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Descriptive systematics of Upper Paleocene–Lower Eocene pollen and spores from the northern Niger Delta, southeastern 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 20\textsuperscript{th} 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 fifteen sediment sediment samples spanning the Upper Paleocene–Lower Eocene of southeastern 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 Paleocene to the Eocene in this region. Samples from the Paleocene
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
Paleocene in the Neotropics.

Key words: Tropical rainforests; West Africa; vegetation evolution; palaeoecology;
taxonomy

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 Paleocene 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 focused 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,b; 1957a,b; 1958; van Hoeken-Klinkenberg 1964; Van der
Hammen and Wymstra 1964; Belskey et al. 1965; Jardine and Magloire 1965; Clarke
1966; Leidelmeyer 1966; Van der Hammen and Garcia 1966; van Hoeken-
Klinkenberg 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 (Germereaad et al. 1968). It was suggested that the boundaries of each palynological zone are marked by the first stratigraphic 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 biostratigraphic value at large geographic scales (Germereaad et al. 1968).

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*, *Psilatritporites*, *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 2011; Sigwart et al. 2018). Such taxonomic problems are perhaps of less concern in a stratigraphic context because of the focus on a relatively small number of taxa. For example, while Germereaad et al. (1968) noted the high diversity of pollen and spore morphotypes encountered in palynological preparations from the tropical Cretaceous–Palaeogene, their concern was with pruning this diversity down and focussing on taxa that have biostratigraphic 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.” (Germereaad 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 stratigraphic succession. Consequently, workers have begun revising the taxonomy of tropical palynofloras in order 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-Camina et al. 2010; D’Apolito et al. 2021), some as part of wider studies of tropical vegetation evolution and biogeography (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 timescales (Jaramillo et al. 2006), biogeographical observations that the latitudinal diversity gradient among plants was reduced in the Paleocene compared to the Holocene (Jaramillo et al. 2007) and that higher temperatures and more seasonally dry climates during the Paleocene–Eocene Thermal Maximum led to the northward range expansion of tropical plants (Korasidis 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 20th century on western African tropical palynology (e.g. Belsky et al. 1965; Jardine and Magloire 1965; Boltenhagen, 1967; Adegoke 1969; Jan du Chêne 1977; Legoux 1978; Salard-Cheboldaeff 1979), while recent palynological studies in tropical West Africa have focused on stratigraphy and basin evolution, often in the context of oil exploration.
(e.g. Ikegwuonu and Umeji 2016; Lucas 2017; Chiadikobi et al. 2018; Ikegwuonu et al. 2020; Bolai et al. 2020; Agharanya et al. 2022). Nevertheless, in order 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 fifteen sediment samples spanning the Upper Paleocene–Lower Eocene of southeastern Nigeria. This interval of time was a period of major plant diversification in tropical West Africa (Morley 2000), and our aims are as follows: (1) describe the pollen and spores preserved in these samples and revise the systematics where necessary; and (2) make some preliminary observations on the general character of the palynoflora—including recovery, diversity and composition—in order to guide future work.

2. Materials and methods
Fifteen sediment samples were examined through the Upper Paleocene–Lower Eocene of the northern Niger Delta (formerly the Anambra Basin), Nigeria (Fig. 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%) acid, oxidised with Schultze Solution, sieved at 10µm and stained with safranine. 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 40x 0.85Na objective and a 60x 1.4Na 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 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 Palaeogene fossil pollen and spores of tropical West Africa (van Hoeken-Klinkenberg 1964; Belskey et al. 1965; Jardine and Magloire 1965; Clarke 1966; van Hoeken-Klinkenberg 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-Cheboldaeff 1979; Doyle et al. 1982; Boltenhagen and Salard-Cheboldaeff 1987; Oboh and Salami 1989; Salami 1990; Salard-Cheboldaeff 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 have been observed and measured and the material is of sufficient quality. We made one exception to this in proposing *Syncolporites rostron* n. sp., 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.

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 provided. 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 side, 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 written in italic typeface between
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, fig. 1

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

Description. Monad, amb sub-circular–oval; alete, sporoderm 1-layered, exospore 2µm thick; surface ornamentation rugulate over entire body, muri 3–10µm in length, 1µm in width, grooves 0.5µm in width.

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

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

Monolette Spores

Genus Cicatricososporites Pflug and Thomson in Thomson and Pflug 1953

Type. Cicatricososporites eocenicus (Selling 1944) Jansonius and Hills 1976

Cicatricososporites eocenicus (Selling 1944) Jansonius and Hills 1976

Plate 1, figs 2–3

Synonymy.

Cicatricososporites norrisii Srivastava 1971

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

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

**Dimensions.** Equatorial diameter 45µm, polar axis 31µm; 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, fig. 4

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

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

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

**Comparisons.** Laevigatosporite 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.** Marattiacae (Balme 1995; Wang et al. 2001)

Laevigatosporites ovatus Wilson and Webster 1946

Plate 1, fig. 5

**Diagnosis.** Monolete, equatorial diameter 34µm, 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 1–1.5µm thick; surface ornamentation laevigate.

**Dimensions.** Equatorial diameter 29–(34)–39µm; 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 and Gelletich 1933 ex Potonié 1956, emend. Kahn and Martin 1972

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

*Polypodiisporites specious* Sah 1967

Plate 1, fig. 6

**Synonymy.**

*Polypodiisporites* aff. *specious* Jaramillo and Dilcher 2001

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

**Description.** Monad, lateral shape oval and plano-convex, reniform; monolete, laesura 20µm; sporoderm 1-layered, exospore 0.5–1µm thick; surface ornamentation psilate on proximal face, rest of spore verrucate, verrucae 1–3.5µm in diameter, 0.5–1µm high and spaced up to 1.5µm apart, verrucae irregularly shaped, some verrucae rounded, others polygonal with up to 6 distinct faces, verrucae denser on the distal face (spaced <0.5µm apart) than elsewhere on the spore.

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

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

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

**Botanical affinity.** Polypodiaceae (D’Apolito et al. 2020).

*Polypodiisporites sp.*

Plate 1, fig. 7

**Diagnosis.** Monolete, equatorial diameter 28µm, 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 (20µm); sporoderm 1-layered, exospore 1µm thick; surface ornamentation granulate–verrucate, verrucae scarce and isolated, 0.5µm high and
irregularly shaped, granulæ faint and distributed densely over the spore surface, granulæ denser on the proximal face.

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

**Comparisons.** *Scabramonoletes microreticuloides* Ramanujam 1966 lacks verrucae and has granulæ which fuse into a microreticulum.

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

### Trilete Spores

**Genus Apiculatasporites Ibrahim 1933**

**Type.** *Apiculatasporites spinulistriatus* Potonié and Kremp 1955

**Apiculatasporites sp. 1**

Plate 1 fig. 8

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

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

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

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

**Apiculatasporites sp. 2**

Plate 1, fig. 9

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

**Description.** Monad, amb triangular and slightly convex; trilete, kyrtomate, kyrtome surrounds trilete mark, 1.5µm wide; sporoderm 1-layered, exospore 1.5µm thick; surface ornamentation echinate, spines 4µm in height and 2µm in diameter, spines taper sharply from a relatively wide base to a narrow tip, spines distributed over the spore surface at 1–5µm intervals.
**Dimensions.** Equatorial diameter 18µm; nm: 1; no: 11.

