed, pori costate and clearly defined, lalongate, 10 µm wide, costae 2 µm wide and 1 µm thick; tectate, collumellae indistinct, nexine 0.5 µm, sexine 0.5 µm thick,

thickening slightly around the pori; surface ornamentation psilate to micropitted, lumina <0.5 µm.

Dimensions. Equatorial diameter 23.5–(27.5)–31 µm; nm: 6; no: 10.

Comparisons. *Psilabrevitricolporites* sp. 2 Jaramillo & Dilcher 2001 is atectate; *Psilabrevitricolporites simpliformis* Van der Kaars 1983 is atectate and has thickened apocolpia.

Material. Holotype Amaogugu 1.1 (T60), Plate 6, figures 20–21, polar view; paratype Amaogugu 1.1 (M48,1), Plate 6, figures 22–23, polar view.

Genus *Rhoipites* Wodehouse 1933

Type. *Rhoipites bradleyi* Wodehouse 1933

Rhoipites guianensis (Van der Hammen & Wymstra 1964)
Jaramillo & Dilcher 2001

Plate 6, figure 24

Synonymy. *Retitricolporites guianensis* Van der Hammen & Wymstra 1964.

Retitricolporites guianensis (Van der Hammen & Wymstra 1964) Germeraad et al. 1968.

Retitricolporites guianensis (Van der Hammen & Wymstra 1964) Regali et al. 1974.

Retitricolporites guianensis (Van der Hammen & Wymstra 1964) Lorente 1986.

Diagnosis. Tricolporate, prolate, colpi marginate, pori lalongate, tectate, reticulate, heterobrochate, equatorial diameter 20 µm.

Description. Monad, radial, prolate; tricolporate, colpi 25 µm long, borders straight, ends pointed, marginate, margo 2 µm wide, pori lalongate, 1.3 µm high, 4 µm wide; tectate, columellae distinct, exine 1.5 µm thick; surface ornamentation reticulate, heterobrochate and mesh-like, muri 0.5 µm wide, lumina 0.5–1.5 µm wide and polygonal, decreasing in size towards apocolpia.

Dimensions. Equatorial diameter 20 µm; nm: 1; no: 4.

Material. Ameke 1.1 (T65), equatorial view.

Botanical affinity. Malvaceae (Germeraad et al. 1968).

Genus *Rugutricolporites* González Guzmán 1967

Type. *Rugutricolporites felix* González Guzmán 1967

Rugutricolporites cumulus sp. nov.

Plate 6, figures 25–27

Diagnosis. Tricolporate, sub-triangular, colpi marginate and costate, pori costate, tectate, collumellae indistinct, rugulate at mesocolpium, psilate elsewhere, equatorial diameter 28 µm.

Etymology. After the cloud-like appearance of the mesocolpia.

Description. Monad, radial, amb sub-triangular; tricolporate, colpi 13 µm long, 0.5 µm wide, borders straight, marginate, margo 1–2 µm wide, costate, costa 0.5 µm thick, colpi do not anastomose at pole, apocolpium small (5 µm wide), pori

2.5 µm wide, costate, costae 0.5–1 µm thick; tectate, columellae indistinct, exine 1–2 µm thick; surface ornamentation rugulate, rugulae 1 µm wide, 2–4 µm long, sculptural elements restricted to mesocolpium, psilate elsewhere.

Dimensions. Equatorial diameter 24.5–(27.5)–31 µm; nm: 7; no: 8.

Comparisons. *Rugutricolporites felix* González Guzmán 1967 has rugulae over the entire surface of the grain. *Rugutricolporites intensus* Jaramillo et al. 2011 is larger (38–40 µm), has fastigate pori and has foveolae over the entire surface of the grain. *Striatricolporites nigeriensis* van Hoeken-Klinkenberg 1966 is striate in the mesopodium and lacks ornamentation around the pori.

Material. Holotype Ozuitem 6.1 (O33,2), Plate 6, figure 25, polar view; paratype Ozuitem 3.1 (V40,4), Plate 6, figures 26–27, polar view;

Genus *Striatricolporites* Van der Hammen ex Leidelmeyer 1966

Type. *Striatricolporites pimulis* Leidelmeyer 1966

Striatricolporites cf. *pimulis* Leidelmeyer 1966

Plate 6, figure 28

Diagnosis. Tricolporate, sub-triangular, intectate, striate, equatorial diameter 22 µm.

Description. Monad, radial, amb sub-triangular; tricolporate, colpi 9 µm long, 5 µm wide at equator, narrowing to 1 µm, ends pointed, borders curved, pore circular, 3 µm in diameter; intectate, exine 1 µm thick; surface ornamentation striate, muri 0.5–1 µm wide, striae 0.5–1 µm wide, striae orientated perpendicular to colpi.

Dimensions. Equatorial diameter 22 µm; nm: 1; no: 1.

Comparisons. *Striatricolporites pimulis* Leidelmeyer 1966 has costate pori.

Material. Ozuitem 3.1 (W65,2), oblique view.

Genus *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type. *Tetracolporopollenites sapotoides* Pflug & Thomson in Thomson & Pflug 1953

Tetracolporopollenites maculosus (Regali et al. 1974) Jaramillo & Dilcher 2001

Plate 6, figures 29–30

Synonymy. *Psilatricolporites maculosus* Regali et al. 1974.

Psilatricolporites maculosus (Regali et al. 1974) Lorente 1986.

Diagnosis. Tetracolporate, prolate to prolate spheroidal, pori lalongate and annulate, atectate, psilate, equatorial diameter 27 µm.

Description. Monad, radial, prolate to prolate spheroidal; tetracolporate (four colpi), colpi 12 µm long, 0.5 µm wide, pori lens-shaped and lalongate, 8 µm wide, 2 µm high, pori annulate, annulus 2 µm wide; atectate, exine <0.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 26.2–(27)–28 µm; nm: 3; no: 16.

Material. Ameke 1.1 (T44), equatorial view.

Botanical affinity. Sapotaceae (Lorente 1986).

Tetracolporopollenites transversalis (Dueñas 1980) Jaramillo & Dilcher 2001

Plate 6, figures 31–32

Synonymy. *Psilatricolporites transversalis* Dueñas 1980.

Diagnosis. Tricolporate, prolate, pori lalongate and costate, tectate, psilate, equatorial diameter 25 µm.

Description. Monad, radial, prolate; tricolporate, colpi 11 µm long, indistinct, pori lalongate, 6 µm wide, 2 µm high, pori costate; tectate, exine 0.5 µm thick; exine thickens to 1.5 µm at the equator, thickening forms a continuous band 12 µm high around the equator, thickening formed by the nexine; surface ornamentation psilate.

Dimensions. Equatorial diameter 25 µm; nm: 1; no: 10.

Comparisons. *Lugopollis tetraporites* (Venkatachala & Rawat 1972) Venkatachala & Rawat 1984 has shorter colpi and reticulate surface ornamentation at the poles.

Material. Amaogugu 1.1 (L60), equatorial view.

Botanical affinity. Sapotaceae (Lorente 1986).

Tetracolporopollenites cryptoporus (Boltenhagen 1976) comb. nov.

Basonym = *Psilatricolporites cryptoporus* Boltenhagen 1976

Plate 6, figure 33

Diagnosis. Tricolporate, prolate, colpi costate, atectate, psilate, equatorial diameter 18 µm.

Description. Monad, radial, prolate; tricolporate, colpi 13 µm long, narrow, colpi costate, costae 1 µm wide, 1 µm thick, pori indistinct; atectate, exine 2 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 17–(18)–19.4 µm; nm: 4; no: 23.

Comparisons. *Psilatricolporites* Van der Hammen 1956 ex Pierce 1961 is an obligate later synonym of *Tricolporites* Van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as the latter is illegitimate and a later synonym of *Clethra*, so is *Psilatricolporites* (vide *Tricolporites* Van der Hammen – non Erdtman 1949) (Jansonius and Hills 1976, card 2234). *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953 accommodates tri- and tetracolporate pollen grains.

Material. Okigwe B6.1 (W40,1), equatorial view.

Tetracolporopollenites torus sp. nov.

Plate 6, figures 34–39

Diagnosis. Tricolporate, prolate to prolate spheroidal, pori with annulus, tectate, psilate–micropitted, equatorial diameter 23 µm.

Etymology. After the prominent annulate pori.

Description. Monad, radial, prolate to prolate spheroidal; tricolporate, colpi 11 µm long, simple, borders slightly irregular, ends pointed, slit-like, pori circular, 2 µm wide, annulate, annulus 1.5 µm wide, 1 µm thick, pori lalongate; tectate, columellae indistinct, exine 1.5 µm thick, nexine 0.5 µm, sexine 1 µm; surface ornamentation psilate to micropitted.

Dimensions. Equatorial diameter 19.5–(22.5)–25.5 nm; 10; no: 20.

Comparisons. *Psilatricolporites* Van der Hammen 1956 ex Pierce 1961 is an illegitimate genus (Jansonius and Hills 1976, card 2234). *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953, accommodates tri- and tetracolporate pollen grains. *Lakiapollis ovatus* Venkatachala & Kar 1969 has very short colpi and is larger; *Tetracolporopollenites?* sp. 2 Jaramillo & Dilcher 2001 has marginate colpi.

Material. Holotype Amaogugu 1.1 (W67,1), Plate 6, figures 34–36, oblique view; paratype Okigwe A1.1 (F66), Plate 6, figures 37–39, equatorial view.

Genus *Tricolporites* Cookson 1947

Type. *Tricolporites prolata* Cookson 1947

Tricolporites densus sp. nov.

Plate 6, figures 40–42

Diagnosis. Tricolporate, subprolate, pori lalongate, tectate, reticulate, homobrochate, equatorial diameter 31 µm.

Etymology. After the dense and even lumina of the reticulum.

Description. Monad, radial, subprolate; tricolporate, colpi 12 µm long, borders straight, ends pointed, costate, pori lalongate; tectate, columellae distinct, exine 1.5 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5–1 µm wide, spaced densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 28–(30.5)–33 µm; nm: 2; no: 19.

Comparisons. *Retitricolporites ninghesikanus* Boltenhagen 1976 is heterobrochate with a coarser reticulum and irregular lumina (2.5 µm).

Material. Holotype Okigwe B2.1 (W61,2), Plate 6, figure 40, polar view; paratype Okigwe B3.1 (S46), Plate 6, figures 41–42, equatorial view.

Tricolporites 'reticulomargites'

Plate 7, figures 1–2

Diagnosis. Tricolporate, sub-circular, colpi marginate, pore costate at equator, tectate, simplicicolumellate, reticulate, heterobrochate, equatorial diameter 56 µm.

Description. Monad, radial, amb sub-circular; tricolporate, colpi 21 µm long, 15 µm wide, borders irregular, ends rounded, marginate, margo 2 µm wide, formed by reduction of the reticulum; pore costate at equator, costa 0.5 µm thick, tectate, columellae distinct, 0.6 µm wide, spaced 0.5 µm apart, nexine 1 µm thick in mesocolpium, nexine thickens to 1.5 µm adjacent to colpi, columellae 1.5 µm thick, tectum 0.5 µm thick; surface ornamentation reticulate, heterobrochate, muri 0.5–1 µm, simplicicolumellate, lumina 1.5 µm.

Dimensions. Equatorial diameter 56 µm, nm: 1; no: 1.

Comparisons. *Retitricolporites ninghesikanus* Boltenhagen 1976 has coarser reticulum with irregular lumina (2.5 µm), is smaller (equatorial diameter 32 µm), and the pori are not costate.

Material. Ozuitem 6.1 (H36), polar view.

Tricolporites sp. 1

Plate 7, figures 3–5

Diagnosis. Tricolporate, sub-circular, pori circular, tectate, reticulate, homobrochate, equatorial diameter 23 µm.

Description. Monad, radial, amb sub-circular; tricolporate, colpi 9 µm long, 3 µm wide, borders slightly irregular, ends pointed, pori circular, simple, 2 µm in diameter; tectate, columellae distinct, exine 1 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm wide, spaced densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 21–(22.5)–24; nm: 2; no: 8.

Comparisons. *Retitricolporites ogowensis* Boltenhagen 1976 has indistinct pori and the reticulum is coarser at the equator.

Material. Ameke 1.1 (T51,4), oblique view.

Tricolporites sp. 2

Plate 7, figures 6–7

Diagnosis. Tricolporate, sub-triangular, colpi costate, pori indistinct, tectate, reticulate, heterobrochate, equatorial diameter 22 µm.

Description. Monad, radial, amb sub-triangular; tricolporate, colpi 10 µm long, 3 µm wide, borders straight, ends rounded, costate, costa 3 µm wide at equator and tapering towards the pole, pori indistinct; tectate, columellae distinct, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, muri 0.5 µm wide, curvilinear, simplicicolumellate, lumina in mesocolpium 1–1.5 µm wide, lumina decrease to 0.5 µm at pole and adjacent to colpi.

Dimensions. Equatorial diameter 22 µm; nm: 1; no: 2.

Comparisons. *Retitricolporites salardii* Boltenhagen 1976 is larger (34 µm) and lacks a conspicuous margo; *Retitricolporites ninghesikanus* Boltenhagen 1976 lacks a conspicuous margo.

Material. Ozuitem 3.1 (S38,2), polar view.

Tricolporites sp. 3

Plate 7, figures 8–9

Diagnosis. Tricolporate, subprolate, pori sub-circular–lalongate, tectate, reticulate, homobrochate, equatorial diameter 16 µm.

Description. Monad, radial, subprolate, tricolporate, colpi 6–11 µm long and narrow (1–2 µm wide), colpi simple, pori sub-circular–lalongate, 1–2 µm wide and 2–3 µm high; tectate, columellae distinct, exine 1–1.5 µm thick, nexine 0.5 µm thick, sexine 0.5–1 µm thick; surface ornamentation reticulate, homobrochate, muri 0.5 µm wide, lumina 0.5 µm wide, spaced densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 13–(16)–19.3 µm; nm: 10; no: 23.

Material. Ameke 1.1 (S52,4), equatorial view.

Tricolporites sp. 4

Plate 7, figures 10–12

Diagnosis. Tricolporate, subprolate–prolate spheroidal, colpi costate, tectate, micropitted–reticulate homobrochate, equatorial diameter 18 µm.

Description. Monad, radial, subprolate–prolate spheroidal, tricolporate, colpi 10–15 µm long and narrow (1–2 µm wide), colpi

costate, pori sub-circular, 1–2 µm wide and 2–3 µm high; tectate, columellae distinct, exine 1–2 µm thick, nexine 0.5 µm thick, sexine 0.5–1.5 µm thick; surface ornamentation micropitted–reticulate homobrochate, muri 0.5 µm wide, lumina 0.5–1 µm wide, spaced densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 14.8–(17.5)–20.4 µm; nm: 14; no: 60.

Material. Okigwe B2.1 (M60,1), equatorial view.

Tricolporites sp. 5

Plate 7, figures 13–14

Diagnosis. Tricolporate, circular, colpi costate, tectate, scabrate, equatorial diameter 25 µm.

Description. Monad, radial, amb circular; tricolporate, colpi 7 µm long, 3 µm wide, ends pointed, costate, costae 1 µm wide, pore indistinct; tectate, columellae distinct, nexine 0.5 µm thick, sexine 0.5 µm thick; surface ornamentation scabrate, sculptural elements spaced 0.5 µm apart, distributed densely over the surface of the pollen grain.

Dimensions. Equatorial diameter 25 µm; nm: 1; no: 15.

Comparisons. *Psilatricolporites lehmanii* Boltenhagen 1976 is atectate and psilate.

Material. Ozuitem 3.1 (U56,1), polar view.

Tricolporites sp. 6

Plate 7, figures 15–16

Diagnosis. Tricolporate, circular, colpi simple, pore indistinct, tectate, columellae distinct, echinate, equatorial diameter 25 µm.

Description. Monad, radial, amb circular; tricolporate, colpi simple, pore indistinct; exine tectate, columellae distinct, 2 µm thick; surface ornamentation echinate, echinae densely spaced 3–5 µm wide at base, 8–11 µm high.

Dimensions. Equatorial diameter 23–(24.5)–25.5 µm; nm 8; no: 30.

Comparisons. *Echitricolporites spinosus* (Van der Hammen) Germeraad et al. 1968 has distinctive columellae that increase in length beneath the echinae.

Material. Okigwe B4.1 (O54), polar view.

Tricolporites? sp.

Plate 7, figure 17

Diagnosis. Tricolporate, circular, colpi costate, tectate, columellae indistinct, echinate, equatorial diameter 22 µm.

Description. Monad, radial, amb circular; tricolporate, colpi 2 µm wide, 4 µm long, costate, costae 2 µm thick, 4 µm wide at equator decreasing to 2 µm wide at tip of colpi; exine tectate, columellae indistinct, 1 µm thick; surface ornamentation echinate, echinae spaced 1–2 µm, 0.5 µm wide at base, 1.5 µm high.

Dimensions. Equatorial diameter 22 µm; nm 1; no: 1.

Comparisons. The colpi of *Echitricolporites minutus* Regali et al. 1974 lack costae and the colpi are shorter. *Brevitricolpites macroexinatus* Jaramillo & Dilcher 2001 has larger spines and the costae are narrower. *Echitricolporites*

Van der Hammen 1956 ex. Germeraad et al. 1968 is an invalid genus (Jansonius and Hills 1976, card 901).

Material. Ozuitem 6.1 (V48), polar view.

Triporate pollen

Genus *Casuarinidites* Cookson & Pike 1954

Type. *Casuarinidites cainozoicus* Cookson & Pike 1954

Casuarinidites foveolatus sp. nov.

Plate 7, figures 18–20

Diagnosis. Triporate, oval, pori strongly aspidate, intectate, foveolate, equatorial diameter 30 µm.

Etymology. After the foveolate surface ornamentation.

Description. Monad, radial, amb oval; triporate, pori circular 2 µm in diameter and aspidate, aspis 4 µm wide and differentiated into an inner psilate band 2 µm wide and an outer foveolate band 2 µm wide, annulus 8 µm high; exine intectate, 1.5 µm thick; surface ornamentation foveolate, lumina 0.5 µm, spaced 1 µm apart, densely and evenly distributed.

Dimensions. Equatorial diameter 24.7–(30)–35 µm; nm: 3; no: 5.