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

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**Genus Deltoidospora** Miner 1935

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

**Deltoidospora sp. 1**

Plate 1, fig. 10–11

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

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

**Dimensions.** Equatorial diameter 27–(35)–42.5µm; 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, fig. 12

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

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

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

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

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

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

**Type.** *Densoisporites velatus* (Weyland and Krieger 1953) Potonié 1956
**Densoisporites sp.**
Plate 1, figs 13–14

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

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

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


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

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**Genus Dictyophyllidites** Couper 1958 emend. Dettman 1963

**Type.** *Dictyophyllidites harrisii* Couper 1958

**Dictyophyllidites cf. equiexinus** (Couper 1958) Dettmann 1963
Plate 1, fig. 15

**Diagnosis.** Trilete, equatorial diameter 65µm, 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 3–4.5µm thick; surface ornamentation psilate.

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

**Comparisons.** *Dictyophyllidites equiexinus* (Couper 1958) Dettmann 1963 has longer laesurae and a triangular amb. *Psilatriletes* Van der Hammen 1954 ex Potonié 1956 has laesurae that extend between 3/4 and 4/4 of the amb radius. *Calamospora* Schopf
Wilson and Bentall 1944 has a thin sporoderm, less than 2µm in spores less than 100µm 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, figs. 16–17

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

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

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

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

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

**Distaverrusporites? sp.**

Plate 1, fig. 18

**Diagnosis.** Trilete, equatorial diameter 32µm, 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 (9µm); sporoderm 1-layered, exospore 1µm thick; surface ornamentation at the equator verrucate, verrucae 1–5µm wide and 1–4µm high, surface ornamentation on proximal and distal faces scabrate.

**Dimensions.** Equatorial diameter 32µm; 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 *Foveotriletes* Potonié 1956

**Type.** *Foveotriletes scrobiculatus* (Ross ex Weyland and Krieger 1953) Potonié 1956

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

![Plate 1, fig. 19](image)

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

**Description.** Monad, amb sub-circular; trilete, laesurae straight and slightly indistinct, do not reach equator, unequal length (5–17µm); sporoderm 1-layered, exospore 2µm thick; surface ornamentation of exospore foveo- reticulate, lumina 0.5–2µm, muri 0.5µm anastomosing across the spore.

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

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

*Foveotriletes sp.*

![Plate 1, fig. 20](image)

**Diagnosis.** Trilete, sub-triangular, equatorial diameter 43.5µm, 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 1µm; surface ornamentation foveolate, lumina polygonal and densely distributed over the entire spore surface.

**Dimensions.** Equatorial diameter 38.5–(43.5)–48µm; 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 phlebopteroides* Couper 1958

*Matonisporites sp.*

Plate 1, figs 21–22

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

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

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

**Comparisons.** *Matonisporites phlebopteroides* Couper 1958 is wholly psilate, smaller, has a more continuous and pronounced thickening of the exine in the interradial 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, figs 23–24

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

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

**Dimensions.** Equatorial diameter 30µm; nm: 1; no: 3.
**Comparisons.** *Microreticulatisporites uniformis* Singh 1964 has a coarser reticulum (lumina 2–3µm wide).

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

**Genus Osmundacidites Couper 1953 emend. Norris 1986**

**Type.** *Osmundacidites wellmanii* Couper 1953

*Osmundacidites minor* Jaramillo and Dilcher 2001

Plate 1, figs 25–26

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

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

**Dimensions.** Equatorial diameter 30–(31)–32µm; 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 and Dilcher 2001

Plate 1, figs 27–28

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

**Description.** Monad, amb sub-triangular, cingulum uniform in thickness, 4.5µm in the interradial regions and at the apices of the outline; trilete, commissure distinct, laesurae do not extend into cingulum, kyrtoame present and formed of fused verrucae; sporoderm 1-layered, exospore 1.5µm 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 and Dilcher 2001 except for the measurements of the cingulum, which is thickened in the interradial region in *Polypodiaceoisporites? fossulatus* Jaramillo and Dilcher 2001.

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

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

### *Polypodiaceoisporites “striatus”*
Plate 1, figs 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 interradial 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.** *Polypodiaceoisporites pseudopsilatus* Lorente 1986 is rugulate on the distal face but psilate on the proximal face.

**Material.** Amaogugu 7.1 (T44), polar view.

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**Genus Psilatriletes Van der Hammen 1954 ex Potonié 1956**

**Type.** *Psilatriletes detortus* (Weyland and Krieger) Potonié 1956

### *Psilatriletes brevilaesuratus* n. sp.
Plate 2, fig. 1
Synonymy.

*Psilatriletes* “brevilaesuratus” Jaramillo et al. 2014

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

**Etymology.** After the short laesurae.

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

**Dimensions.** Equatorial diameter 75–(79)–83µm; 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, fig. 1.

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

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**Genus Pteridacidites Sah 1967**

**Type.** *Pteridacidites africanus* Sah 1967

**Pteridacidites sp. 1**

Plate 2, figs 2–3

**Diagnosis.** Trilete, equatorial diameter 36µm, 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 1.5µm wide, laesurae straight and long, do not extend into cingulum (12µm), cingulum 4µm thick and psilate; sporoderm 1-layered, exospore 1µm; surface ornamentation on the distal face verrucate, verrucae 3–5µm wide and 1–4µm high, distributed 1–3µm over the spore surface, surface ornamentation on the proximal face granulate–verrucate, granules distributed sparsely over the spore.
surface, verrucae 1µm high and 0.5µm wide distributed sparsely over the spore surface.

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

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

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

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**Pteridacidites sp. 2**

Plate 2, figs 4–5

**Diagnosis.** Trilete, equatorial diameter 31µm, 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 1µm short of the cingulum (13µm), cingulum 3µm thick and psilate; sporoderm 1-layered, exospore 1µm; surface ornamentation on the distal face rugulate, surface ornamentation on the proximal face verrucate, verrucae 1µm high and <0.5µm wide distributed densely over the spore surface.

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

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

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

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**Genus Punctatisporites Ibrahim 1933**

**Type.** *Punctatisporites punctatus* (Ibrahim 1932) Ibrahim 1933

**Punctatisporites interfoveolatus n. sp.**

Plate 2, figs 6–9

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

**Etymology.** After the foveolate interradial area.

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

**Dimensions.** Equatorial diameter 34–(39)–43.5µm; 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, figs 6–7, polar view; paratypes Okigwe B1.1 (E43, Plate 2, fig. 8, polar view; X50, Plate 2, fig. 9, polar view).

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

**Type.** *Verrucosisporites verrucosus* Ibrahim 1933

*Verrucosisporites major* (Couper 1958) Burden and Hills 1989

Plate 2, figs 10–11

**Synonymy.**

*Leptolepidites major* Couper 1958

*Converrucosisporites saskatchewanensis* Pocock 1962

*Verrucosisporites rarus* Burger 1966

**Diagnosis.** Trilete, sub-circular, equatorial diameter 32µm, 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 (13µm); sporoderm 1-layered, exospore 1µm thick; surface ornamentation verrucate. verrucae at the equator rounded (1–1.5µm high), verrucae elsewhere polygonal 1–3µm wide, and coalescing into rugulae on the distal face, surface ornamentation around the laesurae granulate.

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

**Comparisons.** *Tuberositriletes montuosus* Doring 1964 is triangular and larger (60–78µm), *Tuberositriletes verrucatus* Jaramillo and 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. verricosus Ibrahim 1933**

Plate 2, fig. 12

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

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

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

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

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

**Genus Verrutriletes Pierce 1961**

**Type.** *Verrutriletes verus* Pierce 1961

**Verrutriletes virueloides Jaramillo et al. 2007)**

Plate 2, fig. 13

**Synonymy.**

*Verrutriletes “viruelensis”* Instituto Colombiano del Petróleo (Colombian Petroleum Institute)

**Diagnosis.** Trilete, equatorial diameter 44µm, 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 (10µm); sporoderm 1-layered, exospore 1µm thick; surface ornamentation scabrate, scabrae distributed sparseley over the spore surface (spaced 1–2µm apart).
Dimensions. Equatorial diameter 44µm; 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, fig. 14

**Synonymy.**

*Triporolletes blanensis* (Pacltová) Srivastava 1975

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

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

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

Material. Amaogugu 1.1 (U44), polar view.

Botanical affinity. Marchantiaceae (Elsawi and Schrank 2008).

Gymnosperm Pollen

Genus *Cycadopites* Wodehouse 1933 emend. Herbst 1965

Type. *Cycadopites follicularis* Wilson and Webster 1946

*Cycadopites deterius* (Balme 1957) Pocock 1970

Plate 2, fig. 15

**Synonymy.**

*Entylissa deterius* Balme 1957

**Diagnosis.** Monocolpate, elliptic, atectate, psilate, length 49µm, width 22µm.
Description. Monad, bilateral, heteropolar, amb elliptic; monocolpate, colpus long, borders curved, ends flared; exine atectate, 0.5µm thick; surface ornamentation psilate.

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


**Genus Cyclusphaera Elisk 1966**

Type. *Cyclusphaera euribeii* Elisk 1966

*Cyclusphaera scabrata* Jaramillo and Dilcher 2001

Plate 2, fig. 16

Synonymy.

*Cyclusphaera cf. euribeii* Schuler and Doubinger 1970

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

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

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

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

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

Angiosperm Pollen

Inaperturate Pollen

**Genus Inaperturopollenites Pflug and Thomson in Thomson and Pflug 1953**

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

*Inaperturopollenites fossulatus* n. sp.
Plate 2, figs 17–18

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

**Etymology.** After the fossulate surface ornamentation.

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

**Dimensions.** Largest dimension 24.5–(27)–29µm; 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, fig 17–18.

*Inaperturopollenites?* sp. 1

Plate 2, fig. 19

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

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

**Dimensions.** Largest dimension 50µm; 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, fig. 20

**Diagnosis.** Inaperturate?, oval, tectate, clavate with scattered gemmae, largest dimension 95µm.
Description. Monad, amb oval; inaperturate?; exine tectate, columellae indistinct, nexine 0.5µm thick, tectum 1µm thick; surface ornamentation clavate, clavae 1µm wide, 2µm high, densely distributed over the grain surface, scattered gemmae, 8µm wide, 7µm high.

Dimensions. Largest dimension 95µm; 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 (95µm), but the material is insufficient to erect a new species.

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

**Genus Praedapollis Boltenhagen and Salard 1973**

**Type.** *Praedapollis africanus* Boltenhagen and Salard 1973

*Praedapollis africanus* Boltenhagen and Salard 1973

Plate 2, figs 21–22

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

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

Dimensions. Inner body smallest dimension 28µm, largest dimension 35µm wide, outer body smallest dimension 42µm, largest dimension 46µm; 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) collumellae. *Periretiricolpites anambraensis* Jan du Chêne et al. 1978 is tricolpate. *Praedapollis africanus* Boltenhagen and Salard 1973 is described as triporate (Jansonius and Hills 1976, card
but the specimens examined here lack endoapertures. The holotype specimen of *P. africanus* Boltenhagen and 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 and Salard 1973 that consists of an inner body with apertures together with an enclosing reticulum. On specimens of *P. africanus* Boltenhagen and Salard 1973 recovered from the Neogene Niger Delta, Legoux (1978, p. 280) commented “Dans certains cas, on devine des « encoches » sur les 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 dechire laisse entrevoir une grande partie de la nexine: aucun port n'est visible.” [In some cases, we can guess “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 and 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 and Salard 1973 to Arapatiella (Fabaceae). However, in Arapatiella the reticulum is attached to the inner body whereas in *P. africanus* Boltenhagen and 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 and Jan du Chêne 1975

Plate 3, fig. 1

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

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 1µm thick; surface ornamentation micropitted, coarsening slightly to form rugulae in proximal area of the grain, muri 1.5µm wide, extent of rugulae slightly variable, sometimes covering up to half the grain.

Dimensions. Equatorial diameter 43–(48)–53µm; 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 and Garcia 1966

Plate 3, fig. 2

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

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 1µm thick; surface ornamentation foveolate, lumina 0.5–1µm densely and evenly distributed, some lumina coalesce to form irregular grooves.
**Dimensions.** Equatorial diameter width 42µm, equatorial diameter length 49.2–(54)–58µm; 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 and Garcia 1966

Plate 3, figs 3–4

**Synonymy.**

*Longapertites proxapertitoides var. reticuloides* González Guzmán 1967

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

**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 1µm thick; surface ornamentation reticulate, heterobrochate, lumina 1–3µm wide, muri 1µm wide, lumina gradually increase in size from the distal to the proximal face.

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

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

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

*Longapertites vaneendenburgi* Germaraad et al. 1968

Plate 3, fig. 5

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

**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 1µm thick; surface ornamentation micropitted, lumina 0.4µm densely and evenly distributed.

**Dimensions.** Equatorial diameter 60.5–(70)–78.5µm; nm: 5; no: 121.
Botanical affinity. Areceae (Germeraad et al. 1968; Morley 2000).

Longapertites cf. marginatus van Hoeken-Klinkenberg 1964
Plate 3, fig. 6

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

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 1µm 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 1µm, muri 1µm, in some specimens the variation in lumina size is not prominent and the lumina are mostly 1µm with a very subtle coarsening towards the proximal area of the grain.

Dimensions. Equatorial diameter 30.5–(31.5)–33µm; 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 1µm 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 Paleocene of Sudan (Assemblage Zone IV of Eisawi and Schrank (2008)) L. marginatus var. parvus Schrank 1994 has uniformly fine foveolate surface ornamentation.

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

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

Longapertites crassireticuloides n. sp.
Plate 3, figs 7–8

Synonymy.

Longapertites sp. 1 Jaramillo and Dilcher 2001

Diagnosis. Monocolpate (longaperturate), suboblate, tectate, surface ornamentation reticulate curvimurate, heterobrochate, equatorial diameter 42µm.
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 0.5µm in diameter spaced 0.5µm apart, exine 2µm thick, nexine 0.5µm sexine 1.5µm; surface ornamentation reticulate, curvimurate, heterobrochate, lumina 1–5µm, muri 1µm wide.