Comparisons. *Corsinipollenites oculusnoctis* (Thiergart 1940) Nakoman 1965 lacks foveolae. Aspidate germinals are not mentioned in the diagnosis of *Corsinipollenites* Nakoman 1965 (Jansonius & Hills 1976, card 613). *Casuarinidites* Cookson & Pike 1954 accommodates aspidate grains with smooth or fine surface ornamentation (Jansonius and Hills 1976, card 412). *Casuarinidites cainozoicus* Cookson & Pike 1954 lacks foveolae.

Material. Holotype Ameke 11.1 (N52,1), Plate 7, figures 18–20, polar view.

Genus *Clavatriporites* gen. nov.

A new genus is required because these grains do not fit into established genera and are found in sediments from both tropical Africa and South America.

Description. Triporate pollen grains with clavate (occasionally baculate) surface ornamentation and very large pori that have irregular borders.

Genotype. *Clavatriporites dispersiclavatus* sp. nov.

Clavatriporites dispersiclavatus sp. nov.

Plate 7, figures 21–22

Synonymy. *Clavatriporites 'dispersiclavatus'* Jaramillo & Rueda 2023.

Diagnosis. Triporate, sub-circular, pori borders irregular, intectate, clavate with some baculae, equatorial diameter 28 µm.

Etymology. After the sparse clavate surface ornamentation.

Description. Monad, radial, amb sub-circular; triporate, pori wide (12 µm), borders of pori slightly irregular; exine intectate, 1 µm thick; surface ornamentation clavate with some baculate, clavae and baculae 1 µm high and distributed sparsely and evenly over pollen surface, clavae and baculae spaced 3 µm apart at equator, 1–2 µm apart at poles.

Dimensions. Equatorial diameter 25–(27.5)–30 µm; nm: 4; no: 4.

Comparisons. *Clavatricolpites densiclavatus* Jaramillo & Dilcher 2001 is tricolpate, *Crototricolpites finitus* Silva-Caminha et al. 2010 is tricolpate, with more densely distributed clavae (0.5–1 µm apart). *Bacutripurites orluensis* Jan du Chêne et al. 1978 has smaller annulate pori with larger baculae scattered unevenly over the surface of the pollen grain. *Clavatriporites spicatus* sp. nov. has coarser surface ornamentation. This genus and species conforms to the informal taxon *Clavatriporites 'dispersiclavatus'* (see Jaramillo and Rueda 2023) and is formalised here.

Material. Holotype, Okigwe A7.1 (O63,4), Plate 7, figure 21, polar view, paratype Okigwe B1.1 (K48,4), Plate 7, figure 22, polar view.

Clavatriporites spicatus sp. nov.

Plate 7, figures 23–25

Synonymy. *Clavatriporites 'spicatus'* Jaramillo & Rueda 2023.

Diagnosis. Triporate, sub-circular, pori faintly annulate, pori borders irregular, intectate, clavate, equatorial diameter 33 µm.

Etymology. From the latin *spica*, meaning head.

Description. Monad, radial, amb sub-circular; triporate, pori 10–12 µm wide, lolongate, borders of pore irregular, pori faintly annulate (4 µm wide), borders of annulus irregular; exine intectate, 1 µm thick; surface ornamentation clavate, clavae 1.5–2.5 µm high, 0.5–1.5 µm wide, sub-circular in shape, spaced 1–2 µm, densely and evenly distributed.

Dimensions. Equatorial diameter 31–(32.5)–33.5 µm; nm: 4; no: 9.

Comparisons. *Clavatricolpites prolatus* Pierce 1961 has colpi with smooth borders and is smaller (16–20 µm), *Clavatricolpites gracilis* González Guzmán 1967 has colpi with smooth borders. *Clavatriporites dispersiclavatus* sp. nov. has finer surface ornamentation. This genus and species conforms to the informal taxon *Clavatriporites 'spicatus'* (see Jaramillo and Rueda 2023) and is formalised here.

Material. Holotype Okigwe B6.1 (S47,4), Plate 7, figure 23, polar view, paratype Okigwe A5.1 (T45,2), Plate 7, figures 24–25, polar view.

Genus *Corsinipollenites* Nakoman 1965

Type. *Corsinipollenites oculusnoctis* (Thiergart 1940) Nakoman 1965

Corsinipollenites psilatus Jaramillo & Dilcher 2001

Plate 7, figure 26

Diagnosis. Triporate, sub-triangular convex, pori annulate, atectate, psilate, equatorial diameter 45 µm.

Description. Monad, radial, amb sub-triangular convex; triporate, pori 4 µm wide and annulate, annulus 2.5 µm wide; exine atectate, 1 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 45 µm; nm: 1; no: 3.

Material. Ozuitem 3.1 (S52), polar view.

Botanical affinity. Onagraceae (Morley 2000; Jaramillo et al. 2014).

Corsinipollenites undulatus (González Guzmán 1967) Jaramillo & Dilcher 2001

Plate 7, figure 27

Synonymy. *Jussitripurites undulatus* González Guzmán 1967.

Diagnosis. Triporate, triangular and rounded at apices, pori annulate and micropitted, atectate, exine psilate, equatorial diameter 40 µm.

Description. Monad, radial, amb triangular slightly rounded at the apices; triporate, pori lolongate (3.5 µm × 2 µm) and annulate, annulus 6 µm wide; exine atectate, 2 µm thick; surface ornamentation psilate, pori micropitted.

Dimensions. Equatorial diameter 40 µm; nm: 1; no: 7.

Material. Ameke 11.1 (Q45,4), polar view, specimen fragmented.

Botanical affinity. Onagraceae (Morley 2000; Jaramillo et al. 2014).

Corsinipollenites cf. *psilatus* Jaramillo & Dilcher 2001

Plate 7, figure 28

Diagnosis. Triporate, sub-triangular convex, pori annulate, atectate, psilate, equatorial diameter 20 µm.

Description. Monad, radial, amb sub-triangular convex; triporate, pori oval (3 µm × 1.5 µm) and annulate, annulus 1.5 µm wide and 3 µm high; exine atectate, 1 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 20 µm; nm: 1; no: 8.

Comparisons. *Corsinipollenites psilatus* Jaramillo & Dilcher 2001 is larger (28–40 µm).

Material. Ameke 1.1 (O61,1), oblique view.

Botanical affinity. Onagraceae (Morley 2000; Jaramillo et al. 2014).

Corsinipollenites 'striatus'

Plate 7, figures 29–30

Diagnosis. Triporate, sub-triangular, pori annulate, intectate, striate, equatorial diameter 34 µm.

Description. Monad, radial, amb sub-triangular convex; triporate, pori 2 µm wide, annulate, annulus 4.5 µm wide, 4 µm thick; intectate, exine 1.5 µm thick; surface ornamentation striate, muri 0.5 µm wide, striae 0.5 µm wide, striae arranged irregularly over the surface of the pollen grain.

Dimensions. Equatorial diameter 34 µm, nm: 1; no: 1.

Comparisons. No other species of *Corsinipollenites* are striate. *Striatitripurites nigeriensis* van Hoeken-Klinkenberg 1966 lacks ornamentation around the pori, which are themselves markedly less protuberant, and the costa pori are thinner (1 µm thick).

Material. Ozuitem 3.1 (X58,2), polar view.

Botanical affinity. Onagraceae (Morley 2000; Jaramillo et al. 2014).

Genus *Cricotripurites* Leideimayer 1966

Type. *Cricotripurites guianensis* Leideimayer 1966

Cricotripurites fragilis van Hoeken-Klinkenberg 1966

Plate 7, figure 31

Diagnosis. Triporate, sub-circular, pori costate and annulate, tectate, exine 1 µm thick, scabrate, equatorial diameter 23 µm.

Description. Monad, radial, amb sub-circular; triporate, pori rounded, 3 µm in diameter, costate, costa 1–1.5 µm wide, annulate, annulus 1 µm wide; exine tectate, 1 µm thick, sexine thickened by 0.5 µm around the pore forming a slight annulus; surface ornamentation scabrate, scabrae distributed evenly.

Dimensions. Equatorial diameter 23 µm; nm 1; no: 4.

Material. Amaogugu 1.1 (J51), polar view.

Cricotriporites macroporus Jaramillo & Dilcher 2001

Plate 7, figure 32

Diagnosis. Triporate, sub-circular, pori annulate and lolongate, intectate, exine 0.5 µm thick, scabrate, equatorial diameter 33 µm.

Description. Monad, radial, amb sub-circular; triporate, pori lolongate (10 µm long, 6 µm wide), annulate, annulus 3 µm wide, 1 µm thick; exine intectate, 0.5 µm thick; surface ornamentation scabrate, scabrae distributed densely and evenly distributed.

Dimensions. Equatorial diameter 33 µm; nm 1; no: 1.

Comparisons. *Cricotriporites elongatoporus* Jaramillo & Dilcher 2001 has lolongate pori.

Material. Amaogugu 1.1 (V35,2), polar view.

Cricotriporites cf. *macroporus* Jaramillo & Dilcher 2001

Plate 7, figures 33–34

Diagnosis. Triporate, sub-circular, pori annulate, intectate, exine 1 µm thick, scabrate–faintly rugulate, equatorial diameter 34 µm.

Description. Monad, radial, amb circular; triporate, pori rounded, 5 µm in diameter, annulate, annulus 1 µm wide; exine intectate, 1 µm thick, thickened slightly around pori to form a slight annulus; surface ornamentation faintly scabrate–faintly rugulate, granulae spaced 1 µm apart, evenly distributed.

Dimensions. Equatorial diameter 34 µm; nm 1; no: 2.

Comparisons. *Cricotriporites macroporus* Jaramillo & Dilcher 2001 lacks rugulae and has a thinner exine (0.5 µm thick).

Material. Okigwe B4.1 (K58), polar view.

Cricotriporites aff. *minutiporus* (Muller 1968) Jaramillo & Dilcher 2001

Plate 7, figure 35

Diagnosis. Triporate, sub-circular, pori costate, intectate, exine 0.5 µm thick, scabrate, equatorial diameter 27 µm.

Description. Monad, radial, amb sub-circular; triporate, pori circular, 3 µm in diameter, and costate, costae 1 µm in width; exine intectate, 0.5 µm thick, 1 µm thick around pori; surface ornamentation scabrate–verrucate, sculptural elements 1 µm wide, spaced 0.5–2 µm apart, and distributed evenly.

Dimensions. Equatorial diameter 27 µm; nm 1; no: 1.

Comparisons. *Cricotriporites minutiporus* (Muller 1968) Jaramillo & Dilcher 2001 has finer scabrae and a slight

thickening at the apoporia. *Cricotriporites guianensis* Leidekmeyer 1966 (*Cricotriporites operculatus* of van Hoeken-Klinkenberg 1966) has a thicker exine (1–2 µm).

Material. Amaogugu 1.1 (F34,4), polar view.

Genus *Echitriporites* Van der Hammen ex van Hoeken-Klinkenberg 1964

Type. *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964

Echitriporites suescae (Van der Hammen 1954) Cárdenas, de La Parra & Espinoza-Campuzano 2019

Plate 7, figures 36–38

Synonymy. *Triporites suescae* Van der Hammen 1954.

Proteacidites sigali Boltenhagen 1978.

Diagnosis. Triporate, triangular obtuse-straight, pori annulate, intectate, echinate, equatorial diameter 26 µm.

Description. Monad, radial, amb triangular obtuse-straight; triporate, pori 2 µm wide, annulate, annulus 1 µm thick, 2 µm wide, slightly protruding; exine intectate, 0.5–1 µm thick; surface ornamentation echinate, echinae spaced 1–2 µm apart, 0.5 µm wide at base, 0.5–1 µm high.

Dimensions. Equatorial diameter 22.5–(25.5)–28 µm; nm: 4; no: 37.

Comparisons. *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964 is triangular to triangular obtuse-convex and has larger spines (>1 µm).

Material. Okigwe B2.1 (T32; M38,3), polar view.

Botanical affinity. Proteaceae by comparison to *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964.

Echitriporites trianguliformis van Hoeken-Klinkenberg 1964

Plate 7, figures 39–40

Diagnosis. Triporate, triangular to triangular obtuse-convex, pori annulate, intectate, echinate, equatorial diameter 26 µm.

Description. Monad, radial, amb triangular to triangular obtuse-convex; triporate, pori 2 µm wide, annulate, annulus 1 µm thick, 2 µm wide, slightly protruding; exine intectate, 0.5–1 µm thick; surface ornamentation echinate, echinae spaced 1–2 µm apart, 0.5–1 µm wide at base, 1–2 µm high.

Dimensions. Equatorial diameter 24–(26)–28 µm; nm: 4; no: 49.

Comparisons. *Echitriporites suescae* (Van der Hammen 1954) Cárdenas, de La Parra & Espinoza-Campuzano 2019 is triangular obtuse-straight and has shorter spines (<1 µm).

Material. Okigwe B2.1 (N50; T41), polar view.

Botanical affinity. Proteaceae (by 'superficial resemblance [to] some Proteaceae (*Embothrium*, *Garnieria*, *Persoonia*, *Telopea*)' Germeraad et al. 1968, p. 312).

Echitriporites trianguliformis var. *orbicularis* Jaramillo & Dilcher 2001

Plate 7, figures 41–42

Synonymy. *Echitriporites trianguliformis* Forma A Muller et al. 1987.

Diagnosis. Triporate, circular, pori annulate, intectate, echinate, equatorial diameter 28 µm.

Description. Monad, radial, amb circular to sub-circular; triporate, pori 2 µm wide, annulate, annulus 1–1.5 µm thick, 1 µm wide, slightly protruding; exine intectate, 0.5–1 µm thick; surface ornamentation echinate, echinae spaced 0.5–1 µm apart, 0.5 µm wide at base, 0.5–2.5 µm high.

Dimensions. Equatorial diameter 23.5–(27.5)–31 µm; nm: 4; no: 46.

Comparisons. *Echitriporites trianguliformis* van Hoeken Klinkenberg 1964 is triangular to triangular obtuse-convex.

Material. Okigwe B2.1 (P48,3; Q33,2), polar view.

Botanical affinity. Proteaceae by comparison to *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964.

Genus *Momipites* Wodehouse 1933 emend. Frederiksen & Christopher 1978

Type. *Momipites coryloides* Wodehouse 1933

Momipites cf. *africanus* van Hoeken-Klinkenberg 1966

Plate 7, figure 43

Diagnosis. Triporate, sub-circular, pori annulate and vestibulate, tectate, psilate, equatorial diameter 25 µm.

Description. Monad, radial, amb sub-circular; triporate, pore 2 µm wide, annulate, annulus 2 µm wide, vestibulate; tectate, columellae indistinct, exine 1.5 µm thick; surface ornamentation psilate, scabrate around pori.

Dimensions. Equatorial diameter 25 µm; nm: 1; no: 9.

Comparisons. *Momipites africanus* van Hoeken-Klinkenberg 1966 is sub-triangular, and each pore has an atrium. *Momipites* sp. 1 Jaramillo & Dilcher 2001 is larger and intectate, and *Momipites macroexinatus* Jaramillo et al. 2007 has a thicker, intectate exine.

Material. Ozuitem 3.1 (V51,2), polar view.

Botanical affinity. Betulaceae (Jaramillo et al. 2014).

Genus *Proteacidites* Cookson 1950 ex Couper 1953

Type. *Proteacidites adenanthoides* Cookson 1950 ex Couper 1953

Proteacidites cooksonii Salard-Chebaldoeff 1978

Plate 8, figure 1

Diagnosis. Triporate, triangular, pori large, tectate, micropitted, equatorial diameter 25 µm.

Description. Monad, radial, amb triangular; triporate, pori large, 7 µm wide; tectate, columellae indistinct; surface ornamentation micropitted, lumina <0.5 µm in size, spaced <0.5 µm apart, densely and evenly distributed across the pollen grain surface.

Dimensions. Equatorial diameter 25 µm; nm: 1; no: 1.

Material. Okigwe B4.1 (X60), polar view, specimen folded.

Botanical affinity. Proteaceae (Salard-Chebaldoeff 1978).

Genus *Retitriporites* Ramanujam 1966

Type. *Retitriporites curvimurati* Ramanujam 1966

Retitriporites aff. *simplex* Van der Kaars 1983

Plate 8, figures 2–3

Diagnosis. Triporate, sub-triangular, pori indistinct, tectate, collumellae indistinct, reticulate, heterobrochate, equatorial diameter 19 µm.

Description. Monad, radial, amb sub-triangular; triporate, pori indistinct, possibly due to poor preservation; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation reticulate, heterobrochate, muri 0.5 µm wide, lumina 0.5–1 µm wide and polygonal.

Dimensions. Equatorial diameter 19 µm; nm: 1; no: 1.

Comparisons. *Retitriporites simplex* Van der Kaars 1983 is intectate and has a more rounded outline.

Material. Ameke 11.1 (V67,1), polar view.

Retitriporites irregularis sp. nov.

Plate 8, figures 4–7

Diagnosis. Triporate, triangular and slightly rounded, tectate, reticulate, heterobrochate, equatorial diameter 26 µm.

Etymology. After the irregular distribution of the lumina on the surface of the pollen grain.

Description. Monad, radial, amb triangular and slightly rounded; triporate, pori 4 µm wide, borders distinct, pori costate, costae 1 µm thick; tectate, columellae distinct, nexine <0.5 µm thick, columellae 0.5 µm thick, tectum very thin (<0.5 µm thick); surface ornamentation reticulate, heterobrochate, simplicolumellate, muri 0.5 µm wide, slightly curvimate, lumina 0.5–3 µm wide and polygonal, lumina of different sizes occur randomly over the surface of the pollen grain.

Dimensions. Equatorial diameter 25–(25.5)–26 µm; nm: 2; no: 3.

Comparisons. *Retitriporites simplex* Van der Kaars 1983 is smaller, has a homobrochate reticulum, and has an obtuse-convex amb. *Retitriporites 'heterobrochatus'* Jaramillo et al. 2014 has a thicker exine (3.5 µm).

Material. Holotype Ozuitem 6.1 (H40,4), Plate 8, figures 4–6, polar view; paratype Ozuitem 3.1 (M43), Plate 8, figure 7, polar view, specimen slightly broken.

Retitriporites 'robustus'

Plate 8, figures 8–9

Diagnosis. Triporate, sub-circular, pori costate, tectate, reticulate–rugulate, heterobrochate, equatorial diameter 21 µm.

Description. Monad, radial, amb sub-circular; triporate, pori 3 µm wide, costate, costae 2 µm wide, 1 µm thick; tectate, nexine 0.5 µm thick, columellae 1 µm thick, tectum 0.5 µm thick; surface ornamentation reticulate–rugulate, heterobrochate, curvimate, muri 0.5 µm wide, lumina 0.5–1 µm wide, rugulae 0.5 µm wide, 1–2 µm long.

Dimensions. Equatorial diameter 19–(20.5)–22.1 µm, nm: 2; no: 2.

Comparisons. *Retitriporites rotundus* Silva-Caminha et al. 2010 has marginate pori; *Retitriporites federicii* González Guzmán 1967 has annulate pori; *Retitriporites variabilis* Muller 1968 has simple pori.

Material. Ameke 1.1 (M65,1), polar view.

Genus *Rugulitriporites* Muller 1968

Type. *Rugulitriporites vestibulipori* Muller 1968

Rugulitriporites 'umbrabilis'

Plate 8, figures 10–11

Diagnosis. Triporate, sub-triangular, pori annulate, tectate, rugulate, equatorial diameter 29 µm.

Description. Monad, radial, amb sub-triangular; triporate, pori 9 µm wide, annulate, annulus 1.5 µm wide formed by a reduction in the surface ornamentation, pori situated sub-equatorially; tectate, columellae distinct, 1 µm wide spaced irregularly 1–3 µm apart, nexine 1 µm thick, sexine 1 µm thick; surface ornamentation rugulate, rugulae 0.5 µm wide, 2–8 µm long, occasional irregularly distributed granulae.

Dimensions. Equatorial diameter 29 µm; nm: 1; no: 1.

Comparisons. *Cricotriporites* Leidlmeyer 1966 has a circular circumference. *Striatiporites* van Hoeken-Klinkenberg 1966 lacks rugulae. *Rugulitriporites vestibulipori* Muller 1968 is reticulate.

Material. Ozuitem 6.1 (V48,1), polar view.

Genus *Tripototetradites* van Hoeken-Klinkenberg 1964

Type. *Tripototetradites* cf. *scabratus* van Hoeken-Klinkenberg 1964

Tripototetradites cf. *scabratus* van Hoeken-Klinkenberg 1964

Plate 8, figure 12

Diagnosis. Decussate tetrad, monad amb sub-circular, triporate, pori annulate, intectate, scabrate, tetrad equatorial diameter 32 µm, monad equatorial diameter 18 µm.

Description. Decussate tetrad, monad amb sub-circular; triporate, pori 1 µm wide, annulate, annulus 1 µm wide; intectate, exine 0.5 µm thick; surface ornamentation scabrate, sculptural elements spaced 1–2 µm apart.

Dimensions. Tetrad 26–(31.5)–37 µm in diameter, equatorial diameter of monads 13–(18)–23 µm; nm: 3; no: 14

Comparisons. *Tripototetradites scabratus* van Hoeken-Klinkenberg 1964 is larger (tetrad 40 µm × 50 µm, monads 32 µm × 22 µm).

Material. Amaogugu 7.1 (V53,3), oblique view.

Heterocolpate pollen

Genus *Heterocolpites* Van der Hammen 1956

Type. *Heterocolpites incomptus* Van der Hammen 1956

Heterocolpites cf. *laevigatus* Salard-Chebouldaëff 1978

Plate 8, figure 13

Diagnosis. Heterocolpate, circular, atectate, psilate, equatorial diameter 11 µm.

Description. Monad, radial, amb circular; heterocolpate with three colpi and three pseudocolpi, colpi 3 µm wide, borders straight and slightly diffuse, covered by a thin (<0.5 µm) colpus membrane at the equator, pseudocolpi 1.5 µm wide, borders straight and slightly diffuse; atectate, exine 0.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 11 µm; nm: 1; no: 1.

Comparisons. *Heterocolpites laevigatus* Salard-Chebouldaëff 1978 is tectate (nexine 0.5 µm thick and sexine 0.5 µm thick) and slightly larger (14–22 µm).

Material. Ozuitem 6.1 (P55,1), oblique view.

Botanical affinity. Combretaceae (Salard-Chebouldaëff (1978), Morley (2000) and by comparison to *Terminalia*), Melastomataceae (Morley 2000).

Syncolporate pollen

Genus *Syncolporites* Van der Hammen 1954

Type. *Syncolporites lisamae* Van der Hammen 1954

Syncolporites sowunmiai Jan du Chêne et al. 1978

Plate 8, figure 14

Diagnosis. Syncolporate, triangular, colpi marginate, pori costate, intectate, scabrate, equatorial diameter 36 µm.

Description. Monad, radial, amb triangular and slightly convex; syncolporate (three colpi), colpi 20 µm long, 2 µm wide, colpi marginate, margo 2.5 µm wide, thickened by 1 µm, pori costate, costae 1.5 µm thick; intectate, exine 0.5 µm thick, exine thickened to 1 µm in mesocolpium; surface ornamentation scabrate.

Dimensions. Equatorial diameter 36 µm; nm: 1; no: 3.

Material. Ozuitem 6.1 (V45), polar view.

Syncolporites marginatus van Hoeken Klinkenberg 1964

Plate 8, figures 15–18

Diagnosis. Syncolporate, sub-circular, pori costate, tectate, reticulate, homobrochate, equatorial diameter 29 µm.

Description. Monad, radial, amb sub-circular; syncolporate, colpi narrow (0.5 µm wide), borders straight, colpi marginate, margins 1.5 µm wide, formed by thickening of the sexine and a slight coarsening of the reticulum, endoapertures indistinct and costate, costae 1.5 µm thick and 1.5 µm wide; tectate, columellae distinct, exine 1 µm thick, nexine <0.5 µm, sexine 0.5–0.7 µm; surface ornamentation reticulate, homobrochate, lumina rounded and 0.5 µm wide, spaced densely and evenly over the surface of the pollen grain, lumina on margins 0.5–0.7 µm wide, muri 0.5 µm.

Dimensions. Equatorial diameter 24–(28.5)–32.5, nm: 14; no: 43.

Comparisons. The size range of *Syncolporites marginatus* van Hoeken-Klinkenberg 1964 was originally given as 27–30 µm but the specimens examined here cover a larger size range.

Material. Ozuitem 3.1 (J37,4), oblique view; Ozuitem 6.1 (T40), oblique view.

Syncolporites angusticolpatus sp. nov.

Plate 8, figures 19–20

Diagnosis. Parasyncolporate, sub-circular, pori annulate, tectate, columellae indistinct, exine 1 µm thick, micropitted, equatorial diameter 27 µm.

Etymology. After the narrow colpi.

Description. Monad, radial, amb sub-circular; parasyncolporate, pori rounded, 4 µm wide, annulate, annulus 1 µm wide,

1 µm thick and slightly protuberant, large apocolpial field demarcated by prominent slightly curved colpi 15 µm long and 0.5 µm wide, each colpus is separate and there is no division of a single colpus into two branches; exine tectate, 1 µm thick, thickened very slightly around the pori, columellae indistinct; surface ornamentation micropitted.

Dimensions. Equatorial diameter 26–(26.5)–27.1 µm, nm: 2; no: 4.

Comparisons. This grain has been interpreted as parasyncolporate, but the colpi do not divide into two branches and anastomose towards the poles as in *Eugenia uniflora* (Myrtaceae). An alternative interpretation is that these structures represent pseudocolpi, in which case the grain would be triporate, and the apopodium would be characterized by pseudocolpi. We prefer a parasyncolporate interpretation because the colpi extend to the annulus of the pore. *Syncolporites boltenhageni* Jan du Chêne et al. 1978 is psilate.

Material. Holotype Okigwe A7.1 (O66,1), Plate 8, figure 19, polar view; paratype Ozuitem 3.1 (P62,3), Plate 8, figure 20, polar view.

Syncolporites rostro sp. nov.

Plate 8, figures 21–23

Diagnosis. Syncolporate, amb triangular, colpi marginate, pori costate, tectate, reticulate, homobrochate, equatorial diameter 28 µm.

Etymology. After the beak-like appearance of each aperture.

Description. Monad, radial, amb triangular; syncolporate, colpi narrow (1 µm wide), marginate, margo 1 µm wide and psilate, margo formed by a reduction of the reticulum and a slight thinning of the exine, lacking apocolpial field, pori indistinct, pori costate, costae 1.5 µm thick and 1.5 µm wide; tectate, columellae distinct, exine 1 µm thick; surface ornamentation reticulate, homobrochate, lumina rounded and 0.5 µm wide, spaced densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 28 µm, nm: 1; no: 1.

Comparisons. *Cupanieidites acuminatus* Boltenhaegen 1967 is syncolporate.

Material. Holotype Ozuitem 3.1 (X36,1), Plate 8, figures 21–23, polar view.

Syncolporites sp.

Plate 8, figures 24–25

Diagnosis. Parasyncolporate, sub-circular, colpi marginate, tectate, striate, equatorial diameter 34 µm.

Description. Monad, radial, amb sub-circular; parasyncolporate, colpi 14 µm long, 1 µm wide, marginate, margo variable in width (0.5–1.5 µm), apocolpium distinguished by a triangle with sides 3.5 µm long, pori 6 µm wide, pore borders irregular; tectate, columellae distinct, exine 1 µm thick; surface ornamentation striate, muri 1 µm wide and spaced <0.5 µm apart, striae anastomosing.

Dimensions. Equatorial diameter 34 µm; nm: 1; no: 6.

Comparisons. *Syncolporites subtilis* Boltenhagen 1976 is triangular in polar view. *Striasyncolpites zwaardii* Germeraad et al. 1968 is triangular in polar view and has protruding pori.

Material. Amaogugu 1.1 (L39,2), polar view.

Stephanocolpate pollen

Genus *Ctenolophonidites* van Hoeken-Klinkenberg 1966

Type. *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966

Ctenolophonidites costatus (van Hoeken-Klinkenberg 1964)
van Hoeken-Klinkenberg 1966

Plate 8, figure 26

Synonymy. *Stephanocolpites costatus* van Hoeken Klinkenberg 1964.

Diagnosis. Stephanocolpate, circular, tectate, columellae indistinct, rugulate, rugulae pronounced in mesocolpium, equatorial diameter 41 µm.

Description. Monad, radial, amb circular; stephanocolpate (six colpi), colpi 2 µm wide; tectate, columellae indistinct, exine 0.5 µm thick, thickened in the mesocolpium to form rugulae; surface ornamentation rugulate, rugulae 3 µm wide.

Dimensions. Equatorial diameter 41 µm; nm 1; no: 4.

Material. Okigwe A1.1 (N56), polar view.

Botanical affinity. Ctenolophonaceae (by comparison to *Ctenolophon engleri* (Morley 2000)).

Ctenolophonidites aff. *costatus* (van Hoeken-Klinkenberg 1964)
van Hoeken-Klinkenberg 1966

Plate 8, figure 27

Diagnosis. Stephanocolpate, circular, tectate, columellae indistinct, rugulate, rugulae pronounced in mesocolpium, equatorial diameter 25 µm.

Description. Monad, radial, amb circular; stephanocolpate, colpi 1.5 µm wide, exine thickened in the mesocolpium to form rugulae; tectate, columellae indistinct, exine 0.5 µm thick; surface ornamentation rugulate, rugulae 2.5 µm wide, rugulae anastomose in apocolpial region.

Dimensions. Equatorial diameter 25 µm; nm 1; no: 3.

Comparisons. *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966 is larger (35–70 µm).

Material. Ameke 1.1 (V57,3), polar view.

Botanical affinity. Ctenolophonaceae (by comparison to *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966).

Ctenolophonidites? 'apocolpius'

Plate 8, figure 28

Diagnosis. Tricolpate, angular, three pseudocolpi, colpi and pseudocolpi costate, apocolpium distinct and circular, tectate, reticulate, heterobrochate, equatorial diameter 29 µm.

Description. Monad, radial, amb angular; tricolpate, colpi 7 µm long, 12 µm wide, colpi costate, colpi costae 2 µm wide, three pseudocolpi, pseudocolpi 7 µm long, 12 µm wide, pseudocolpi costae 2 µm wide, pseudocolpi infilled with a quantity of thin exine, equator protrudes 2 µm beyond this quantity of thin exine, apocolpium defined by a circular region of thin exine 4 µm in diameter; tectate, columellae distinct, exine 0.5 µm thick, and 1.5 µm thick in thickened

areas; surface ornamentation reticulate, heterobrochate, muri 0.5 µm thick, lumina 0.5–1 µm wide.

Dimensions. Equatorial diameter 29 µm; nm 1; no: 3.

Comparisons. No other species of *Ctenolophonidites* van Hoeken-Klinkenberg 1966 have pseudocolpi. *Margocolporites raувolfii* Salard-Chebaldaff 1978 is tricolporate, with a slightly coarser heterobrochate reticulum (lumina up to 3 µm).

Material. Okigwe A7.1 (R46,2), polar view.

Ctenolophonidites? 'echicolpatus'

Plate 8, figure 29

Diagnosis. Stephanocolpate with three colpi and three pseudocolpi, colpi and pseudocolpi marginate, sub-circular, tectate, scabrate and echinate, equatorial diameter 37 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate, three colpi, three pseudocolpi, colpi 13 µm wide, pseudocolpi 5 µm wide, colpi and pseudocolpi marginate (1 µm wide), borders of margo irregular, edges of colpi lined with echinae 1 µm high; exine intectate, 0.5 µm thick; surface ornamentation scabrate and echinate.

Dimensions. Equatorial diameter 37 µm; nm 1; no: 1.

Comparisons. No other species of *Ctenolophonidites* van Hoeken-Klinkenberg 1966 have pseudocolpi.

Material. Okigwe B7.1 (J50,4), polar view.

Genus *Echistephanocolpites* Wijmstra 1971

Type. *Echistephanocolpites echinatus* Wijmstra 1971

Echistephanocolpites echinatus Wijmstra 1971

Plate 8, figure 30

Diagnosis. Stephanocolpate, colpi simple, tectate, echinate, equatorial diameter 53.5 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (five colpi), colpi simple, 15 µm long; exine tectate, collumellae distinct, exine 2.5 µm thick, nexine 1 µm thick, sexine 1.5 µm thick; nexine characterised by a loose infrareticulum, muri 1 µm wide, lumina 1.5–2.5 µm wide and polygonal, sometimes disconnected; surface ornamentation echinate, echinae 1–2 µm high, 1 µm wide at base.

Dimensions. Equatorial diameter 53.5 µm; nm 1; no: 1.

Material. Okigwe B7.1 (D37,1), polar view.

Genus *Foveostephanocolpites* Leidelmeyer 1966

Type. *Foveostephanocolpites typicus* Leidelmeyer 1966

Foveostephanocolpites sp. 1

Plate 8, figure 31

Diagnosis. Stephanocolpate (four colpi), sub-circular, tectate, foveoreticulate, lumina 1 µm in apocolpial region, 0.5 µm in mesocolpial region, equatorial diameter 44 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (four colpi), colpi 4 µm wide, 14 µm long; exine tectate,

nexine 1 µm thick, columellae 0.5 µm thick, 1 µm wide and spaced 0.5 µm apart, tectum 0.5 µm thick; surface ornamentation foveoreticulate, heterobrochate, lumina irregularly shaped, lumina 1 µm in apocolpial region, 0.5 µm in mesocolpial region.

Dimensions. Equatorial diameter 44 µm; nm 1; no: 1.

Comparisons. *Foveostephanocolpites typicus* Leidelmeyer 1966 has seven costate colpi and is 25 µm in size. *Foveostephanocolpites perfectus* Leidelmeyer 1966 has six marginate colpi and is 29 µm in size.

Material. Ameke 1.1 (K55,2), polar view.

Foveostephanocolpites sp. 2

Plate 8, figure 32

Diagnosis. Stephanocolpate (five colpi), circular, tectate, foveolate, lumina 0.5 µm, equatorial diameter 30 µm.

Description. Monad, radial, amb circular; stephanocolpate (five colpi), colpi 4 µm wide, 10 µm long; exine tectate, columellae distinct, 0.5 µm wide, spaced 1 µm apart, nexine 1.5 µm, sexine 0.5 µm; surface ornamentation foveolate, lumina 0.5 µm wide, spaced 1–2 µm apart.

Dimensions. Equatorial diameter 30 µm; nm 1; no: 1.

Comparisons. *Foveostephanocolpites typicus* Leidelmeyer 1966 has seven costate colpi and is 25 µm in size. *Foveostephanocolpites perfectus* Leidelmeyer 1966 has marginate colpi.

Material. Ozuitem 3.1 (Q62), polar view.

Genus *Psilastephanocolpites* Leidelmeyer 1966

Type. *Psilastephanocolpites maia* Leidelmeyer 1966

Psilastephanocolpites sp.

Plate 8, figure 33

Diagnosis. Stephanocolpate, sub-circular, colpi marginate, tectate, psilate, equatorial diameter 38 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (five colpi), colpi 10 µm long, borders straight, ends slightly curved, marginate, margo 1–1.5 µm wide; tectate, nexine 0.5 µm thick, columellae 0.5 µm thick, 0.5 µm wide and spaced 1 µm apart, tectum 0.5–1 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 38 µm; nm: 1; no: 3.

Comparisons. *Psilastephanocolpites maia* Leidelmeyer 1966 has four colpi and is smaller (25 µm); *Psilastephanocolpites marginatus* González Guzmán 1967 is smaller (22 µm). *Retistephanocolpites williamsi* Germeraad et al. 1968 is foveoreticulate.

Material. Okigwe B6.1 (O39,1), polar view.

Genus *Retistephanocolpites* Leidelmeyer 1966 emend. Saxena 1982

Type. *Retistephanocolpites angoli* Leidelmeyer 1966

Retistephanocolpites regularis van Hoeken-Klinkenberg 1966

Plate 8, figure 34

Diagnosis. Stephanocolpate, sub-circular, tectate, reticulate, homobrochate, equatorial diameter 29 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (five or six colpi), colpi 8 µm long 3 µm wide, colpi simple, borders straight, ends pointed; tectate, exine 1 µm thick, nexine 0.5 µm, sexine 0.5 µm; surface ornamentation reticulate, homobrochate, lumina 1 µm in diameter and rounded, muri 1 µm wide.

Dimensions. Equatorial diameter 25–(28.5)–32.5 µm; nm: 3; no. 7.

Comparisons. The entire description of *Retistephanocolpites regularis* van Hoeken-Klinkenberg 1966 reads 'Reticulate tectate stephanocolpate pollengrains' (van Hoeken-Klinkenberg 1966, p. 42) and the figured specimen has five colpi and measures 24.5 µm in equatorial diameter.

Material. Okigwe B7.1 (F46,2), polar view.

Botanical affinity. Ctenolophonaceae (Morley 2000), Malvaceae (Jaramillo and Rueda 2023).