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

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

Material. Holotype Okigwe A5.1 (M33,4), Plate 3, fig. 7, paratype Okigwe A5.1 (G33,3), Plate 3, fig. 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, figs 9–10

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

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

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

Comparisons. *Mauritiidites franciscoi* var. franciscoi van Hoeken-Klinkenberg 1964 is echinate–baculate with finer sculptural elements (1–2.5µm wide). *Mauritiidites franciscoi* var. minutus Van der Hammen and Garcia 1966 is smaller and has finer sculptural elements (0.5–2µm wide, 1–3µm high). *Mauritiidites crassibaculatus* Van Hoeken-Klinkenberg 1964 is larger and has longer baculae (6µm 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) (32–55µm).

**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, figs 11–13

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

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

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

**Comparisons.** *Mauritiidites crassibaculatus* Van Hoeken-Klinkenberg 1964 has thicker (3µm) baculae. *Mauritiidites franciscoi* var. *minutus* Van der Hammen and 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 and 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 and Garcia 1966 primarily on the basis of their large size (polar view length >35µm) and longer sculptural elements (>3µm).

**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 and Garcia 1966

Plate 3, figs 14–16

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

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

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

Comparisons. Mauritiidites crassibaculatus Van Hoek en-Klinkenberg 1964 is larger and has longer (6µm) and thicker (3µm) baculae. Mauritiidites franciscoi var. franciscoi van Hoeken-Klinkenberg 1964 is larger, 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 and Garcia 1966 in the material studied here, particularly in surface ornamentation, but specimens assigned to M. franciscoi var. minutus Van der Hammen and 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 <35µm) and shorter sculptural elements (<3µm).

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

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


Type. Monocolpopollenites tranquillus (Potonié 1934) Jansonius and Hills 1976

Monocolpopollenites ovatus Jaramillo and Dilcher 2001

Plate 3, fig. 17

Diagnosis. Monocolpate, elliptic, tectate, micropitted, faintly verrucate at equator, equatorial diameter 36µm.
Description. Monad, bilateral, heteropolar, amb elliptic; monocolpate, colpus long, extending to the poles, borders slightly curved; exine tectate, collumellae indistinct, <1µm thick; surface ornamentation micropitted, lumina <0.5µm spaced 0.5µm apart, surface ornamentation occasionally faintly verrucate at the equator, verrucae 1–3µm wide and 1–2µm high.

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

Comparisons. Arecipites regio Jaramillo and 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 and Hills 1976
Plate 3, fig. 18

Synonymy.

Pollenites tranquillus Potonié 1934

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

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

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

Comparisons. Psilamonocolpites medius (Van der Hammen 1956) Van der Hammen and Garcia 1966 is intectate.

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

Botanical affinity. Arecaceae (Morley 2000).

Genus Psilamonocolpites Van der Hammen and Garcia 1966
Type. Psilamonocolpites medius (Van der Hammen 1954) Van der Hammen and Garcia 1966

Psilamonocolpites grandis Van der Hammen and Garcia 1966
Plate 3, fig. 19
**Diagnosis.** Monocolpate, oval, colpus marginate, atectate, psilate, equatorial diameter 42µm.

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

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

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

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

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

*Psilamonocolpites medius* (Van der Hammen 1954) Van der Hammen and Garcia 1966

Plate 3, fig. 20

**Synonymy.**

*Monocolpites medius* Van der Hammen 1954

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

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

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

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

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

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

**Genus Retimonocolpites** Pierce 1961

**Type.** *Retimonocolpites dividuus* Pierce 1961
*Retimonocolpites aff. nigeriensis* van-Hoeken-Klinkenberg 1966

Plate 3, figs 21–23

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

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

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

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

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

**Botanical affinity.** Arecaceae (Morley 2000).

Trichotomocolpate Pollen

**Genus Luminidites** Pocknall and Mildenhall 1984

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

**Luminidites microreticulatus** n. sp.

Plate 3, figs 24–29

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

**Etymology.** After the fine reticulate surface ornamentation.

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

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

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

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

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

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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, figs 30–31

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

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

**Dimensions.** Equatorial diameter 34–(37)–40.5µm; 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
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 124µm.

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

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

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

*Proxapertites magnus* Muller et al. 1987

Plate 3, fig. 33

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

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

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

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

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

Plate 3, figs 34–35

**Synonymy.**

*Monocolpites operculatus* Van der Hammen 1954

**Diagnosis.** Zonasulculate, sub-circular, tectate, reticulate, homobrochate, equatorial diameter 35µm.
**Description.** Monad, amb sub-circular; zonasulcate, sulculus extending around the circumference of the outline, margin of the sulcus irregular; tectate, nexine 0.5µm thick, columellae 0.5µm thick, tectum 0.5µm thick; surface ornamentation reticulate, homobrochate, lumina 0.5–1µm and sub-circular, muri 0.5µm.

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

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

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

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**Proxapertites psilatus Sarmiento 1992**
Plate 3, figs 36–37

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

**Description.** Monad, amb circular; zonasulcate, sulculus extending around the circumference of the outline, margin of the sulcus irregular, tectate, columellae indistinct, exine 1µm 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)–32µm; 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)), Nymphaceae (D’Apolito et al. 2021).

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

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

**Spinizonocolpites prominatus** *(McIntyre 1965) Stover and Evans 1973*
Plate 4, figs 1–3

**Synonymy.**

*Spinizonocolpites echinatus* Muller 1968

**Diagnosis.** Zonasulcate, tectate, columellae distinct, echinate, equatorial diameter 45µm.
Description. Monad, radial, amb sub-circular; zonosulcate, borders of sulculus irregular; tectate, columellae distinct, exine 1µm thick; surface ornamentation echinate, echinae 5µm–9µm high with blunt rounded apices and expanded bases, echinae spaced 3µm–11µm apart, surface ornamentation elsewhere reticulate, muri 0.5µm–1µm wide, lumina 0.5µm–1µm wide.

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

Comparisons. Spinizonocolpites echinatus Muller 1968 is a junior synonym of Spinizonocolpites prominatus (McIntyre 1965) Stover and 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. bacula Muller 1968

Plate 4, fig. 4

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

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

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

Comparisons. This species conforms to Spinizonocolpites aff. bacula 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 and Evans 1973 and Nypa fruticans)

Genus Saturna Salard-Cheboldaeff 1978

Type. Saturna enigmaticus Salard-Cheboldaeff 1978

Saturna enigmaticus Salard-Cheboldaeff 1978
Plate 4, fig. 5

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

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

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

**Comparisons.** *Spirosoncolpites brunii* Legoux 1978 is homobrochate and has considerably larger lumina. The description of the type species *Saturna enigmaticus* Salard-Cheboldaeff 1978 begins “Spores or pollen?” (Jansonius and Hills 1976, Card 3611). *Saturna enigmaticus* Salard-Cheboldaeff 1978 is included among angiosperm pollen here on the basis of the possible sub-equatorial furrow, which may represent a zonasulculus, and the presence of collumellae.

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

Monoporate Pollen

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

**Type.** *Milfordia hypolaenoides* Erdtman 1960

*Milfordia confossus* (Fairchild in Stover et al. 1966) n. comb.

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

Plate 4, fig. 6

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

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

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

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 and Partridge 1973

Plate 4, fig. 7

Synonymy.

*Monoporopollenites homeopunctatus* McIntyre 1965

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

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

Dimensions. Equatorial diameter 28µm; 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 and 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, fig. 8

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

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

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


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

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

**Genus Retimonoporites** Brenner and Bickoff 1992

**Type.** *Retimonoporites operculatus* Brenner and Bickoff 1992

*Retimonoporites heterobrochatus* n. sp.

Plate 4, figs 9–12

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

**Etymology.** After the heterobrochate reticulum.

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

**Dimensions.** Equatorial diameter 27.5–32.5–37.8µm; nm: 5; no: 8.
Comparisons. *Retimonoporites operculatus* Brenner and Bickoff 1992 is smaller (13µm) and homobrochate.

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

### Diporate Pollen

**Genus Retidiporites** Varma and Rawat 1963

**Type.** *Retidiporites bengalensis* Varma and Rawat 1963

*Retidiporites magdalenensis* Van der Hammen and Garcia 1966

Plate 4, fig. 13

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

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

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

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

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

### Tricolpate Pollen

**Genus Bacubrevitricolpites** Rao and Ramanujam 1982

**Type.** *Bacubrevitricolpites rotundus* Rao and Ramanujam 1982

*Bacubrevitricolpites sp.*

Plate 4, figs 14–15

**Diagnosis.** Tricolpate, triangular, colpi short and costate, tectate, baculate, baculae spaced 2–4µm apart, equatorial diameter 38µm.
**Description.** Monad, radial, amb triangular obtuse-convex; tricolpate, colpi short (9µm), costate (costae 2µm wide); exine tectate, columellae indistinct, 1µm thick; surface ornamentation baculate, baculae 1–2µm high, spaced 2–4µm and distributed irregularly, pollen surface elsewhere densely covered with microechinae.

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

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

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

**Genus Crototricolpites Leidelmeyer 1966**

**Type.** *Crototricolpites annemariae* Leidelmeyer 1966

*Crototricolpites densus* Salard-Chaeboldaeff 1978

Plate 4, fig. 16

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

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

**Dimensions.** Equatorial diameter 28µm; 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-Chaeboldaeff 1978).

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

Plate 4, fig. 17

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

**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, 1–2µm thick; surface ornamentation clavate, clavae 1µm high, 0.5µm
wide, spaced 1–1.5µm apart, densely and evenly distributed, and arranged in a Croton-like pattern in some areas of the exine.

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

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

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

**Botanical affinity.** Euphorbiaceae (Jaramillo and Rueda 2023).

**Crototricolpites “superatus”**

Plate 4, fig. 18

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

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

**Dimensions.** Equatorial diameter 29µm; 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** n. sp.

Plate 4, figs 19–21

**Synonymy.**

Echitricolpites sp. 1 Jaramillo and Dilcher 2001

Echitricolpites "guaneorum" Jaramillo and Rueda 2023
**Diagnosis.** Tricolpate, prolate, tectate, columellae distinct, echinate and micropitted, equatorial diameter 30µm.

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

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

**Dimensions.** Equatorial diameter 25–(29.5)–33.5µm, 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, fig. 19, equatorial view; paratype Okigwe A1.1 (S40,4), Plate 4, figs 20–21, equatorial view.

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**Echitricolpites aff. communis** Regali et al. 1974

Plate 4, fig. 22

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

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

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

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

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

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**Genus Foveotricolpites** Pierce 1961
Type. *Foveotricolpites sphaeroides* Pierce 1961

*Foveotricolpites simplex* (González Guzmán 1967) D’Apolito et al. 2021
Plate 4, figs 23–24

**Synonymy.**
*Retitricolpites simplex* González Guzmán 1967

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

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

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

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

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

Genus *Ladakhipollenites* Mathur and Jain 1980

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

Plate 4, figs 25–26

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

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

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

**Dimensions.** Equatorial diameter 27µm; 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).

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*Ladakhipollenites simplex* (González Guzmán 1967) Jaramillo and Dilcher 2001

Plate 4, fig. 27–28

**Synonymy.**

*Psilatricolpites simplex* González Guzmán 1967

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

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

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

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

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*Ladakhipollenites hammenii* (Boltenhagen 1976) n. comb.

**Basonym = *Psilatricolpites hammenii* Boltenhagen 1976

Plate 4, fig. 29

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

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

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

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

*Ladakhipollenites sp. 1*

Plate 4, figs 30–31

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

**Description.** Monad, radial, amb sub-circular; tricolpate, colpi 7µm long, 3µm wide, margins of colpi straight and pointed–sub-rounded in apocolpium; tectate, columellae indistinct, exine 1µm thick at the centre of the mesocolpia, thickens gradually to 1.5µm close to the colpi and thins gradually to 1µm thick adjacent to the colpi; surface ornamentation psilate.

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

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

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

*Ladakhipollenites sp. 2*

Plate 4, fig. 32

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

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

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

**Comparisons.** *Scabratricolpites thomasi* Sarmiento 1992 has simple colpi.
Material. Okigwe A5.1 (U40.3), polar view.


**Basonym** = *Scabratricolpites thomasi* Sarmiento 1992

Plate 4, figs 33–34

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

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

**Dimensions.** Equatorial diameter 24.5µm; 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 and 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 and 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, figs 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 27µm.

**Description.** Monad, radial, amb triangular and slightly rounded; brevitricolpate, colpi 4µm wide, borders distinct; tectate, exine 1µm thick; surface ornamentation reticulate, heterobrochate, simplicolumellate, muri 0.5µm wide, lumina 0.5µm–2µm 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 27µm; nm: 1; no: 1.

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

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

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**Genus Retitrescolpites Sah 1967**

**Type.** *Retitrescolpites typicus* Sah 1967

*Retitrescolpites cecryphalium* (Leidelmeyer 1966) n. comb.

**Basonym = Retitricescolpites cecryphalium** Leidelmeyer 1966

Plate 5, figs 3–6

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

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

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

**Comparisons.** *Retitricescolpites cecryphalium* Leidelmeyer 1966 is larger (48–50µm) and has a thinner exine (3µm) but otherwise is very similar. *Retitricescolpites?*
irregularis (Van der Hammen and Wymstra 1964) Jaramillo and Dilcher 2001 is tricolporate. *Retitrescolpites definidus* Jaramillo et al. 2007 has a thinner exine (2.5µm) and costate colpi. *Retritricolpites* (Van der Hammen 1956) Van der Hammen and Wijmstra 1964 is an illegitimate genus (Janosonius 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 and Dilcher 2001
Plate 5, figs 7–8

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

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

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

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

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

*Retitrescolpites cf. "opitaeorum"
Plate 5, figs 9–10

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

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

**Dimensions.** Equatorial diameter 21–(23)–25.2µm; 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 miriabilis* n. sp.

**Plate 5, figs 11–12**

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

**Etymology.** After the striking morphology.

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

**Dimensions.** Equatorial diameter 54–(54.6)–55.2µm; 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, fig. 11, polar view; paratype Amaogugu 7.1 (L64,3), Plate 5, fig 12, polar view.