Retistephanocolpites williamsi Germeraad et al. 1968

Plate 8, figure 35

Diagnosis. Stephanocolpate, polygonal, tectate, reticulate, heterobrochate, equatorial diameter 37 µm.

Description. Monad, radial, amb polygonal; stephanocolpate (six colpi), colpi 12 µm long and 2 µm wide, ends pointed; tectate, columellae distinct, spaced 2 µm apart, exine 1 µm thick, nexine 0.5 µm, sexine 0.5 µm; surface ornamentation reticulate, lumina 0.5–1 µm in diameter, spaced densely and evenly over the surface of the grain, muri 0.5 µm wide.

Dimensions. Equatorial diameter 35–(36.5)–38 µm; nm: 2; no: 7.

Comparisons. *Jandufouria seamrogiformis* Germeraad et al. 1968 is larger (40–57 µm) and micropitted.

Material. Ozuitem 3.1 (S42,4), polar view.

Botanical affinity. Ctenolophonaceae (by comparison to *Ctenolophon parvifolius* (Germeraad et al. 1968; Morley 2000)).

Genus *Scabrastephanocolpites* Van der Hammen & Garcia 1966

Type. *Scabrastephanocolpites scabratus* Van der Hammen & Garcia 1966

Scabrastephanocolpites vanegensis Van der Hammen & Garcia 1966

Plate 8, figure 36

Diagnosis. Stephanocolpate, sub-circular, colpi marginate, tectate, columellae indistinct, scabrate, equatorial diameter 33 µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (four colpi), colpi long (16 µm), 9 µm wide, borders well defined, ends rounded, marginate, margo 0.5 µm wide, margo produced by slight thickening of the sexine; tectate, columellae indistinct; surface ornamentation scabrate, sculptural elements spaced 0.5–2 µm over the pollen surface.

Dimensions. Equatorial diameter 31–(33)–35 µm; nm: 7; no: 13.

Comparisons. *Tetracolpites reticulatus* Vimal ex Srivastava 1966 has reticulate surface ornamentation and lacks marginate colpi.

Material. Okigwe B1.1 (O33,1), polar view.

Scabrastephanocolpites 'irregularis'

Plate 8, figure 37

Diagnosis. Stephanocolpate (four colpi), circular, colpi margins irregular, tectate, columellae indistinct, scabrate, equatorial diameter 27 µm.

Description. Monad, radial, amb circular; stephanocolpate (four colpi), colpi 7 µm long, 6 µm wide, margins irregular, ends pointed; tectate, columellae indistinct, exine 0.5 µm thick; surface ornamentation scabrate, sculptural elements distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 27 µm; nm: 1; no: 3.

Comparisons. *Scabrastephanocolpites scabratus* Van der Hammen & Garcia 1966 has five colpi and is larger (37 µm); *S. guadensis* Van der Hammen 1954 has a thicker exine (2 µm) and shorter colpi; *S. vanegensis* Van der Hammen & Garcia 1966 has marginate colpi, and *S. sp. 1* Jaramillo & Dilcher 2001 has shorter marginate colpi.

Material. Okigwe A5.1 (U50,1), polar view.

Stephanocolporate pollen

Genus *Tetracolporites* Couper 1953 emend. Pocknall & Mildenhall 1984

Type. *Tetracolporites oamaruensis* Couper 1953

Tetracolporites cf. spectabilis Pocknall & Mildenhall 1984

Plate 8, figure 38

Diagnosis. Stephanocolporate, circular, colpi short and costate, tectate, psilate, equatorial diameter 27 µm.

Description. Monad, radial, amb circular; stephanocolporate (five colpi), colpi 5 µm long, 2.5 µm wide, borders straight, ends rounded, costate, costae 1.5 µm wide, pore lalongate indistinct; tectate, nexine 0.5 µm thick, columellae 0.5 µm thick but indistinct, tectum 0.5 µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 27 µm; nm: 1; no: 3.

Comparisons. *Tetracolporites spectabilis* Pocknall & Mildenhall 1984 has simple colpi; *Tetracolporites pachyexinatus* Jaramillo & Dilcher 2001 has a thicker exine (4–5 µm).

Material. Ozuitem 3.1 (M35), polar view.

Stephanoporate pollen

Genus *Echistephanoporites* Leidelmeyer 1966

Type. *Echistephanoporites alfonsi* Leidelmeyer 1966

Echistephanoporites alfonsi Leidelmeyer 1966

Plate 8, figure 39

Diagnosis. Stephanoporate, pori annulate, tectate, columellae indistinct, echinate, equatorial diameter 27.5 µm.

Description. Monad, radial, amb sub-circular; stephanoporate, pori annulate, annulus 2.5 µm wide; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation echinate, echinae spaced 1–2 µm and 1 µm apart.

Dimensions. Equatorial diameter 27.5 µm; nm 1; no: 2.

Material. Okigwe B7.1 (N40,1), polar view.

Genus *Pachydermites* Germeraad et al. 1968

Type. *Pachydermites diderixii* Germeraad et al. 1968

Pachydermites diderixii Germeraad et al. 1968

Plate 8, figure 40

Diagnosis. Stephanoporate, sub-circular, pore margins irregular, tectate, psilate, equatorial diameter 43 µm.

Description. Monad, radial, amb sub-circular; stephanoporate (six pori), pori sub-circular, margins irregular, 4 µm wide; tectate, exine 4.5 µm thick; surface ornamentation psilate, micro-pitted around pori.

Dimensions. Equatorial diameter 43 µm; nm: 1; no: 1.

Material. Ameke 1.1 (U44,1), polar view.

Botanical affinity. Clusiaceae (by comparison to *Symphonia globulifera* Germeraad et al. 1968).

Genus *Retistephanoporites* González Guzmán 1967

Type. *Retistephanoporites angelicus* González Guzmán 1967

Retistephanoporites sp.

Plate 8, figure 41

Diagnosis. Stephanoporate, sub-circular, pori annulate, tectate, reticulate, homobrochate, equatorial diameter 18 µm.

Description. Monad, radial, amb sub-circular; stephanoporate (four pori), pori 1.5 µm wide, annulate, annulus 1.5 µm wide, 1 µm high; tectate, columellae indistinct, exine 1 µm thick; surface ornamentation reticulate, homobrochate, lumina 0.5 µm wide.

Dimensions. Equatorial diameter 18 µm; nm: 1; no: 10.

Comparisons. *Retistephanoporites minutiporus* Jaramillo & Dilcher 2001 has distinct columellae.

Material. Ameke 1.1 (M44,2), polar view.

Pantoporate pollen

Genus *Chenopodipollis* Krutzsch 1966

Type. *Chenopodipollis multiplex* (Weyland & Pflug 1957) Krutzsch 1966

Chenopodipollis multiplex (Weyland & Pflug 1957) Krutzsch 1966

Plate 8, figure 42

Synonymy. *Periporopollenites multiplex* Weyland & Pflug 1957.

Diagnosis. Pantoporate, circular, tectate, columellae indistinct, scabrate, equatorial diameter 23 µm.

Description. Monad, radial, amb circular; pantoporate (>46 pori), pori circular, annulate, and 1.5 µm in diameter; tectate, columellae indistinct, exine 1.5 µm thick; surface ornamentation scabrate.

Dimensions. Equatorial diameter 23 µm; nm: 1; no: 4.

Material. Okigwe A7.1 (W48,2).

Botanical affinity. Amaranthaceae (by comparison with *Amaranthus*, see also Morley (2000)).

Genus *Clavaperiporites* Ramanujam 1966

Type. *Clavaperiporites jacobi* Ramanujam 1966

Clavaperiporites cf. *jacobi* Ramanujam 1966

Plate 8, figures 43–44

Diagnosis. Pantoporate, circular, intectate, reticulate, clavate, clavae arranged in *Croton* pattern, equatorial diameter 39 µm.

Description. Monad, radial, amb circular; pantoporate (6–14 pori), pori circular, simple, 2–4 µm in diameter; exine intectate, 2 µm thick; surface ornamentation clavate, clavae 1.5 µm high, 1–1.5 µm wide, triangular in plan view, arranged in a *Croton* pattern, clavae bases connect in the nexine to form a heterobrochate infrareticulum, muri 1 µm wide, lumina 1–1.5 µm wide and polygonal.

Dimensions. Equatorial diameter 34–(39)–44 µm; nm: 3; no: 4.

Comparisons. The sexine in *Clavaperiporites jacobi* Ramanujam 1966 has clavae placed on a baculate platform, with small spinules surmounting the clavae, and the grain has 5–10 pori (Jansonius and Hills 1976, card 509). The reticulum in *Clavaperiporites jacobi* Ramanujam 1966 is formed by the arrangement of the clavae heads: ‘clavae heads polygonal or triangular forming a loose reticulum’ (Jansonius and Hills 1976, card 509). However, in the specimens assigned here to *Clavaperiporites* cf. *jacobi* Ramanujam 1966, the clavae bases are connected to form the reticulum and the clavae heads therefore surmount the reticulum. *Thymelipollis amazonicus* D’Apolito et al. 2021 is smaller and the pore is annulate.

Material. Amaogugu 1.1 (E48,4), oblique view.

Genus *Echiperiporites* Van der Hammen & Wymstra 1964

Type. *Echiperiporites akanthos* Van der Hammen & Wymstra 1964

Echiperiporites aff. *scabrannulatus* Jaramillo et al. 2010

Plate 8, figure 45

Diagnosis. Pantoporate, pori annulate, intectate, echinate, equatorial diameter 25 µm.

Description. Monad, radial, amb sub-circular; pantoporate, pori spaced 2–7 µm apart, pori annulate, annulus 1.5 µm wide; exine intectate, 1 µm thick; surface ornamentation echinate, echinae spaced 1.5–3.5 µm apart, 1 µm wide at base, 2–3.5 µm high, ornamentation elsewhere scabrate.

Dimensions. Equatorial diameter 25 µm; nm 1; no: 3.

Comparisons. *Echiperiporites scabrannulatus* Jaramillo et al. 2010 is larger (67 µm); *Echiperiporites ‘psilatus’* is larger (35–

44 µm) (Jaramillo and Rueda 2023); *Echiperiporites akanthos* Van der Hammen & Wymstra 1964 is tectate and has more densely distributed echinae.

Material. Okigwe B6.1 (M57).

4. Results and discussion

4.1. Palynostratigraphy

The samples we have studied contain a diverse assemblage of fossil pollen and spores consisting of 29 spores, two gymnosperm pollen grains, and 138 angiosperm pollen grains (Plates 1–8). Recovery was high in the samples from Okigwe A and Ozuitem, but lower in some samples from Okigwe B as well as Ameke and Amaogugu (Table 1). Pollen and spores were generally well preserved, but differential uptake of staining may reflect some preservational differences among the sections studied here. In general, specimens from the Upper Nsukka Formation were slightly paler in colour than specimens from the Imo and Ameke formations, and this can be illustrated by comparing *Longapertites proxapertitoides* var. *proxapertitoides* (Plate 3, figure 2, from sample Okigwe A5.1), *Longapertites proxapertitoides* var. *reticuloides* (Plate 3, figure 3, from sample Amaogugu 1.1), and *Longapertites proxapertitoides* var. *reticuloides* (Plate 3, figure 4, from sample Ozuitem 3.1). It has been shown that the PETM in the Bighorn Basin, USA, is characterised by extensive reworking of Cretaceous palynomorphs (Korasidis et al. 2022), and while the paler colour of samples from the Okigwe sections could indicate reworking, no early Cretaceous forms such as *Dicheiropollis etruscus* Trevisan 1971 that would indicate general long-range reworking were present in the samples we have studied. Similarly, the Maastrichtian *Proteacidites dehanii* Zone is characterised in Nigeria by the co-occurrence of *Buttinia andreevi* Boltenhagen 1967 and *Proteacidites dehaani* Germeraad et al. 1968 together with high percentages of *Foveotrilletes margaritae* (Van der Hammen 1954) Germeraad et al. 1968 (Germeraad et al. 1968) and the presence of *Retimonocolpites pluribaculatus* Salard-Cheboldaëff 1978 (Salard-Cheboldaëff 1990). All of these diagnostic taxa are absent from the samples we have examined apart from a single well-preserved specimen of *Foveotrilletes margaritae* (Van der Hammen 1954) Germeraad et al. 1968 in the sample Amaogugu 7.1 (Plate 1, figure 19) (figure 2), and this suggests that reworking of pollen and spores from the Cretaceous is unlikely. However, as noted by Salard-Cheboldaëff (1990, p. 6), ‘many forms are common to the Upper Maastrichtian, Paleocene and Eocene’ (see Figure 2), and it is possible that taxa other than these zone fossils that are found in both the Maastrichtian and Palaeocene have been reworked in the samples we have studied. Further work will examine the nature of pollen and spore preservation and the extent of reworking in these sediments.

The samples we have studied have a palynofloral composition that places them within the pantropical *Proxapertites operculatus* Zone (Germeraad et al. 1968) (Figure 2). As noted above, the samples do not have a composition that is consistent with the Maastrichtian *Proteacidites dehanii* Atlantic Zone of

Germeraad et al. (1968) (Dataset S1). The samples from the Upper Nsukka Formation contain *Retidiporites magdalenensis* together with *Echitriporites trianguliformis* and *Proxapertites operculatus* (Dataset S1), which places these samples within the *Retidiporites magdalenensis* Atlantic Zone of Germeraad et al. (1968) (Figure 2). The samples from the Imo and Ameke formations contain both *Striatopollis catatumbus* and *Lanagiopollis crassa* (Dataset S1), and while no specimens of *Retibrevitricolpites triangulatus* van Hoeken-Klinkenberg 1966 were observed, these samples may represent the *Retibrevitricolpites triangulatus* Atlantic Zone of Germeraad et al. (1968) (Figure 2).

4.2. Species diversity and composition

The richness of each sample in terms of the number of sporomorph species observed ranged from 29 (Okigwe B4.1) to 76 (Amaogugu 1.1), and these two samples remained end-members when richness was compared at 100 and 150 specimens following rarefaction (Table 1). When compared at 150 specimens, samples from the Palaeocene (Upper Nsukka Formation and Imo Formation) have a lower average richness compared to the Eocene (Ameke Formation), the difference being significant (t -test, $p = .003$, $df = 6.337$, Palaeocene = 37.4, Eocene = 54.7) (Table 1). If the ages tentatively assigned to these formations are correct (figure 1) this may suggest an increase in Eocene diversity, but this will be tested in further work. Samples from Okigwe A and B (Palaeocene Upper Nsukka Formation) are dominated by pollen with botanical affinities to the Arecaceae (palms) including *Longapertites* spp.; *Monocolpopollenites ovatus*; *Mauritiidites franciscoi* var. *franciscoi* and *Mauritiidites crassibaculatus*, which both closely resemble the pollen of extant *Mauritia*; and *Proxapertites operculatus* and *P. cursus* (Araceae (arums) (Zetter et al. 2001)) (Figure 3a). This assemblage is very similar to the Palaeocene in the Neotropics (e.g. Jaramillo et al. 2007). In comparison, the number of top-ranked taxa with botanical affinities to palms and arums is lower in samples from the Ozuitem, Ameke and Amaogugu sections. Rather, samples from these three sections contain more spores such as *Polypodiisporites speciosus* (Polypodiaceae) and *Laevigatosporites ovatus* (Marattiaceae), together with tricolpate pollen such as *Striatopollis catatumbus* (Fabaceae) and *Foveotricolpites simplex* (Euphorbiaceae) (Figure 3a). However, it is perhaps noteworthy that *Spinizonocolpites prominatus* and *Spinizonocolpites* cf. *Spinizonocolpites* aff. *baculatus*, which are thought to have been produced by a plant with close affinities to the extant palm *Nypa fruticans*, are almost absent from the Okigwe sections (four specimens) but are present in greater numbers (22 specimens) in samples from these three sections (Figure 3a). The lithology (Table 1) and palynofacies (Obboh-Ikuenobe et al. 2005) of the samples studied here are indicative of fluvial-lagoonal-estuarine depositional environments, and considering the palynoflora as a whole, the general vegetation type represented by these samples is one of palm-dominated swamps, perhaps with mangroves represented by *Spinizonocolpites prominatus* (see Morley 2000, p. 135).

Compositional differences between samples are summarized in an NMDS ordination (Figure 3b). Samples are

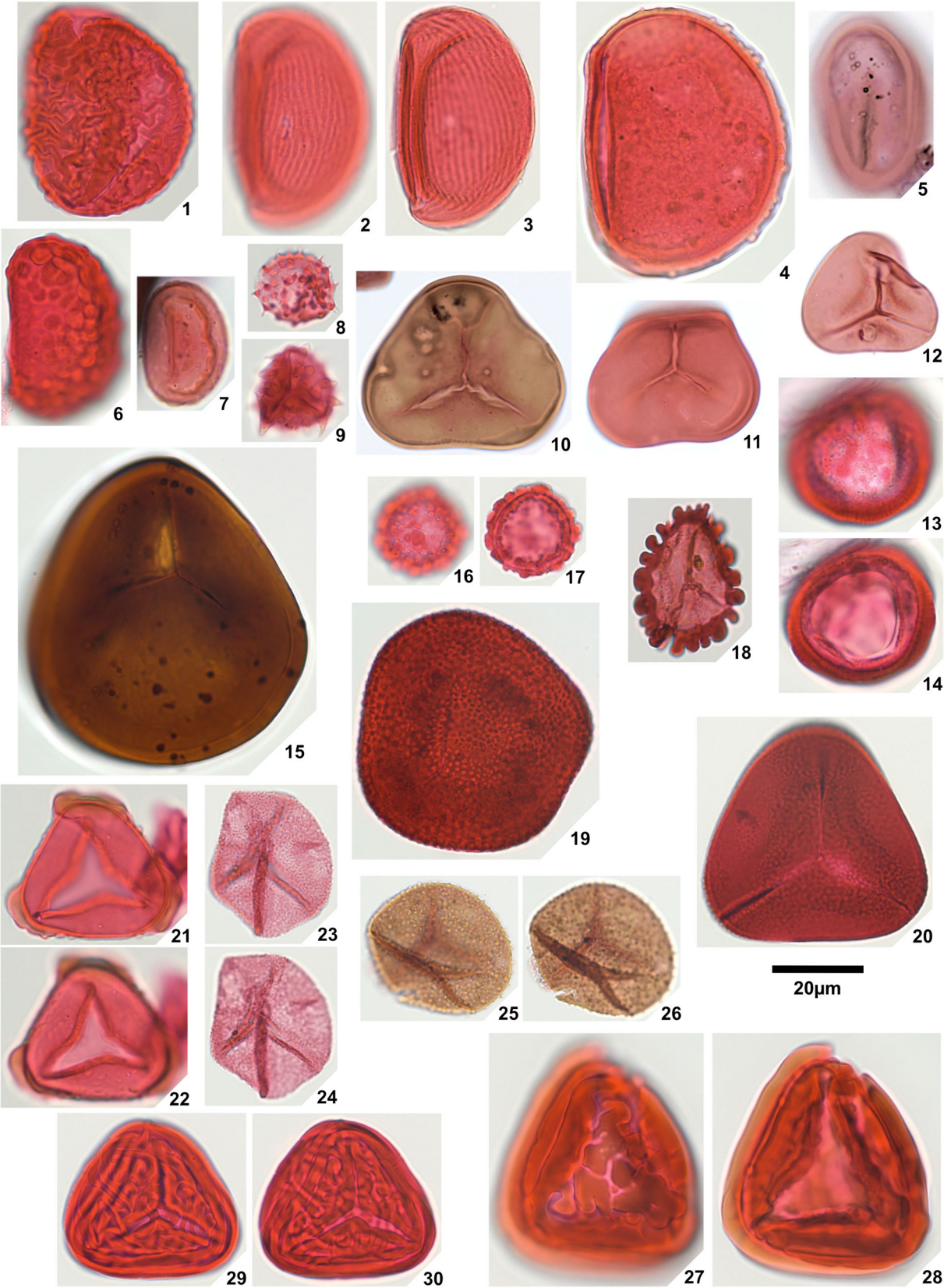


Plate 1.