*Retitrescolpites sp. 1*

**Plate 5, fig. 13**

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

**Description.** Monad, radial, amb circular; tricolpate, colpi 10µm long, 8µm wide, borders straight, ends pointed, marginate, margo1.5µm wide, defined by marked decrease in size of lumina of reticulum; tectate, columellae distinct, exine 1.5µm thick; surface ornamentation reticulate, heterobrochate, muri 1µm wide, duplicolumellate, lumina decrease in size from 3–4µm at the equator to 1.5µm at the pole, ornamentation of margo reticulate, muri 0.5µm wide, duplicolumellate, lumina 0.5µm–1µm.

**Dimensions.** Equatorial diameter 35µm; nm: 1; no: 1.
Comparisons. *Retitrescolpites baculatus* Jaramillo and 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, figs 14–15

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

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

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

**Comparisons.** *Retitricolpites microreticulatus* (Van der Hammen 1954) Van der Hammen and 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, fig. 16

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

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

**Dimensions.** Equatorial diameter 43µm; nm: 1; no: 2.
**Material.** Ameke 1.1 (W38), polar view, specimen slightly fragmented.

*Retitrescolpites sp. 4*
Plate 5, fig. 17

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

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

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

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

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

**Genus Rousea Srivastava 1969**

**Type.** Rousea subtillis Srivastava 1969

*Rousea florentina* (González Guzmán 1967) Jaramillo and Dilcher 2001
Plate 5, figs. 18–19

**Synonymy.**

*Retitricolpites florentinus* González Guzmán 1967

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

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

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

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

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

*Rousea heteroreticulatus* (Boltenhagen 1976) n. comb.

**Basonym** = *Retitricolpites heteroreticulatus* Boltenhagen 1976

Plate 5, figs 20–21

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

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

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


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

Genus Striatopollis Krutzsch 1959

**Type.** Striatopollis sarstedtensis Krutzsch 1959

*Striatopollis catatumbus* (González Guzmán 1967) Takahashi and Jux 1989

Plate 5 figs 22–23

**Synonymy.**

*Striatricolpites catatumbus* González Guzmán 1967

*Striatricolpites catatumbus* Germeraad et al. 1968
**Diagnosis.** Tricolpate, prolate, tectate, striate, equatorial diameter 29µm.

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

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

**Comparisons.** No tricolporate specimens of *Striatopollis catatumbus* Takahashi and 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).

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**Striatopollis sp.**
Plate 5, figs 24–25

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

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

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

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

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

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

**Type.** *Tricolpites reticulata* Cookson ex Couper 1953

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*Tricolpites clarensis* (González Guzmán 1967) Jaramillo and Dilcher 2001
Plate 5, figs 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 32µm.

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

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

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

Tricolpites gageonnetii (Boltenhagen 1976) n. comb.

Basonym = Retitricolpites gageonnetii Boltenhagen 1976
Plate 5, figs 28–29

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

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

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

Comparisons. Retitricolpites caquetanus Hoorn 1994 has shorter colpi, Tricolpites microreticulatus Belsky, Boltenhagen and Potonié 1965 has costate colpi, Tricolpites clarensis (González Guzmán 1967) Jaramillo and 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 n. sp.
Plate 5, figs 30–33

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

**Etymology.** After the multiple types of surface ornamentation.

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

**Dimensions.** Equatorial diameter 24.4–(26)–28µm; 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 and Rueda 2023 has a thinner exine and indistinct columellae.

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

Tricolpites brevicolpatus n. sp.
Plate 5, figs 34–36

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

**Etymology.** After the short colpi.

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

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

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

*Tricolpites sp. 1*
Plate 5, figs 37–38

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

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

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

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


*Tricolpites sp. 2*
Plate 5, fig. 39

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

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

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

**Comparisons.** *Tricolpites clarensis* (González Guzmán 1967) Jaramillo and 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, figs 40–41

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

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

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

**Comparisons.** *Tricolpites* sp. 4 is heterobrochate.

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

### Tricolpites sp. 4
Plate 5, figs 42–43

**Diagnosis.** Tricolpate, circular–oval, tectate, reticulate, heterobrochate, simplicollumellate, curvimurate, equatorial diameter 18µm.

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

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

**Comparisons.** *Tricolpites* sp. 3 is homobrochate.

Tricolporate Pollen

Genus *Bombacacidites* Couper 1960 emend. Krutzsch 1970

Type. *Bombacacidites bombaxoides* Couper 1960

*Bombacacidites aff. brevis* Muller et al. 1987

Plate 6, fig. 1

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

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

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

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

Material. Ozuiem 3.1 (X40), polar view.


*Bombacacidites “pluricolumellatus”*

Plate 6, fig. 2

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

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

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

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

**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).

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**Genus Fillaeopsidites Salard-Chaeboldaef 1979**

**Type.** *Fillaeopsidites reticulatus* (Guinet and Salard-Chaeboldaef 1975) Salard-Chaeboldaef 1979

*Fillaeopsidites cf. reticulatus* (Guinet and Salard-Chaeboldaef 1975) Salard-Chaeboldaef 1978

Plate 6, figs 3–4

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

**Description.** Tetrahedral tetrad, monad amb sub-triangular; monads tricolporate, colpi simple, and 10–12µm long, port indistinct; tectate, exine 2µm thick, nexine 0.5–1µm, sexine 1µm; surface ornamentation micropitted.

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

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

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

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**Genus Foveotricolporites Pierce 1961**

**Type.** *Foveotricolporites rhombohedralis* Pierce 1961
Foveotricolporites cf. crassiexinus van Hoeken-Klinkenberg 1966

Plate 6, figs 5–10

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

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

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

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

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 and Wymstra 1964) Frederiksen 1988

Plate 6, figs 11–14

Synonymy.

Psilatricolporites crassus Van der Hammen and Wymstra 1964

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

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

Description. Monad, radial, amb sub-circular; tricolporate, occasionally tetracolporate (one specimen), colpi 27µm long, 1µm wide, margins well defined, ends pointed, pori lalongate, 7µm wide; tectate, exine 2.5µm thick, nexine 1µm thick, collumellae 0.5µm thick, each collumella 0.5µm wide, collumellae spaced 1µm apart, tectum 1µm thick; surface ornamentation psilate, over the majority of the grain surface the tectum has degraded to expose the collumellae.
Dimensions. Equatorial diameter 49.2–(51.6)–54µm; 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)).


**Type.** *Margocolporites tsukadai* Ramanujam 1966 ex Srivastava 1969

**Margocolporites cf. mandjicus** Boltenhagen 1976
Plate 6, fig. 15

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

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

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

**Comparisons.** The margines of *Margocolporites mandjicus* Boltenhagen 1976 are more conspicuous and the reticulum is slightly coarser in the mesocolpium (1–3µm). The colpi of *Margocolporites rauvolfi* Salard-Cheboldaeff 1979 is larger (35µm) have margines 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-Cheboldaeff 1979
Plate 6, fig. 16

**Diagnosis.** Tricolporate, sub-circular, colpi marginate, pori costate, tectate, reticulate homobrochate, equatorial diameter 37µm.
Description. Monad, radial, amb sub-circular; tricolporate, colpi 13µm long, borders straight, end pointed, marginate, margo 4µm wide and formed by a thinning of the sexine, pori 5µm wide and costate, costae 1µm wide; tectate, nexine 1µm thick, columellae 0.5µm thick, columellae indistinct in certain areas, tectum 0.5µm thick, exine thickens slightly in mesocolpia, formed by thickening of the nexine and sexine; surface ornamentation reticulate, homobrochate, muri 0.5µm wide, lumina 0.5µm wide.