1. *Rugaletes playfordii* Foster 1979, Amaogugu 1.1 (P58,1), specimen damaged,
2. *Cicatricosporites eocenicus* (Selling 1944) Jansonius & Hills 1976, Ozuitem 6.1 (Q42,1), high focal plane,
3. *Cicatricosporites eocenicus* (Selling 1944) Jansonius & Hills 1976, Ozuitem 6.1 (Q42,1), low focal plane,
4. *Laevigatosporites* aff. *catanejensis* Muller et al. 1987, Amaogugu 1.1 (X68,3),
5. *Laevigatosporites ovatus* Wilson & Webster 1946, Okigwe B4.1 (D44),
6. *Polypodiisporites speciosus* Sah 1967, Ozuitem 3.1 (W62, 3),
7. *Polypodiisporites* sp., Okigwe B4.1 (S42,1),
8. *Apiculatasporites* sp. 1, Amaogugu 1.1 (W54,1),
9. *Apiculatasporites* sp. 2, Okigwe B4.1 (X33),
10. *Deltoidospora* sp. 1, Okigwe B3.1 (M53,2),
11. *Deltoidospora* sp. 1, Ameke 11.1 (J58),
12. *Deltoidospora* sp. 2, Okigwe A5.1 (Q43,4),
13. *Densoisporites* sp., Okigwe B4.1 (X57,1), distal face,
14. *Densoisporites* sp., Okigwe B4.1 (X57,1), low focal plane,
15. *Dictyophyllidites* cf. *equixinus* (Couper 1958) Dettmann 1963, Okigwe A1.1 (D48,3),
16. *Distaverrusporites margaritatus* Muller 1968, Okigwe B4.1 (V56), distal face,
17. *Distaverrusporites margaritatus* Muller 1968, Okigwe B4.1 (V56), low focal plane,
18. *Distaverrusporites?* sp., Okigwe A7.1 (P48,1),
19. *Foveotrilites margaritae* (Van der Hammen 1954) Germeraad et al. 1968, Amaogugu 7.1 (K51,4),
20. *Foveotrilites* sp., Okigwe B1.1 (L45,4),
21. *Matonisporites* sp., Ameke 11.1 (O44,2), high focal plane,
22. *Matonisporites* sp., Ameke 11.1 (O44,2), low focal plane,
23. *Microreticulatisporites* cf. *uniformis* Singh 1964, Okigwe B1.1 (Y63,1), high focal plane,
24. *Microreticulatisporites* cf. *uniformis* Singh 1964, Okigwe B1.1 (Y63,1), low focal plane,
25. *Osmundacidites minor* Jaramillo & Dilcher 2001, Okigwe A1.1 (P41), high focal plane,
26. *Osmundacidites minor* Jaramillo & Dilcher 2001, Okigwe A1.1 (P41), low focal plane,
27. *Polypodiaceoisporites?* *fossulatus* Jaramillo & Dilcher 2001, Ameke 11.1 (V57,2), distal face,
28. *Polypodiaceoisporites?* *fossulatus* Jaramillo & Dilcher 2001, Ameke 11.1 (V57,2), proximal face,
29. *Polypodiaceoisporites* 'striatus', Amaogugu 7.1 (T44), distal face,
30. *Polypodiaceoisporites* 'striatus', Amaogugu 7.1 (T44), proximal face.

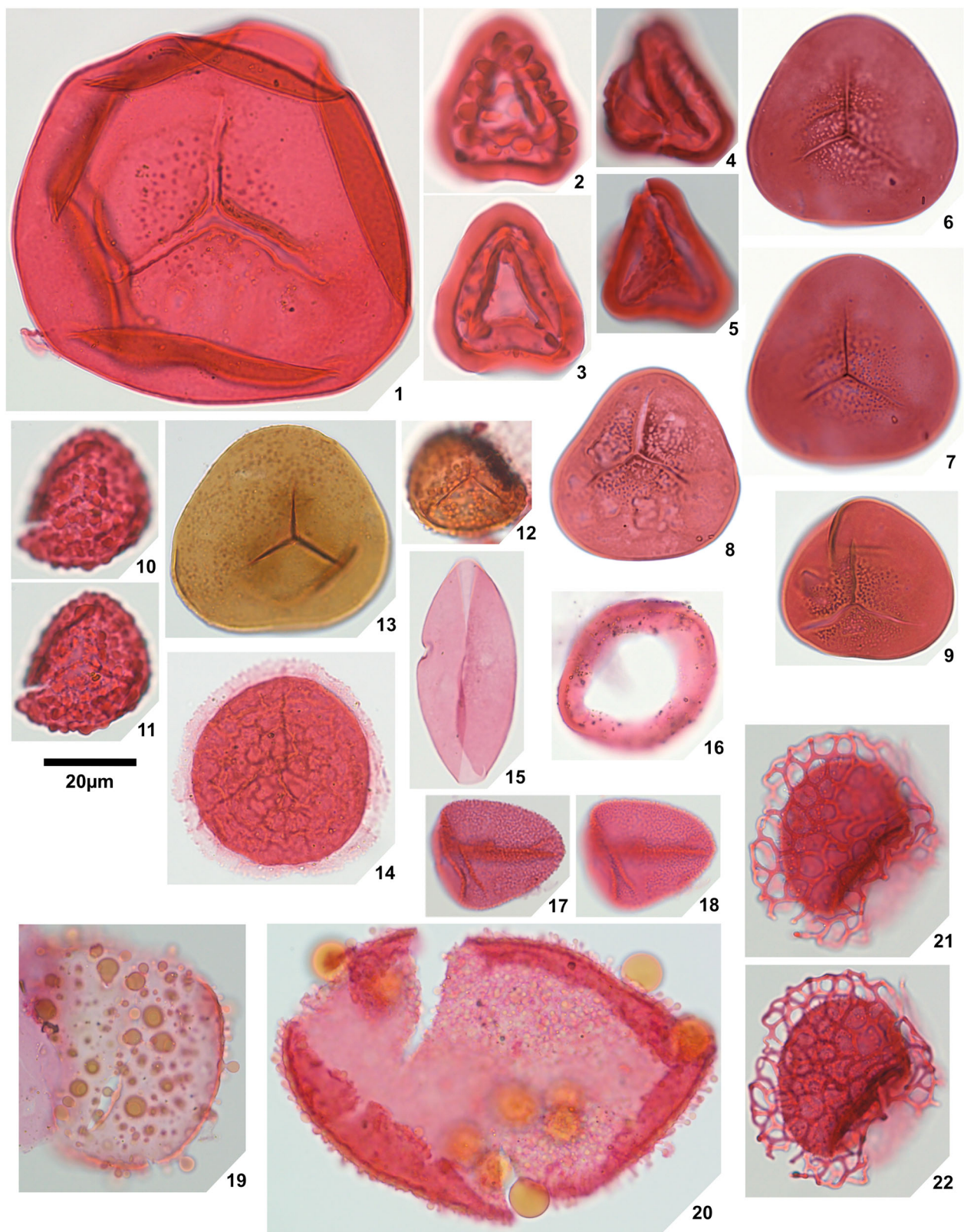


Plate 2.

1. *Psilatrilletes breviaesuratus* sp. nov., Amaogugu 1.1 (V42,3), holotype,
2. *Pteridacidites* sp. 1, Ameke 1.1 (V48,2), distal face,
3. *Pteridacidites* sp. 1, Ameke 1.1 (V48,2), proximal face,
4. *Pteridacidites* sp. 2, Ameke 1.1 (T46), distal face,
5. *Pteridacidites* sp. 2, Ameke 1.1 (T46), proximal face,
6. *Punctatisporites interfoveolatus* sp. nov., Okigwe B1.1 (R33,4), holotype, high focal plane,
7. *Punctatisporites interfoveolatus* sp. nov., Okigwe B1.1 (R33,4), holotype, low focal plane,
8. *Punctatisporites interfoveolatus* sp. nov., Okigwe B1.1 (E43), paratype,
9. *Punctatisporites interfoveolatus* sp. nov., Okigwe B1.1 (X50), paratype,
10. *Verrucosisporites major* (Couper 1958) Burden & Hills 1989, Ameke 1.1 (N49), distal face,
11. *Verrucosisporites major* (Couper 1958) Burden & Hills 1989, Ameke 1.1 (N49), proximal face,
12. *Verrucosisporites* cf. *verrucosus* Ibrahim 1933, Okigwe B3.1 (R37,4),
13. *Verrutrilletes virueloides* Jaramillo et al. (2007), Okigwe A1.1 (E45),
14. *Zlivisporis blanensis* Pacltová 1961, Amaogugu 1.1 (U44),
15. *Cycadopites deterius* (Balme 1957) Pocock 1970, Okigwe B1.1 (V55),
16. *Cyclusphaera scabrata* Jaramillo & Dilcher 2001, Okigwe B4.1 (L46,2),
17. *Inaperturopollenites fossulatus* sp. nov., Ozuitem 3.1 (W34,2), high focal plane,
18. *Inaperturopollenites fossulatus* sp. nov., Ozuitem 3.1 (W34,2), low focal plane,
19. *Inaperturopollenites*? sp. 1, Ameke 1.1 (K51),
20. *Inaperturopollenites*? sp. 2, Ozuitem 3.1 (X42,1),
21. *Praedapollis africanus* Boltenhagen & Salard 1973, Ameke 1.1 (S47), high focal plane,
22. *Praedapollis africanus* Boltenhagen & Salard 1973, Ameke 1.1 (S47), low focal plane.

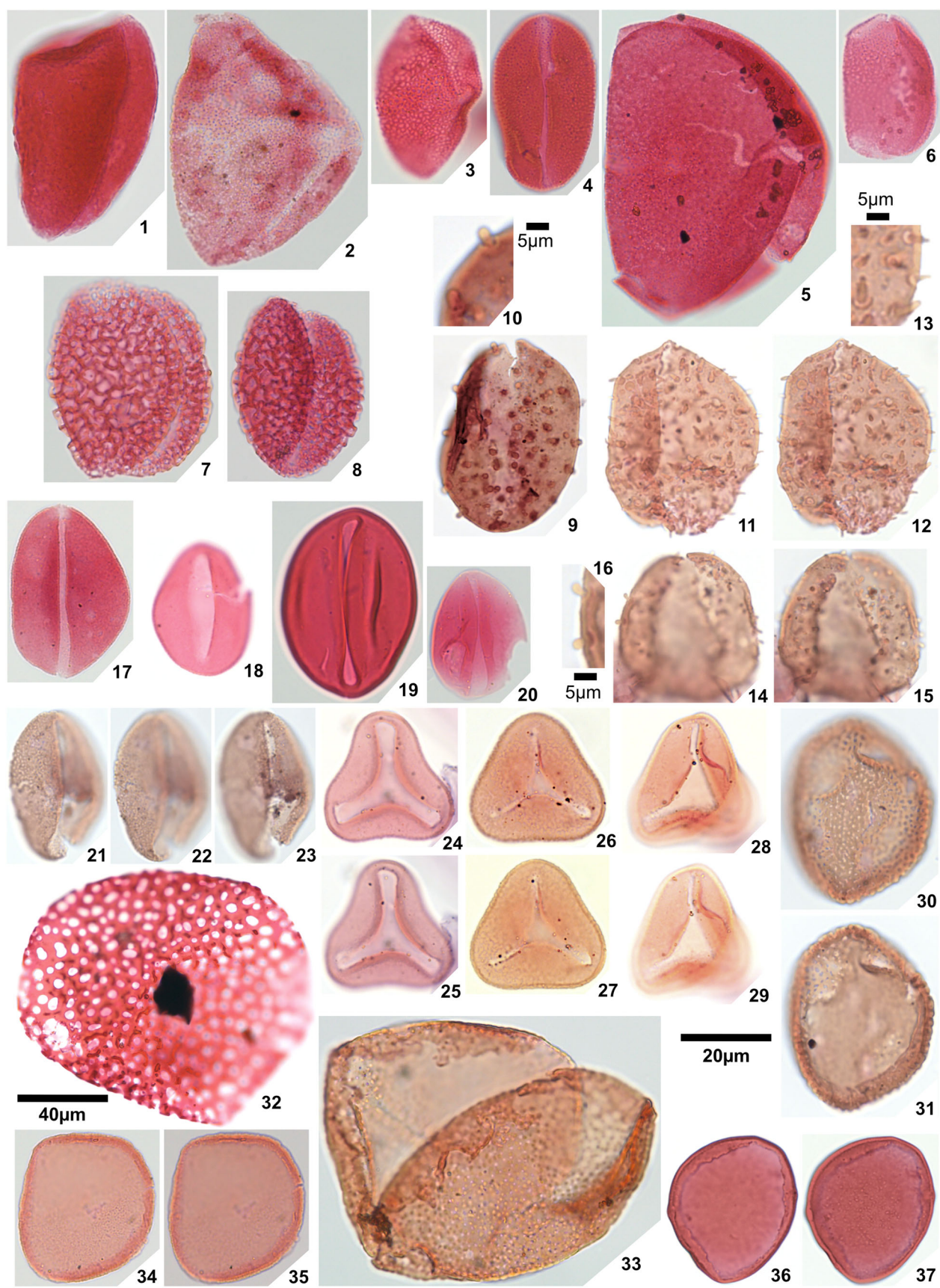


Plate 3.

1. *Longapertites microfoveolatus* Adegoke & Jan du Chêne 1975, Okigwe B1.1 (X38,3),
2. *Longapertites proxapertitoides* var. *proxapertoides* Van der Hammen & Garcia 1966, Okigwe A5.1 (X44,2),
3. *Longapertites proxapertitoides* var. *reticuloides* Van der Hammen & Garcia 1966, Amaogugu 1.1 (T38), equatorial view,
4. *Longapertites proxapertitoides* var. *reticuloides* Van der Hammen & Garcia 1966, Ozuitem 3.1 (V65,1), polar view,
5. *Longapertites vaneendenburgi* Germeaad et al. 1968, Okigwe B2.1 (L39,2),
6. *Longapertites* cf. *marginatus* van Hoeken-Klinkenberg 1964, Amaogugu 1.1 (S58,3),
7. *Longapertites crassireticuloides* sp. nov., Okigwe A5.1 (M33,4), holotype,
8. *Longapertites crassireticuloides* sp. nov., Okigwe A5.1 (G33,3), paratype,
9. *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964, Okigwe A1.1 (D53,4),
10. *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg 1964, Okigwe A1.1 (D53,4), details of sculptural elements, note 5 µm scale bar,
11. *Mauritiidites franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964, Okigwe B3.1 (M33,2), high focal plane,
12. *Mauritiidites franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964, Okigwe B3.1 (M33,2), low focal plane,
13. *Mauritiidites franciscoi* var. *franciscoi* van Hoeken-Klinkenberg 1964, Okigwe B3.1 (M33,2), details of sculptural elements, note 5 µm scale bar,
14. *Mauritiidites franciscoi* var. *minutus* Van der Hammen & Garcia 1966, Okigwe B6.1 (R46), high focal plane,
15. *Mauritiidites franciscoi* var. *minutus* Van der Hammen & Garcia 1966, Okigwe B6.1 (R46), low focal plane,
16. *Mauritiidites franciscoi* var. *minutus* Van der Hammen & Garcia 1966, Okigwe B6.1 (R46), details of sculptural elements, note 5µm scale bar,
17. *Monocolpopollenites ovatus* Jaramillo & Dilcher 2001, Okigwe B1.1 (Y57,4),
18. *Monocolpopollenites tranquillus* (Potonié 1934) Jansonius & Hills 1976, Ameke 1.1 (V52,1),
19. *Psilamonocolpites grandis* Van der Hammen & Garcia 1966, Ozuitem 6.1 (V55,4),
20. *Psilamonocolpites medius* (Van der Hammen 1956) Van der Hammen & Garcia 1966, Amaogugu 7.1 (T56,3),
21. *Retimonocolpites* aff. *nigeriensis* van-Hoeken-Klinkenberg 1966, Okigwe B7.1 (N56,3), high focal plane,
22. *Retimonocolpites* aff. *nigeriensis* van-Hoeken-Klinkenberg 1966, Okigwe B7.1 (N56,3), mid focal plane,
23. *Retimonocolpites* aff. *nigeriensis* van-Hoeken-Klinkenberg 1966, Okigwe B7.1 (N56,3), low focal plane,
24. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (H53,3), holotype, high focal plane,
25. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (H53,3), holotype, low focal plane,
26. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (F48), paratype, high focal plane,
27. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (F48), paratype, low focal plane,
28. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (P52,2), paratype, high focal plane,
29. *Luminidites microreticulatus* sp. nov., Okigwe B4.1 (P52,2), paratype, mid focal plane showing columellae tips,
30. *Proxapertites cursus* van Hoeken-Klinkenberg 1966, Okigwe B6.1 (T35), high focal plane,
31. *Proxapertites cursus* van Hoeken-Klinkenberg 1966, Okigwe B6.1 (T35), low focal plane,
32. *Proxapertites humbertoides* (Van der Hammen 1954) Sarmiento 1992, Okigwe B2.1 (P62), note 40 µm scale bar,
33. *Proxapertites magnus* Muller et al. 1987, Okigwe B6.1 (U54,2),
34. *Proxapertites operculatus* (Van der Hammen 1954) Van der Hammen 1956, Okigwe B2.1 (U51,2), high focal plane,
35. *Proxapertites operculatus* (Van der Hammen 1954) Van der Hammen 1956, Okigwe B2.1 (U51,2), low focal plane,
36. *Proxapertites psilatus* Sarmiento 1992, Ozuitem 6.1 (Q34), high focal plane,
37. *Proxapertites psilatus* Sarmiento 1992, Ozuitem 6.1 (Q34), low focal plane.

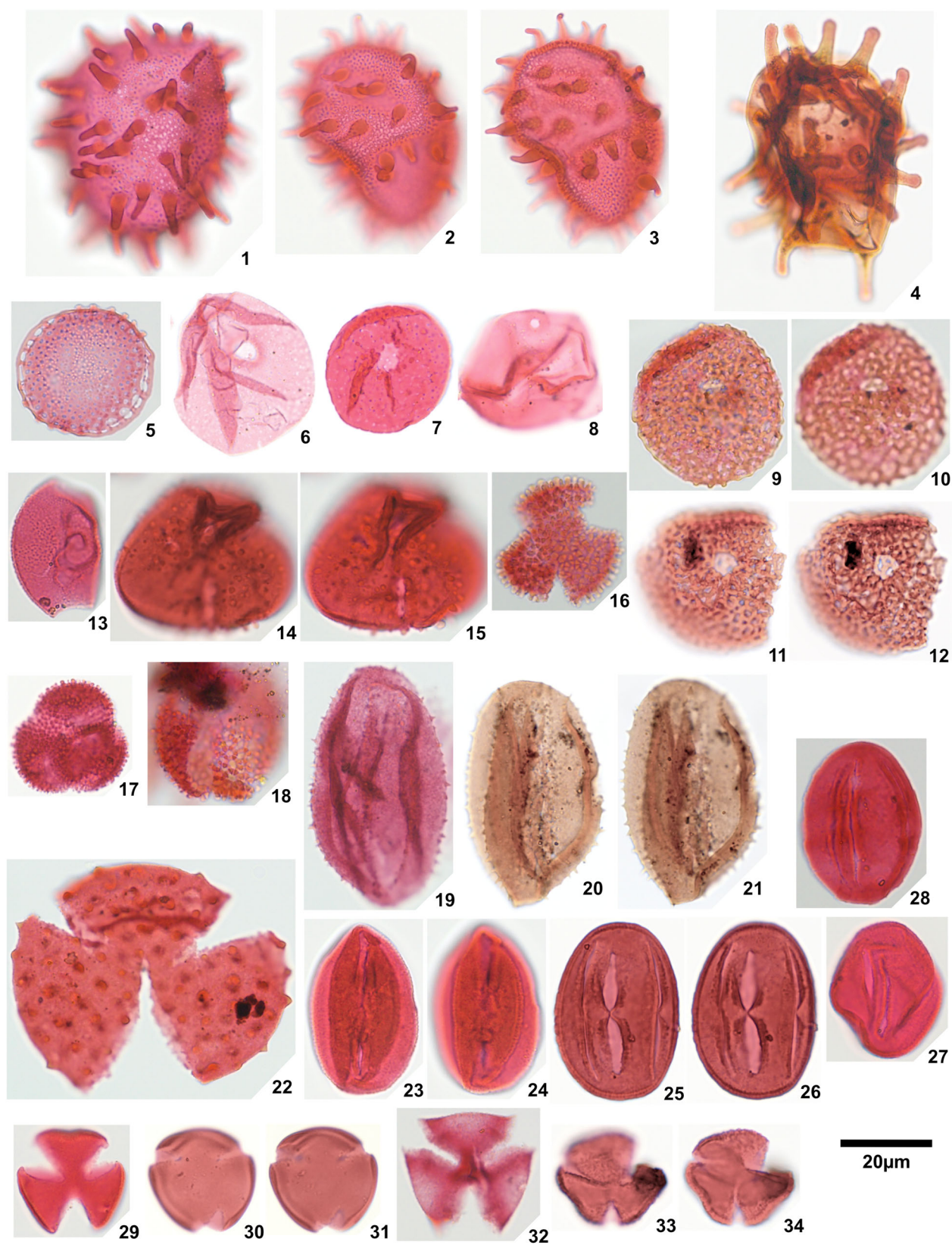


Plate 4.

1. *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973, Ameke 1.1 (Q30),
2. *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973, Amaogugu 7.1 (Q45), details of collumellae,
3. *Spinizonocolpites prominatus* (McIntyre 1965) Stover & Evans 1973, Amaogugu 7.1 (Q45), details of exine,
4. *Spinizonocolpites* cf. *Spinizonocolpites* aff. *baculatus* Muller 1968, Okigwe B7.1 (J40,1),
5. *Saturna enigmaticus* Salard-Chebouldaeff 1978, Okigwe B1.1 (H32,2),
6. *Milfordia confossus* (Fairchild 1966) comb. nov. Okigwe B1.1 (S48),
7. *Milfordia homeopunctata* (McIntyre 1965) Partridge in Stover & Partridge 1973, Ozuitem 3.1 (W65,2),
8. *Monoporopollenites annulatus* (Van der Hammen 1954) Jaramillo & Dilcher, 2001, Okigwe B4.1 (V56,1),
9. *Retimonoporites heterobrochatus* sp. nov., Okigwe B3.1 (G33), holotype, high focal plane,
10. *Retimonoporites heterobrochatus* sp. nov., Okigwe B3.1 (G33), holotype, low focal plane,
11. *Retimonoporites heterobrochatus* sp. nov., Okigwe B3.1 (F40,2), paratype, high focal plane,
12. *Retimonoporites heterobrochatus* sp. nov., Okigwe B3.1 (F40,2), paratype, low focal plane,
13. *Retidiporites magdalenensis* Van der Hammen & Garcia 1966, Okigwe B1.1 (T30,2),
14. *Bacubrevitricolpites* sp., Amaogugu 1.1 (P56,4), high focal plane,
15. *Bacubrevitricolpites* sp., Amaogugu 1.1 (P56,4), low focal plane,
16. *Crototricolpites densus* Salard-Chaebouldaeff 1978, Okigwe B2.1 (M35),
17. *Crototricolpites* aff. *finitus* Silva-Caminha et al. 2010, Okigwe B1.1 (H40,1),
18. *Crototricolpites* 'superatus', Okigwe A7.1 (W37,3),
19. *Echitricolpites serratus* sp. nov., Okigwe B1.1 (H64,4), holotype,
20. *Echitricolpites serratus* sp. nov., Okigwe A1.1 (S40,4), paratype, high focal plane,
21. *Echitricolpites serratus* sp. nov., Okigwe A1.1 (S40,4), paratype, low focal plane,
22. *Echitricolpites* aff. *communis* Regali et al. 1974, Okigwe B3.1 (G54,2),
23. *Foveotricolpites simplex* (González Guzmán 1967) D'Apolito et al. 2021, Ozuitem 6.1 (Y31,2), high focal plane,
24. *Foveotricolpites simplex* (González Guzmán 1967) D'Apolito et al. 2021, Ozuitem 6.1 (Y31,2), low focal plane,
25. *Ladakhipollenites colpiconstrictus* (van Hoeken-Klinkenberg 1966) D'Apolito et al. 2021, Ozuitem 6.1 (M53), high focal plane,
26. *Ladakhipollenites colpiconstrictus* (van Hoeken-Klinkenberg 1966) D'Apolito et al. 2021, Ozuitem 6.1 (M53), low focal plane,
27. *Ladakhipollenites simplex* Jaramillo & Dilcher 2001, Amaogugu 7.1 (U38,2),
28. *Ladakhipollenites simplex* Jaramillo & Dilcher 2001, Okigwe B2.1 (O54,3),
29. *Ladakhipollenites hammenii* (Boltenhagen 1976) comb. nov., Amaogugu 7.1 (R55,1),
30. *Ladakhipollenites* sp. 1, Amaogugu 1.1 (V34,4), high focal plane,
31. *Ladakhipollenites* sp. 1, Amaogugu 1.1 (V34,4), low focal plane,
32. *Ladakhipollenites* sp. 2, Okigwe A5.1 (U40,3),
33. *Ladakhipollenites?* *thomasi* (Sarmiento 1992) comb. nov., Amaogugu 7.1 (L47,3), high focal plane,
34. *Ladakhipollenites?* *thomasi* (Sarmiento 1992) comb. nov., Amaogugu 7.1 (L47,3), low focal plane.

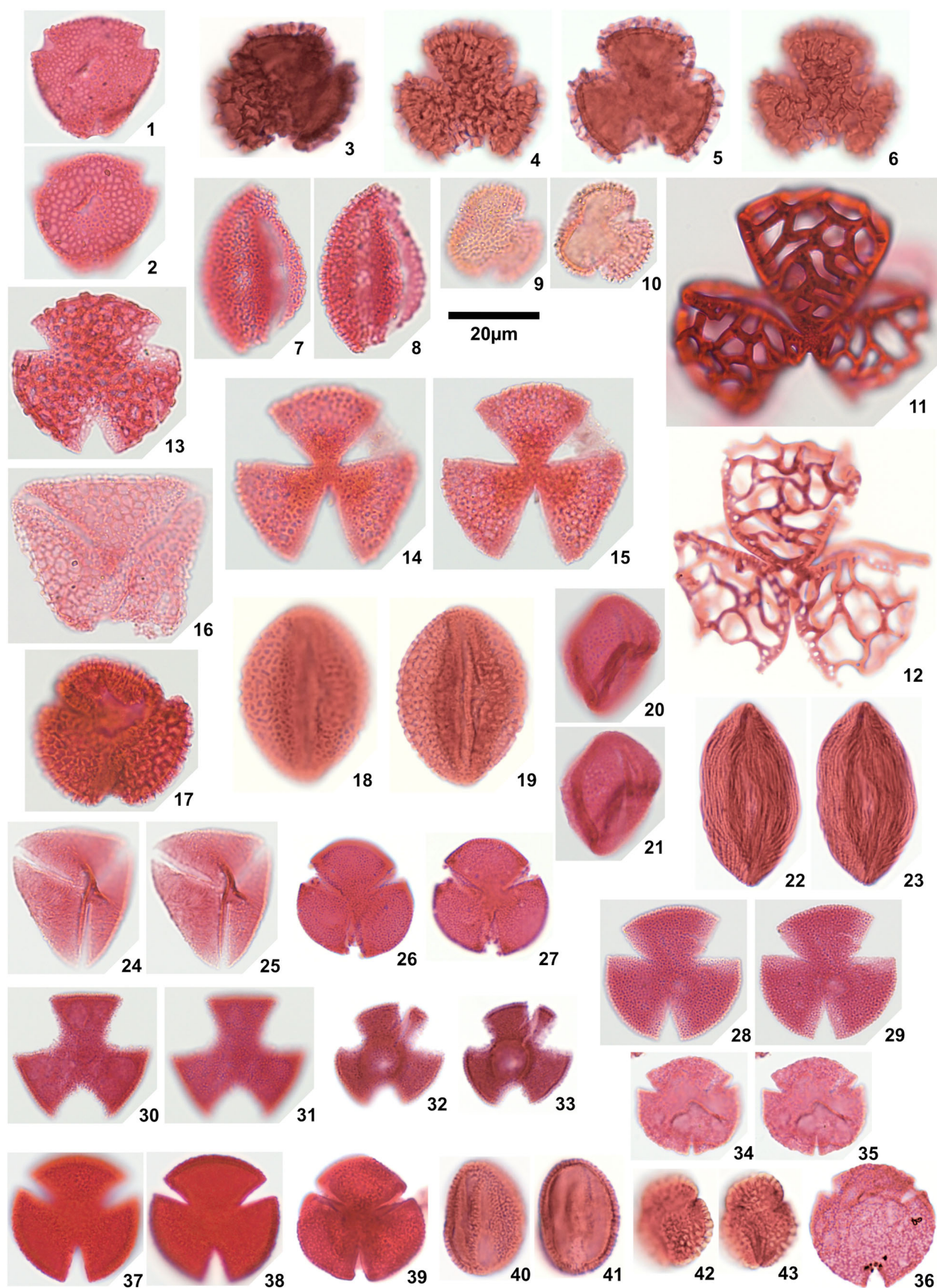


Plate 5.

1. *Retibrevitricolpites* 'reciprocus', Ozuitem 6.1 (X32,2),
2. *Retibrevitricolpites* 'reciprocus', Ozuitem 6.1 (X32,2), opposite pole,
3. *Retitrescolpites cecryphalium* (Leidelmeyer 1966) comb. nov., Ozuitem 6.1 (T32,4),
4. *Retitrescolpites cecryphalium* (Leidelmeyer 1966) comb. nov., Ozuitem 3.1 (N42,3), high focal plane,
5. *Retitrescolpites cecryphalium* (Leidelmeyer 1966) comb. nov., Ozuitem 3.1 (N42,3), mid focal plane,
6. *Retitrescolpites cecryphalium* (Leidelmeyer 1966) comb. nov., Ozuitem 3.1 (N42,3), low focal plane,
7. *Retitrescolpites* aff. *magnus* (González Guzmán 1967) Jaramillo & Dilcher 2001, Ozuitem 6.1 (W35,2), high focal plane,
8. *Retitrescolpites* aff. *magnus* (González Guzmán 1967) Jaramillo & Dilcher 2001, Ozuitem 6.1 (W35,2), low focal plane,
9. *Retitrescolpites* cf. 'opitaeorum', Okigwe B4.1 (K58,1), high focal plane,
10. *Retitrescolpites* cf. 'opitaeorum', Okigwe B4.1 (K58,1), low focal plane,
11. *Retitrescolpites miriabilis* sp. nov., Amaogugu 7.1 (M57,3), holotype,
12. *Retitrescolpites miriabilis* sp. nov., Amaogugu 7.1 (L64,3), paratype,
13. *Retitrescolpites* sp. 1, Ozuitem 6.1 (K60,3),
14. *Retitrescolpites* sp. 2, Ozuitem 6.1 (J42,4), high focal plane,
15. *Retitrescolpites* sp. 2, Ozuitem 6.1 (J42,4), low focal plane,
16. *Retitrescolpites* sp. 3, Ameke 1.1 (W38),
17. *Retitrescolpites* sp. 4, Ozuitem 3.1 (Q35,2),
18. *Rousea florentina* (González Guzmán 1967) Jaramillo & Dilcher 2001, Amaogugu 1.1 (P60,4), high focal plane,
19. *Rousea florentina* (González Guzmán 1967) Jaramillo & Dilcher 2001, Amaogugu 1.1 (P60,4), low focal plane,
20. *Rousea heteroreticulatus* (Boltenhagen 1976) comb. nov., Ameke 1.1 (S55,4), high focal plane,
21. *Rousea heteroreticulatus* (Boltenhagen 1976) comb. nov., Ameke 1.1 (S55,4), low focal plane,
22. *Striatopollis catatumbus* (González Guzmán 1967) Takahashi & Jux 1989, Amaogugu 7.1 (P37,4), high focal plane,
23. *Striatopollis catatumbus* (González Guzmán 1967) Takahashi & Jux 1989, Amaogugu 7.1 (P37,4), low focal plane,
24. *Striatopollis* sp., Okigwe B1.1 (V52,2), high focal plane,
25. *Striatopollis* sp., Okigwe B1.1 (V52,2), low focal plane,
26. *Tricolpites clarensis* (González Guzmán 1967) Jaramillo & Dilcher 2001, Amaogugu 7.1 (S56,1), high focal plane,
27. *Tricolpites clarensis* (González Guzmán 1967) Jaramillo & Dilcher 2001, Amaogugu 7.1 (S56,1), low focal plane,
28. *Tricolpites gageonnetii* (Boltenhagen 1976) comb. nov., Okigwe B1.1 (W42), high focal plane,
29. *Tricolpites gageonnetii* (Boltenhagen 1976) comb. nov., Okigwe B1.1 (W42), low focal plane,
30. *Tricolpites multiornamentus* sp. nov., Okigwe B1.1 (N41,4), holotype, high focal plane,
31. *Tricolpites multiornamentus* sp. nov., Okigwe B1.1 (N41,4), holotype, low focal plane,
32. *Tricolpites multiornamentus* sp. nov., Okigwe B1.1 (M46), paratype, high focal plane, an air bubble rests over the specimen,
33. *Tricolpites multiornamentus* sp. nov., Okigwe B1.1 (M46), paratype, low focal plane, an air bubble rests over the specimen,
34. *Tricolpites brevicolpatus* sp. nov., Okigwe B1.1 (W56), holotype, high focal plane,
35. *Tricolpites brevicolpatus* sp. nov., Okigwe B1.1 (W56), holotype, low focal plane,
36. *Tricolpites brevicolpatus* sp. nov., Okigwe B1.1 (N42,3), paratype,
37. *Tricolpites* sp. 1, Ameke 11.1 (V39), high focal plane,
38. *Tricolpites* sp. 1, Ameke 11.1 (V39), low focal plane,
39. *Tricolpites* sp. 2, Ozuitem 3.1 (P37,2),
40. *Tricolpites* sp. 3, Amaogugu 7.1 (S40,4), high focal plane,
41. *Tricolpites* sp. 3, Amaogugu 7.1 (S40,4), low focal plane,
42. *Tricolpites* sp. 4, Ozuitem 6.1 (T32,2), high focal plane,
43. *Tricolpites* sp. 4, Ozuitem 6.1 (T32,2), low focal plane.