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

Comparisons. Margocolporites sp. 1 Jaramillo and Dilcher 2001 has two distinctive rings around each pore formed by thicking and thinning of the nexine. The colpi of Margocolporites rauwolfii Salard-Cheboldaeff 1979 are shorter and have margines that are rounded at the apocolpium.

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

Botanical affinity. Apocynaceae (Morley 2000).

Genus Paripollis Partridge in Stover and Partridge 1973

Type. Paripollis ochesis Partridge in Stover and Partridge 1973

Paripollis? “dubius”
Plate 6; figs 17–18

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

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

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

Comparisons. Fillaeopsis reticulatus Salard-Cheboldaeff 1978 has long colpi that lack margines, is larger (tetrad 50µm) and has reticulate or foveolate surface.
ornamentation. *Kielmeyerapollenites eocenicus* Sah and Kar 1974 has long funnel-shaped colpi with well-developed pori, is larger (tetrad 65–72µm) and has pilate surface ornamentation that forms a reticulum. The colpi of *Ericipites longisulcus* (Wodehouse 1933) Krutzsch 1970 are narrow slits lacking margines. *Dicotetradites clavatus* (Couper 1953) Crosbie and Clowes 1980 is triporate. *Paripollis ochesis* Partridge in Stover and Partridge 1973 has faint colpi that lack margines and is verrucate with interspersed granulae. Specimens encountered here are tentatively assigned to *Paripollis* Partridge in Stover and 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, fig. 19

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

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

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

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

*Psilabrevitricolporites porolatus* n. sp.  
Plate 6, figs 20–23

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

**Etymology.** After the wide pori.
Description. Monad, radial, amb sub-triangular and convex; tricolporate, colpi 5µm long, simple, borders regular and straight, ends pointed, pori costate and clearly defined, lalongate, 10µm wide, costae 2µm wide and 1µm thick; tectate, collumellae indistinct, nexine 0.5µm sexine 0.5µm thick, thickening slightly around the pori; surface ornamentation psilate to micropitted, lumina <0.5µm.

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

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

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

Genus *Rhoipites* Wodehouse 1933

Type. *Rhoipites bradleyi* Wodehouse 1933

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

Plate 6, fig. 24

Synonymy.

*Retitricolporites guianensis* Van der Hammen and Wymstra 1964

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

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

*Retitricolporites guianensis* (Van der Hammen and Wymstra 1964) Lorente 1986

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

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

Dimensions. Equatorial diameter 20µm; 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* n. sp.

Plate 6, figs. 25–27

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

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

**Description.** Monad, radial, amb sub-triangular; tricolporate, colpi 13µm long, 0.5µm wide, borders straight, marginate, margo 1µm–2µm wide, costate, costa 0.5µm thick, colpi do not anastamose at pole, apocolpium small (5µm wide), pori 2.5µm wide, costate, costae 0.5–1µm thick; tectate, columellae indistinct, exine 1µm–2µm thick; surface ornamentation rugulate, rugulae 1µm wide, 2µm–4µm long, sculptural elements restricted to mesocolpium, psilate elsewhere.

**Dimensions.** Equatorial diameter 24.5–(27.5)–31µm; 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 (38–40µm), has fastigate pori and has foveolae over the entire surface of the grain. Striatriporites nigeriensis van Hoeken-Klinkenberg 1966 is striate in the mesoporium and lacks ornamentation around the pori.

**Material.** Holotype Ozuiem 6.1 (O33,2), Plate 6, fig. 25, polar view; paratype Ozuiem 3.1 (V40,4), Plate 6, figs 26–27, polar view;

**Genus Striatriporites Van der Hammen ex Leidelmeyer 1966**

**Type.** Striatriporites pimulis Leidelmeyer 1966

*Striatriporites cf. pimulis* Leidelmeyer 1966

Plate 6, fig. 28
Diagnosis. Tricolporate, sub-triangular, intectate, striate, equatorial diameter 22µm.
Description. Monad, radial, amb sub-triangular; tricolporate, colpi 9µm long, 5µm wide at equator, narrowing to 1µm, ends pointed, borders curved, pore circular, 3µm in diameter; intectate, exine 1µm thick; surface ornamentation striate, muri 0.5µm–1µm wide, striae 0.5µm–1µm wide, striae orientated perpendicular to colpi.
Dimensions. Equatorial diameter 22µm; nm: 1; no: 1.
Comparisons. Striaticolporites pimulis Leidelmeyer 1966 has costate pori.
Material. Ozuitem 3.1 (W65,2), oblique view.

Genus Tetracolporopollenites Pflug and Thomson in Thomson and Pflug 1953
Type. Tetracolporopollenites sapotoides Pflug and Thomson in Thomson and Pflug 1953
Tetracolporopollenites maculosus (Regali et al. 1974) Jaramillo and Dilcher 2001
Plate 6, figs 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 27µm.
Description. Monad, radial, prolate to prolate spheroidal; tetracolporate (4-colpi), colpi 12µm long, 0.5µm wide, pori lens-shaped and lalongate, 8µm wide, 2µm high, pori annulate, annulus 2µm wide; atectate, exine <0.5µm thick; surface ornamentation psilate.
Dimensions. Equatorial diameter 26.2–(27)–28µm; nm: 3; no: 16.
Material. Ameke 1.1 (T44), equatorial view.
Botanical affinity. Sapotaceae (Lorente 1986).

Tetracolporopollenites transversalis (Dueñas 1980) Jaramillo and Dilcher 2001
Plate 6, figs 31–32
Synonymy.
Psilatricolporites transversalis Dueñas 1980
**Diagnosis.** Tricolporate, prolate, pori lalongate and costate, tectate, psilate, equatorial diameter 25µm.

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

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

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

**Material.** Amaogugu 1.1 (L60), equatorial view.

**Botanical affinity.** Sapotaceae (Lorente 1986).

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**Tetracolporopollenites cryptoporites** (Boltenhagen 1976) n. comb.

*Basonym = Psilatricolporites cryptoporites* Boltenhagen 1976

Plate 6, fig. 33

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

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

**Dimensions.** Equatorial diameter 17–(18)–19.4µm; 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 and Thomson in Thomson and Pflug 1953, accommodates tri- and tetracolporate pollen grains.

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

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**Tetracolporopollenites torus** n. sp.

Plate 6, figs 34–39
**Diagnosis.** Tricolporate, prolate to prolate spheroidal, pori with annulus, tectate, psilate–micropitted, equatorial diameter 23µm.

**Etymology.** After the prominent annulate pori.

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

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


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

**Genus Tricolporites Cookson 1947**

**Type.** *Tricolporites prolata* Cookson 1947

**Tricolporites densus n. sp.**

Plate 6, figs 40–42

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

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

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

**Dimensions.** Equatorial diameter 28–(30.5)–33µm; nm: 2; no: 19.
Comparisons. *Retitricolporites ninghesikanus* Boltenhagen 1976 is heterobrochate with a coarser reticulum and irregular lumina (2.5µm).