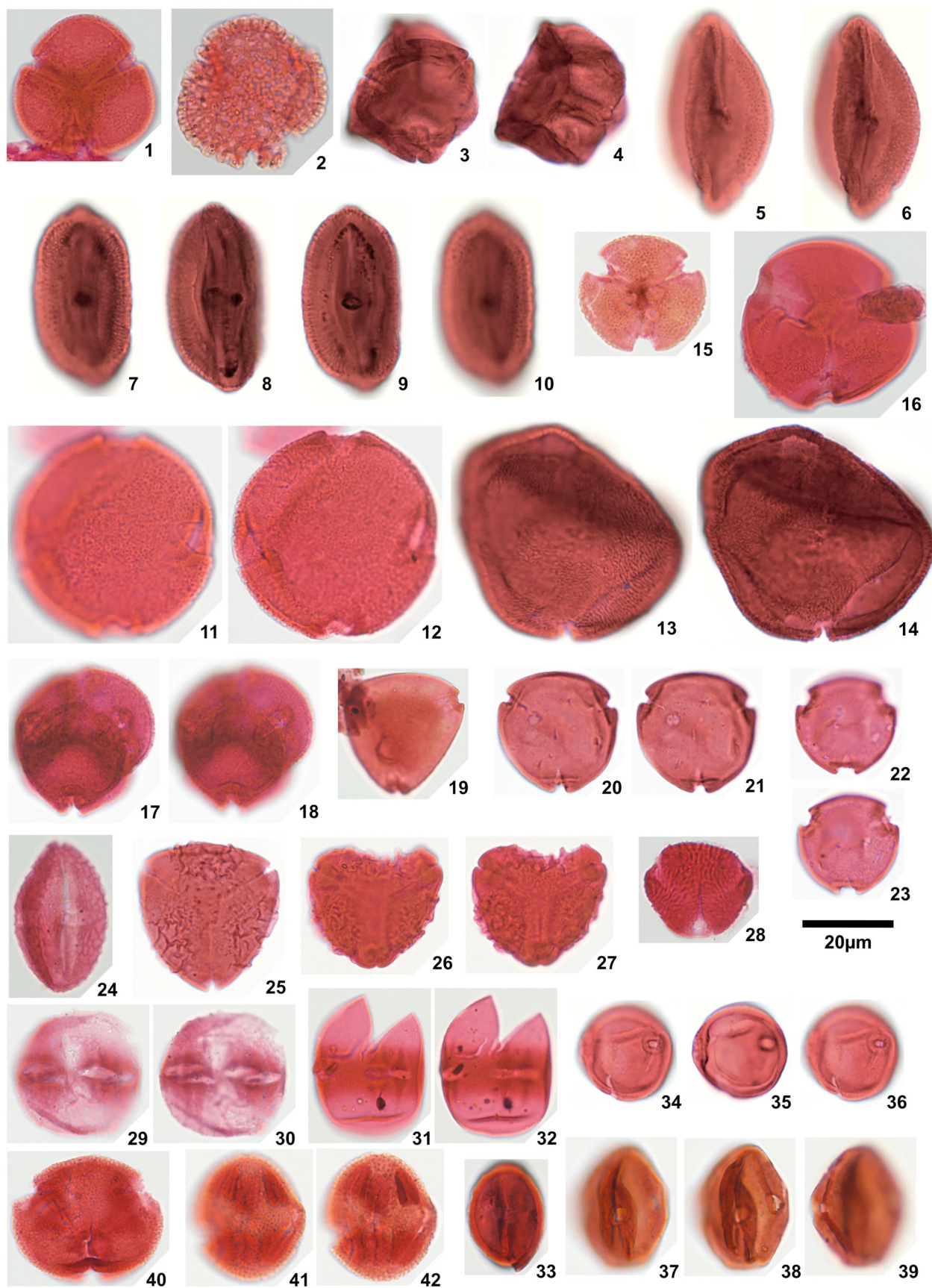


Plate 6.

1. *Bombacacidites* aff. *brevis* Muller et al. 1987, Ozuitem 3.1 (X40),
2. *Bombacacidites* '*pluricolumellatus*', Okigwe B4.1 (H45,2),
3. *Fillaeopsidites* cf. *reticulatus* (Guinet & Salard-Chaeboldaef 1975) Salard-Chaeboldaef 1978, Okigwe A5.1 (E45,4), high focal plane,
4. *Fillaeopsidites* cf. *reticulatus* (Guinet & Salard-Chaeboldaef 1975) Salard-Chaeboldaef 1978, Okigwe A5.1 (E45,4), low focal plane,
5. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 1.1 (H31,3), high focal plane,
6. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 1.1 (H31,3), low focal plane,
7. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 11.1 (R36,1), high focal plane,
8. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 11.1 (R36,1), alternative high focal plane,
9. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 11.1 (R36,1), mid focal plane,
10. *Foveotricolporites* cf. *crassiexinus* van Hoeken-Klinkenberg 1966, Ameke 11.1 (R36,1), low focal plane,
11. *Lanagiopollis* *crassa* (Van der Hammen & Wymstra 1964) Frederiksen 1988, Ozuitem 6.1 (S35,2), tetracolporate specimen, high focal plane,
12. *Lanagiopollis* *crassa* (Van der Hammen & Wymstra 1964) Frederiksen 1988, Ozuitem 6.1 (S35,2), tetracolporate specimen, low focal plane,
13. *Lanagiopollis* *crassa* (Van der Hammen & Wymstra 1964) Frederiksen 1988, Ozuitem 3.1 (W59,3), high focal plane,
14. *Lanagiopollis* *crassa* (Van der Hammen & Wymstra 1964) Frederiksen 1988, Ozuitem 3.1 (W59,3), low focal plane,
15. *Margocolporites* cf. *mandjicus* Boltenhagen 1976, Okigwe B6.1 (M46,2),
16. *Margocolporites* cf. *rauvolfi* Salard-Chaeboldaef 1979, Ameke 1.1 (H43,2),
17. *Paripollis*? '*dubius*', Okigwe B1.1 (W32), high focal plane,
18. *Paripollis*? '*dubius*', Okigwe B1.1 (W32), low focal plane,
19. *Psilabrevitricolporites* *simpliformis* Van der Kaars 1983, Okigwe B3.1 (P44,4),
20. *Psilabrevitricolporites* *porolatus* sp. nov., Amaogugu 1.1 (T60), holotype, high focal plane,
21. *Psilabrevitricolporites* *porolatus* sp. nov., Amaogugu 1.1 (T60), holotype, low focal plane,
22. *Psilabrevitricolporites* *porolatus* sp. nov., Amaogugu 1.1 (M48,1), paratype, high focal plane,
23. *Psilabrevitricolporites* *porolatus* sp. nov., Amaogugu 1.1 (M48,1), paratype, low focal plane,
24. *Rhoipites* *guianensis* (Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001, Ameke 1.1 (T65),
25. *Rugutricolporites* *cumulus* sp. nov., Ozuitem 6.1 (O33,2), holotype,
26. *Rugutricolporites* *cumulus* sp. nov., Ozuitem 3.1 (V40,4), paratype, high focal plane,
27. *Rugutricolporites* *cumulus* sp. nov., Ozuitem 3.1 (V40,4), paratype, low focal plane,
28. *Striatricolporites* cf. *pimulis* Leidelmeyer 1966, Ozuitem 3.1 (W65,2),
29. *Tetracolporopollenites* *maculosus* (Regali et al. 1974) Jaramillo & Dilcher 2001, Ameke 1.1 (T44), high focal plane,
30. *Tetracolporopollenites* *maculosus* (Regali et al. 1974) Jaramillo & Dilcher 2001, Ameke 1.1 (T44), low focal plane,
31. *Tetracolporopollenites* *transversalis* (Dueñas 1980) Jaramillo & Dilcher 2001, Amaogugu 1.1 (L60), high focal plane,
32. *Tetracolporopollenites* *transversalis* (Dueñas 1980) Jaramillo & Dilcher 2001, Amaogugu 1.1 (L60), low focal plane,
33. *Tetracolporopollenites* *cryptoporus* (Boltenhagen 1976) comb. nov., Okigwe B6.1 (W40,1),
34. *Tricolporites* *torus* sp. nov., Amaogugu 1.1 (W67,1), holotype, high focal plane,
35. *Tricolporites* *torus* sp. nov., Amaogugu 1.1 (W67,1), holotype, mid focal plane,
36. *Tricolporites* *torus* sp. nov., Amaogugu 1.1 (W67,1), holotype, low focal plane,
37. *Tricolporites* *torus* sp. nov., Okigwe A1.1 (F66), paratype, high focal plane,
38. *Tricolporites* *torus* sp. nov., Okigwe A1.1 (F66), paratype, mid focal plane,
39. *Tricolporites* *torus* sp. nov., Okigwe A1.1 (F66), paratype, low focal plane,
40. *Tricolporites* *densus* sp. nov., Okigwe B2.1 (W61,2), holotype,
41. *Tricolporites* *densus* sp. nov., Okigwe B3.1 (S46), paratype, high focal plane,
42. *Tricolporites* *densus* sp. nov., Okigwe B3.1 (S46), paratype, low focal plane.

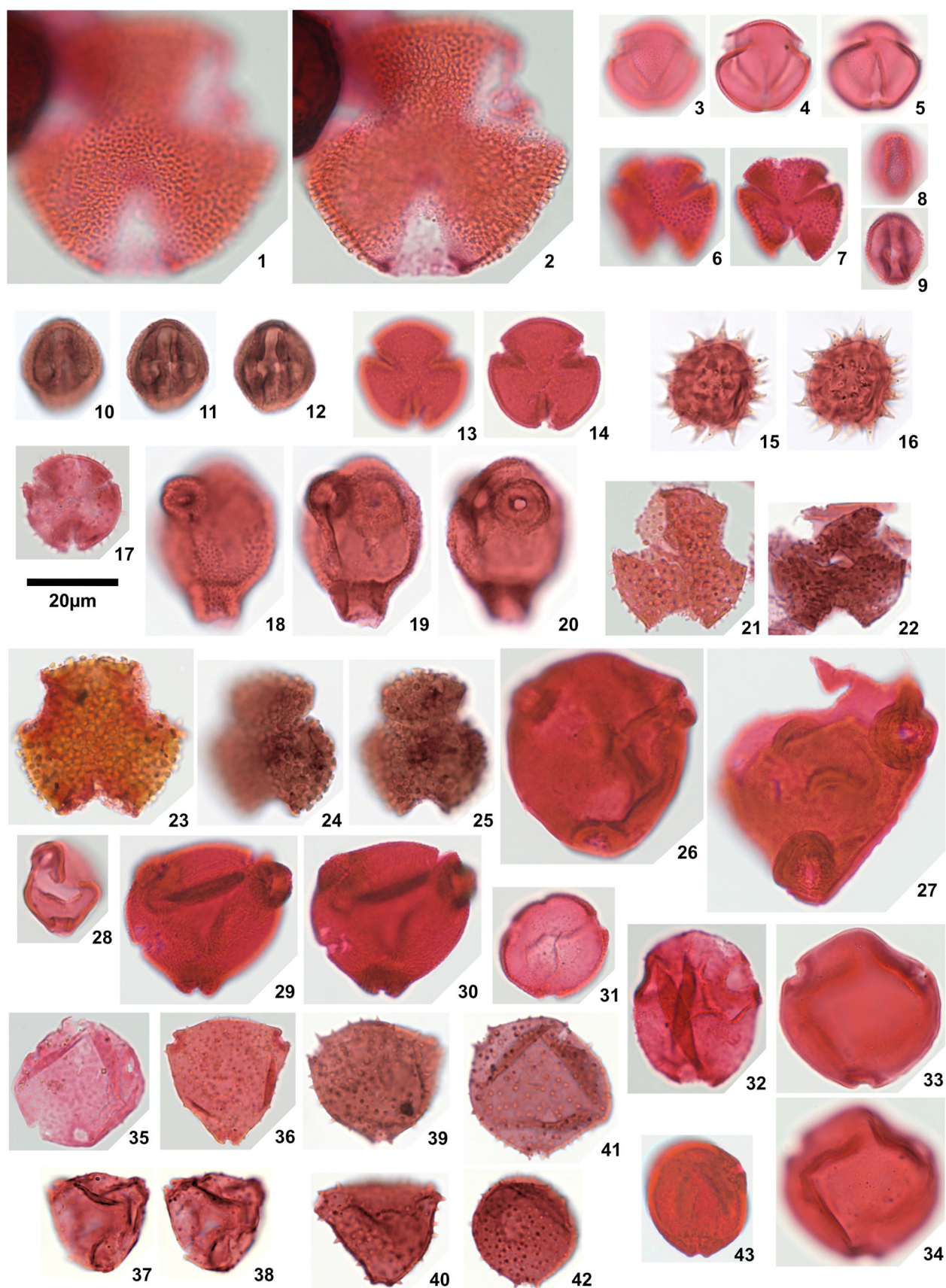


Plate 7.

1. *Tricolporites* 'reticulomargites', Ozuitem 6.1 (H36), high focal plane,
2. *Tricolporites* 'reticulomargites', Ozuitem 6.1 (H36), low focal plane,
3. *Tricolporites* sp. 1, Ameke 1.1 (T51,4), high focal plane showing reticulum,
4. *Tricolporites* sp. 1, Ameke 1.1 (T51,4), mid focal plane,
5. *Tricolporites* sp. 1, Ameke 1.1 (T51,4), low focal plane showing pore,
6. *Tricolporites* sp. 2, Ozuitem 3.1 (S38,2), high focal plane,
7. *Tricolporites* sp. 2, Ozuitem 3.1 (S38,2), mid focal plane,
8. *Tricolporites* sp. 3, Ameke 1.1 (S52,4), high focal plane showing reticulum,
9. *Tricolporites* sp. 3, Ameke 1.1 (S52,4), mid focal plane,
10. *Tricolporites* sp. 4, Okigwe B2.1 (M60,1), high focal plane,
11. *Tricolporites* sp. 4, Okigwe B2.1 (M60,1), mid focal plane,
12. *Tricolporites* sp. 4, Okigwe B2.1 (M60,1), low focal plane,
13. *Tricolporites* sp. 5, Ozuitem 3.1 (U56,1), high focal plane,
14. *Tricolporites* sp. 5, Ozuitem 3.1 (U56,1), low focal plane,
15. *Tricolporites* sp. 6 Okigwe B4.1 (O54), mid focal plane,
16. *Tricolporites* sp. 6 Okigwe B4.1 (O54), high focal plane,
17. *Tricolporites*? sp., Ozuitem 6.1 (V48),
18. *Casuarinidites foveolatus* sp. nov., Ameke 11.1 (N52,1), holotype, high focal plane,
19. *Casuarinidites foveolatus* sp. nov., Ameke 11.1 (N52,1), holotype, details of pore,
20. *Casuarinidites foveolatus* sp. nov., Ameke 11.1 (N52,1), holotype, details of pore band,
21. *Clavatriporites dispersiclavatus* sp. nov., Okigwe A7.1 (O63,4), holotype,
22. *Clavatriporites dispersiclavatus* sp. nov., Okigwe B1.1 (K48,4), paratype,
23. *Clavatriporites spicatus* sp. nov., Okigwe B6.1 (S47,4), holotype,
24. *Clavatriporites spicatus* sp. nov., Okigwe B6.1 (S47,4), paratype, high focal plane,
25. *Clavatriporites spicatus* sp. nov., Okigwe B6.1 (S47,4), paratype, low focal plane,
26. *Corsinipollenites psilatus* Jaramillo & Dilcher 2001, Ozuitem 3.1 (S52),
27. *Corsinipollenites undulatus* (González Guzmán 1967) Jaramillo & Dilcher 2001, Ameke 11.1 (Q45,4),
28. *Corsinipollenites* cf. *psilatus* Jaramillo & Dilcher 2001, Ameke 1.1 (O61,1),
29. *Corsinipollenites* 'striatus', Ozuitem 3.1 (X58,2), high focal plane,
30. *Corsinipollenites* 'striatus', Ozuitem 3.1 (X58,2), low focal plane,
31. *Cricotriporites fragilis* van Hoeken-Klinkenberg 1966, Amaogugu 1.1 (J51),
32. *Cricotriporites macroporus* Jaramillo & Dilcher 2001, Amaogugu 1.1 (V35,2),
33. *Cricotriporites* cf. *macroporus* Jaramillo & Dilcher 2001, Okigwe B4.1 (K58),
34. *Cricotriporites* cf. *macroporus* Jaramillo & Dilcher 2001, Okigwe B4.1 (K58), details of rugulae,
35. *Cricotriporites* aff. *minutiporus* (Muller 1968) Jaramillo & Dilcher 2001, Amaogugu 1.1 (F34,4),
36. *Echitriporites suescae* (Van der Hammen 1954) Cárdenas, de La Parra & Espinoza-Campuzano 2019, Okigwe B2.1 (T32),
37. *Echitriporites suescae* (Van der Hammen 1954) Cárdenas, de La Parra & Espinoza-Campuzano 2019, Okigwe B2.1 (M38,3), high focal plane,
38. *Echitriporites suescae* (Van der Hammen 1954) Cárdenas, de La Parra & Espinoza-Campuzano 2019, Okigwe B2.1 (M38,3), low focal plane,
39. *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964, Okigwe B2.1 (T41),
40. *Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964, Okigwe B2.1 (N50),
41. *Echitriporites trianguliformis* var. *orbicularis* Jaramillo & Dilcher 2001, Okigwe B2.1 (P48,3),
42. *Echitriporites trianguliformis* var. *orbicularis* Jaramillo & Dilcher 2001, Okigwe B2.1 (Q33,2),
43. *Momipites* cf. *africanus* van Hoeken-Klinkenberg 1966, Ozuitem 3.1 (V51,2).

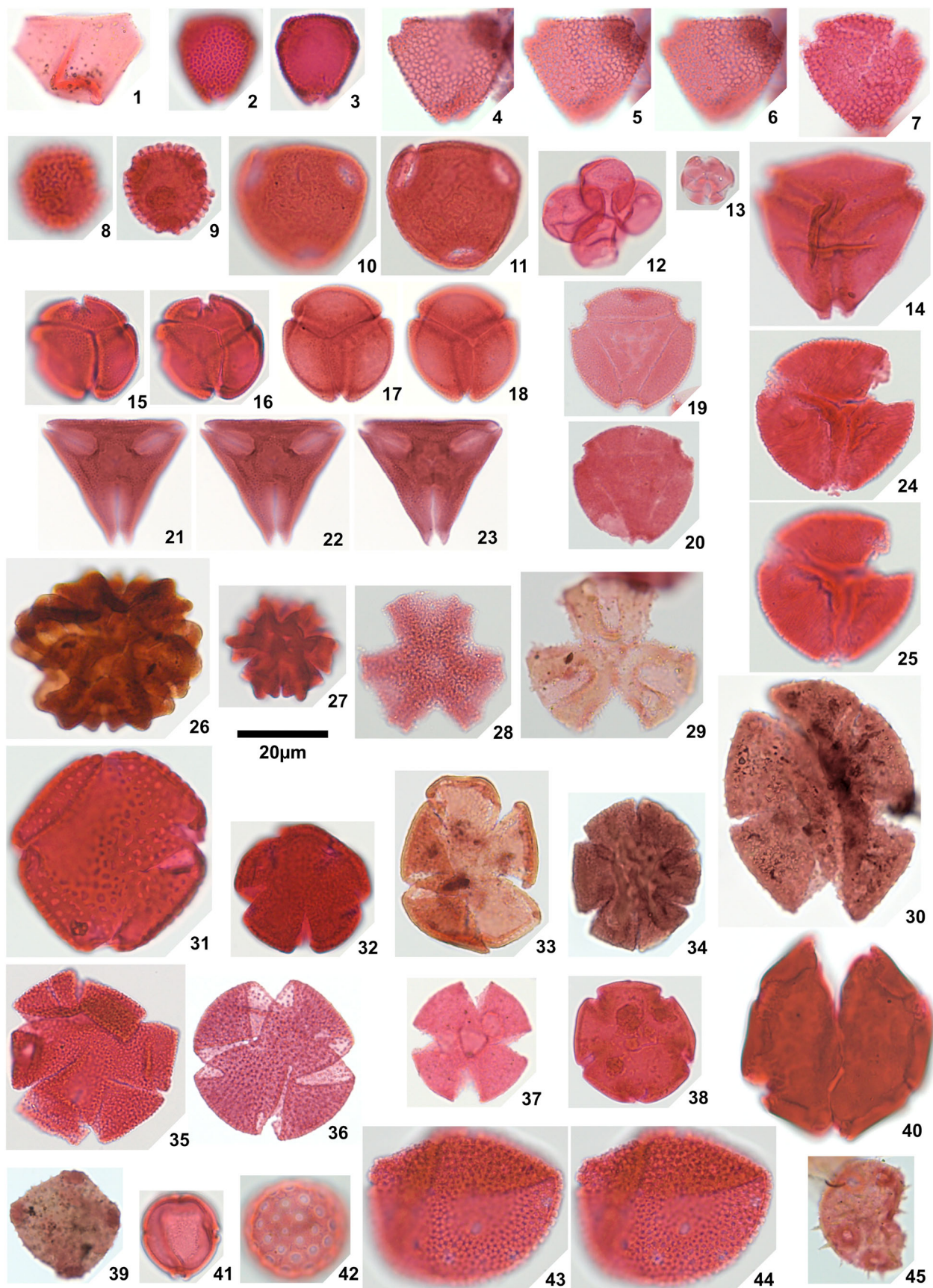


Plate 8.

1. *Proteacidites* cf. *cooksonii* Salard-Cheboldaeff 1978, Okigwe B4.1 (X60),
2. *Retitriporites* aff. *simplex* Van der Kaars 1983, Ameke 11.1 (V67,1), high focal plane,
3. *Retitriporites* aff. *simplex* Van der Kaars 1983, Ameke 11.1 (V67,1), mid focal plane,
4. *Retitriporites irregularis* sp. nov., Ozuiem 6.1 (H40,4), holotype, high focal plane,
5. *Retitriporites irregularis* sp. nov., Ozuiem 6.1 (H40,4), holotype, mid focal plane,
6. *Retitriporites irregularis* sp. nov., Ozuiem 6.1 (H40,4), holotype, low focal plane,
7. *Retitriporites irregularis* sp. nov., Ozuiem 3.1 (M43), paratype, low focal plane,
8. *Retitriporites 'robustus'*, Ameke 1.1 (M65,1), high focal plane,
9. *Retitriporites 'robustus'*, Ameke 1.1 (M65,1), mid focal plane,
10. *Rugulitriporites 'umbrabilis'*, Ozuiem 6.1 (V48,1), high focal plane,
11. *Rugulitriporites 'umbrabilis'*, Ozuiem 6.1 (V48,1), low focal plane,
12. *Triporotetradites* cf. *scabratus* van Hoeken-Klinkenberg 1964, Amaogugu 7.1 (V53,3),
13. *Heterocolpites* cf. *laevigatus* Salard-Cheboldaeff 1978, Ozuiem 6.1 (P55,1),
14. *Syncolporites sowunmiai* Jan du Chêne et al. 1978, Ozuiem 6.1 (V45),
15. *Syncolporites marginatus* van Hoeken Klinkenberg 1964, Ozuiem 3.1 (J37,4), high focal plane,
16. *Syncolporites marginatus* van Hoeken Klinkenberg 1964, Ozuiem 3.1 (J37,4), low focal plane,
17. *Syncolporites marginatus* van Hoeken Klinkenberg 1964, Ozuiem 6.1 (T40), high focal plane,
18. *Syncolporites marginatus* van Hoeken Klinkenberg 1964, Ozuiem 6.1 (T40), mid focal plane,
19. *Syncolporites angusticolpatus* sp. nov., Okigwe A7.1 (O66,1), holotype,
20. *Syncolporites angusticolpatus* sp. nov., Ozuiem 3.1 (P62,3), paratype,
21. *Syncolporites rostro* sp. nov., Ozuiem 3.1 (X36,1), holotype, high focal plane,
22. *Syncolporites rostro* sp. nov., Ozuiem 3.1 (X36,1), holotype, mid focal plane,
23. *Syncolporites rostro* sp. nov., Ozuiem 3.1 (X36,1), holotype, low focal plane,
24. *Syncolporites* sp., Amaogugu 1.1 (L39,2), high focal plane,
25. *Syncolporites* sp., Amaogugu 1.1 (L39,2), mid focal plane showing details of the exine,
26. *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966, Okigwe A1.1 (N56),
27. *Ctenolophonidites* aff. *costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966, Ameke 1.1 (V57,3),
28. *Ctenolophonidites?* *'apocolpius'*, Okigwe A7.1 (R46,2),
29. *Ctenolophonidites?* *'echicolpatus'*, Okigwe B7.1 (J50,4),
30. *Echistephanocolpites echinatus* Wijmstra 1971, Okigwe B7.1 (D37,1),
31. *Foveostephanocolpites* sp. 1, Ameke 1.1 (K55,2),
32. *Foveostephanocolpites* sp. 2, Ozuiem 3.1 (Q62),
33. *Psilastephanocolpites* sp., Okigwe B6.1 (O39,1),
34. *Retistephanocolpites regularis* van Hoeken-Klinkenberg 1966, Okigwe B7.1 (F46,2),
35. *Retistephanocolpites williamsi* Germeraad et al. 1968, Ozuiem 3.1 (S42,4),
36. *Scabrastephanocolpites vanegensis* Van der Hammen & Garcia 1966, Okigwe B1.1 (O33,1),
37. *Scabrastephanocolpites 'irregularis'*, Okigwe A5.1 (U50,1),
38. *Tetracolporites* cf. *spectabilis* Pocknall & Mildenhall 1984, Ozuiem 3.1 (M35),
39. *Echistephanoporites alfonsi* Leideimyer 1966, Okigwe B7.1 (N40,1),
40. *Pachydermites diderixii* Germeraad et al. 1968, Ameke 1.1 (U44,1),
41. *Retistephanoporites* sp., Ameke 1.1 (M44,2),
42. *Chenopodipollis multiplex* Weyland & Pflug 1957, Okigwe A7.1 (W48,2),
43. *Clavaperiporites* cf. *jacobi* Ramanujam 1966, Amaogugu 1.1 (E48,4), high focal plane showing *Croton* pattern,
44. *Clavaperiporites* cf. *jacobi* Ramanujam 1966, Amaogugu 1.1 (E48,4), mid focal plane showing heterobrochate infrareticulum,
45. *Echiperiporites* aff. *scabrannulatus* Jaramillo et al. 2010, Okigwe B6.1 (M57).

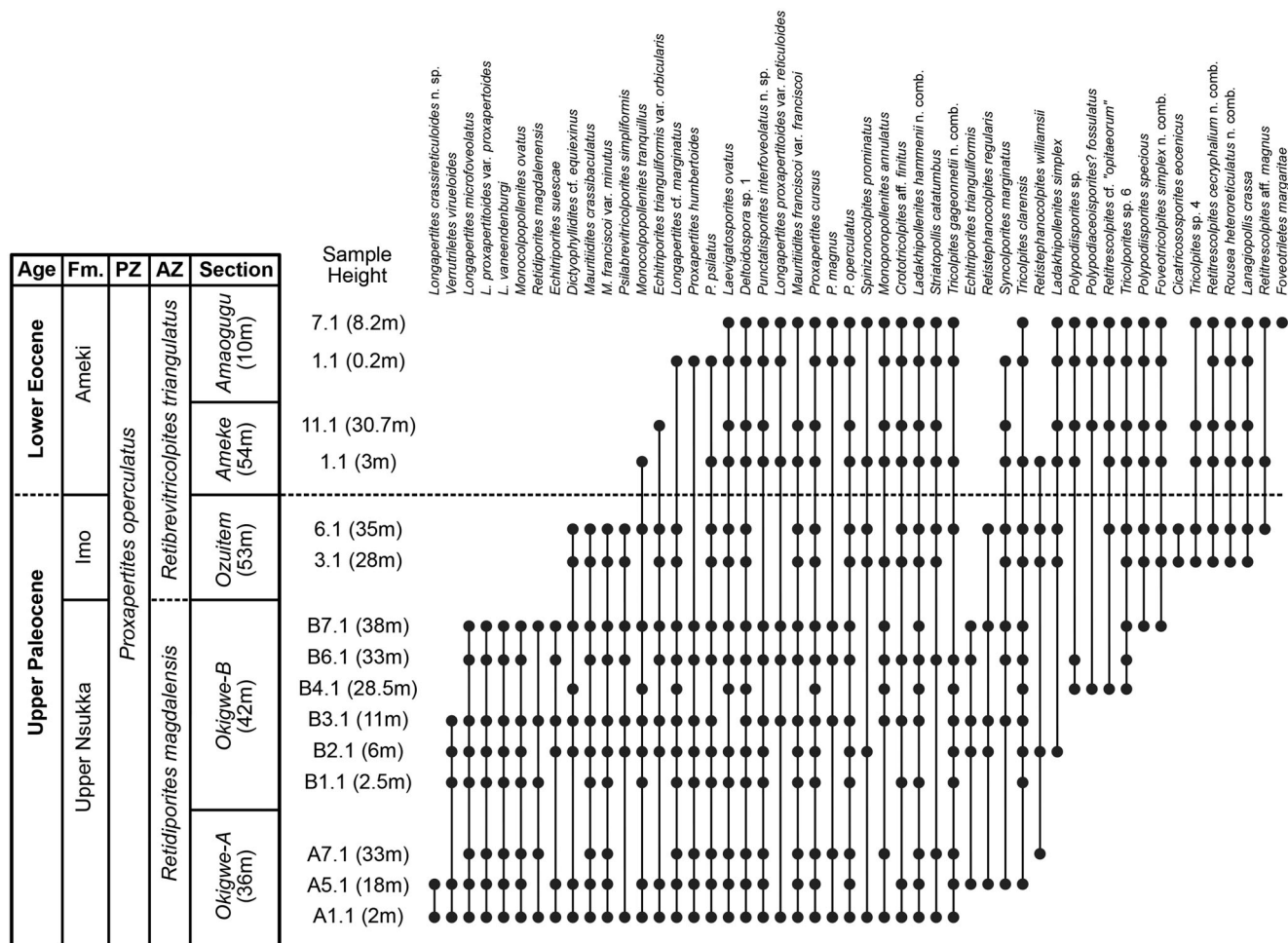


Figure 2. Range chart of 50 selected taxa in the sediment samples studied here. Section heights from Oboh-Ikuenobe et al. (2005) and sample heights from Table 1. Samples positioned schematically for clarity. The Palaeocene–Eocene boundary is placed between the Imo and Ameke formations following Nwajide (1990) and Oboh-Ikuenobe et al. (2005) and shown as a dashed line to indicate uncertainty. Fm. = formation; PZ = Pantropical Zone of Germeraad et al. (1968); AZ = Atlantic Zone of Germeraad et al. (1968).

separated by their age, and those from the Selandian Okigwe A and B sections do not overlap with samples from younger material, but also cluster by formation: samples from the Ameke Formation plot close to each other despite being from two different sections (Ameke and Amaogugu) (Figure 3b). This highlights that further work should explore whether time or lithology exerts the greater control on palynological composition in these sediments. One sample (Okigwe B 4.1) from the Okigwe B section sits as an outlier relative to the other samples taken from the Upper Nsukka Formation (Figure 3b) and is dominated by *Monoporopollenites annulatus* (Van der Hammen 1954) Jaramillo & Dilcher 2001 (48%, Plate 4, figure 8, Poaceae) and *Luminidites microreticulatus* sp. nov. (24%, Plate 3, figures 15–20, Arecaceae). As highlighted by Morley (2000, p. 135), ‘Suggestions regarding the character of other vegetation types at this time should be regarded with caution, since evidence is very fragmentary’, and a single sample is perhaps the most fragmentary evidence possible, but at the very least it highlights a need to investigate – most likely through dense re-sampling of the section itself – the possibility either of open habitats or of grass-dominated palm swamps in the West African Palaeocene.

5. Conclusions

1. A rich and generally well-preserved palynoflora consisting of 29 spores, two gymnosperm pollen grains, and 138 angiosperm pollen grains is described. Two new spore species are proposed, and one new genus and 18 new species of angiosperm pollen are proposed.
2. The composition of the palynoflora is consistent with the pantropical *Proxapertites operculatus* Zone (Germeraad et al. 1968). Samples from the Upper Nsukka Formation (Table 1) may represent the *Retidiporites magdalenensis* Atlantic Zone of Germeraad et al. (1968), while samples from the Imo and Ameke formations (Table 1) may represent the *Retibrevitricolpites triangulatus* Atlantic Zone of Germeraad et al. (1968).
3. The richness of the samples ranges from 29 (Okigwe B4.1) to 76 (Amaogugu 1.1), and when compared at 150 specimens following rarefaction (Table 1), samples from the Palaeocene (Upper Nsukka and Imo formations) have an average richness of 37.4, while samples from the Eocene Ameke Formation have an average richness of 54.7.
4. The top-ranked taxa in samples from the Okigwe A and Okigwe B sections are dominated by pollen with

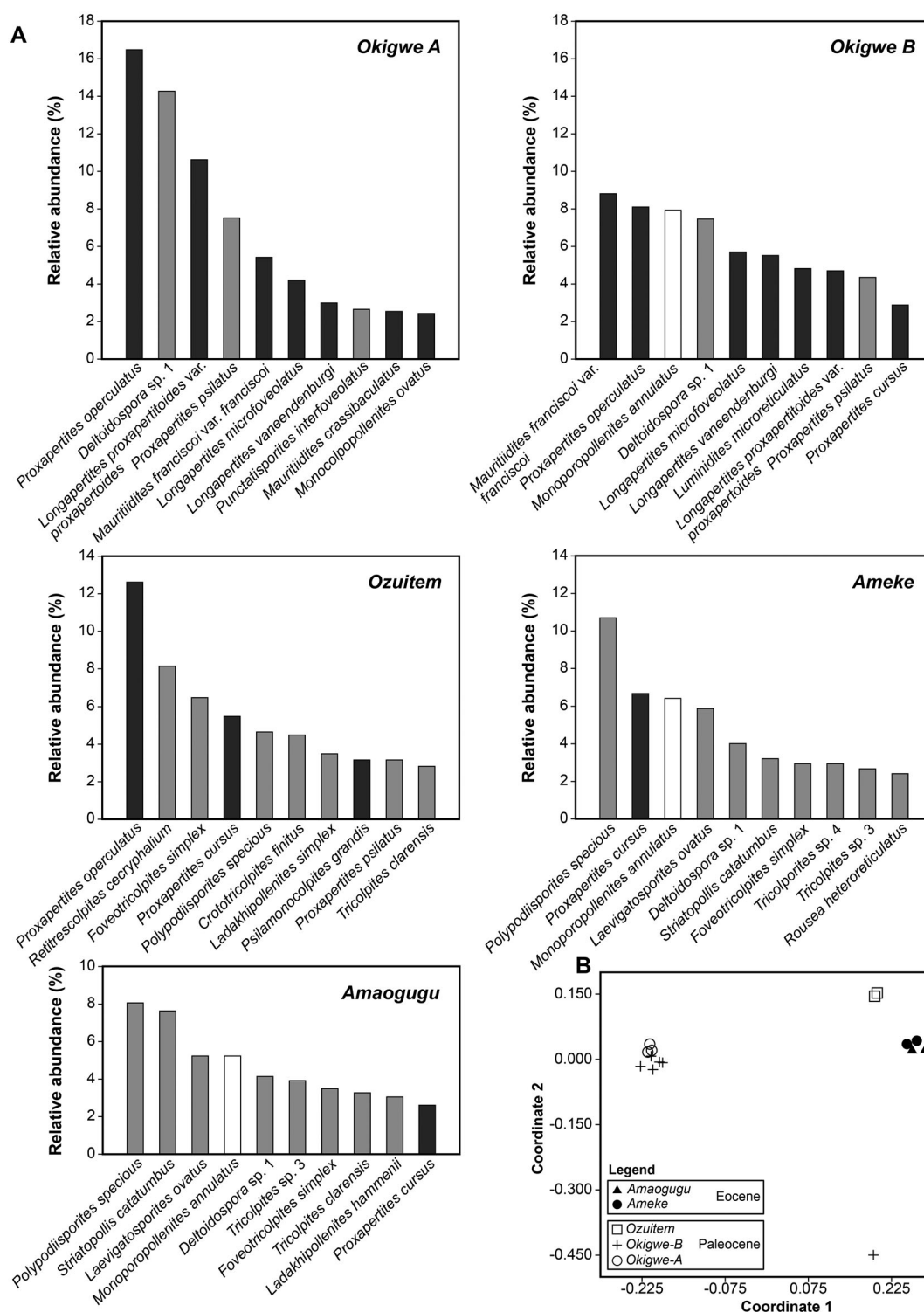


Figure 3. (A) Relative abundance (reported as a percentage) of top-ranked taxa from each of the five sections studied here. Pollen grains with botanical affinities to the Arecaceae (palms) and Araceae (arums; *Proxapertites operculatus* and *P. cursus*) are shown in dark grey, Poaceae (grasses) are shown in white, pollen grains and spores with other botanical affinities are shown in light grey. (B) Non-metric multidimensional scaling ordination of the 15 sediment samples analysed here (stress = 0.116).

botanical affinities to the Arecaceae (palms) and Araceae (arums), while the number of top-ranked taxa with botanical affinities to palms and arums is lower in samples from the Ozuitem, Ameke and Amaogugu sections (Figure 3a). The general vegetation type represented by the palynoflora as a whole consists of palm-dominated swamps, perhaps with mangroves.

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