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

**Tricolporites “reticulomargites”**

Plate 7, figs 1–2

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

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

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

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

Material. Ozuitem 6.1 (H36), polar view.

**Tricolporites sp. 1**

Plate 7 figs 3–5

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

**Description.** Monad, radial, amb sub-circular; tricolporate, colpi 9µm long, 3µm wide, borders slightly irregular, ends pointed, pori circular, simple, 2µm in diameter; tectate, columellae distinct, exine 1µm thick; surface ornamentation reticulate, homobrochate, muri 0.5µm wide, lumina 0.5µm 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 (T514), oblique view.

**Tricolporites sp. 2**
Plate 7, figs 6–7

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

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

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

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

**Material.** Ozuitem 3.1 (S382), polar view.

**Tricolporites sp. 3**
Plate 7, figs 8–9

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

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

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

**Material.** Ameke 1.1 (S524), equatorial view.
**Tricolporites sp. 4**  
Plate 7, figs 10–12

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

**Description.** Monad, radial, subprolate–prolate spheroidal, tricolporate, colpi 10–15µm long and narrow (1–2µm wide), colpi costate, pori sub-circular, 1–2µm wide and 2–3µm high; tectate, columellae distinct, exine 1–2µm thick, nexine 0.5µm thick, sexine 0.5–1.5µm thick; surface ornamentation micropitted–reticulate homobrochate, muri 0.5µm wide, lumina 0.5–1µm wide, spaced densely and evenly over the surface of the pollen grain.

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

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

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**Tricolporites sp. 5**  
Plate 7, figs 13–14

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

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

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

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

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

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**Tricolporites sp. 6**  
Plate 7, figs 15–16

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

**Description.** Monad, radial, amb circular; tricolporate, colpi simple, pore indistinct; exine tectate, columellae distinct, 2µm thick; surface ornamentation echinate, echinae densely spaced 3–5µm wide at base, 8–11µm high.
**Dimensions.** Equatorial diameter 23–(24.5)–25.5µm; 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, fig. 17

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

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

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

**Comparisons.** The colpi of *Echitricolporites minutus* Regali et al. 1974 lack costae and the colpi are shorter. *Brevitricolpites macroexinatus* Jaramillo and 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 and Pike 1954

**Type.** *Casuarinidites cainozoicus* Cookson and Pike 1954

*Casuarinidites foveolatus* n. sp.

Plate 7, figs 18–20

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

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

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


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

Genus Clavatriporites n. gen.

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 n. sp.

Clavatriporites dispersiclavatus n. sp.

Plate 7, figs 21–22

Synonymy.

Clavatriporites "dispersiclavatus" Jaramillo and Rueda 2023

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

Etymology. After the sparse clavate surface ornamentation.

Description. Monad, radial, amb sub-circular; triporate, pori wide (12µm), borders of pori slightly irregular; exine intectate, 1µm thick; surface ornamentation clavate with some baculate, clavae and baculae 1µm high and distributed sparsely and evenly over pollen surface, clavae and baculae spaced 3µm apart at equator, 1–2µm apart at poles.
**Dimensions.** Equatorial diameter 25–(27.5)–30µm; nm: 4; no: 4.

**Comparisons.** *Clavatricolpites densiclavatus* Jaramillo and Dilcher 2001 is tricolpate, *Crototricolpites finitus* Silva–Caminha et al. 2010 is tricolpate, with more densely distributed clavae (0.5–1µm apart). *Bacutriporites 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* n. sp. 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, fig. 21, polar view, paratype Okigwe B1.1 (K48,4), Plate 7, fig. 22, polar view.

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**Clavatriporites spicatus n. sp.**

Plate 7, figs 23–25

**Synonymy.**

*Clavatriporites "spicatus"* Jaramillo and Rueda 2023

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

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

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

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

**Comparisons.** *Clavatricolpites prolatus* Pierce 1961 has colpi with smooth borders and is smaller (16–20µm), *Clavatricolpites gracilis* González Guzmán 1967 has colpi with smooth borders. *Clavatriporites dispersiclavatus* n. sp. 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, fig. 23, polar view, paratype Okigwe A5.1 (T45,2), Plate 7, figs 24–25, polar view.
Genus *Corsinipollenites* Nakoman 1965

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

*Corsinipollenites psilatus* Jaramillo and Dilcher 2001

Plate 7, fig. 26

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

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

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

**Material.** Ozuitem 3.1 (S52), polar view.

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

*Corsinipollenites* cf. *psilatus* Jaramillo and Dilcher 2001

Plate 7, fig. 28

**Diagnosis.** Triporate, sub-triangular convex, pori annulate, atextate, psilate, equatorial diameter 20µm.
**Description.** Monad, radial, amb sub-triangular convex; triporate, pori oval (3µm x 1.5µm) and annulate, annulus 1.5µm wide and 3µm high; exine atectate, 1µm thick; surface ornamentation psilate.

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

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

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

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

*Corsinipollenites “striatus”*
Plate 7, fig. 29–30

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

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

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

**Comparisons.** No other species of *Corsinipollenites* are striate. *Striatriporites nigeriensis* van Hoeken-Klinkenberg 1966 lacks ornamentation around the pori, which are themselves markedly less protuberent, 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 *Cricotriporites* Leidelmayer 1966

Type. *Cricotriporites guianensis* Leidelmayer 1966

*Cricotriporites fragilis* van Hoeken-Klinkenberg 1966
Plate 7, fig. 31

**Diagnosis.** Triporate, sub-circular, pori costate and annulate, tectate, exine 1µm thick, scabrate, equatorial diameter 23µm.
Description. Monad, radial, amb sub-circular; triporate, pori rounded, 3µm in diameter, costa 1–1.5µm wide, annulate, annulus 1µm wide; exine tectate, 1µm thick, sexine thickened by 0.5µm around the pore forming a slight annulus; surface ornamentation scabrate, scabrae distributed evenly.

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

Material. Amaogugu 1.1 (J51), polar view.

\textit{Cricotriporites macroporus} Jaramillo and Dilcher 2001

Plate 7, fig. 32

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

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

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

Comparisons. \textit{Cricotriporites elongatoporus} Jaramillo and Dilcher 2001 has lamellate pori.

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

\textit{Cricotriporites cf. macroporus} Jaramillo and Dilcher 2001

Plate 7, figs 33–34

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

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

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

Comparisons. \textit{Cricotriporites macroporus} Jaramillo and Dilcher 2001 lacks rugulae and has a thinner exine (0.5µm thick).

Material. Okigwe B4.1 (K58), polar view.
**Cricotriporites aff. minutiporus** (Muller 1968) Jaramillo and Dilcher 2001
Plate 7, fig. 35

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

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

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

**Comparisons.** *Cricotriporites minutiporus* (Muller 1968) Jaramillo and Dilcher 2001 has finer scabrae and a slight thickening at the apoporia. *Cricotriporites guianensis* Leidelmeyer 1966 (*Cricotriporites operculatus* of van Hoeken-Klinkenberg 1966) has a thicker exine (1–2µm).

**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 and Espinoza-Campuzano 2019
Plate 7, figs 36–38

**Synonymy.**

*Triporites suescae* Van der Hammen 1954

**Proteacidites sigali** Boltenhagen 1978

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

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

**Dimensions.** Equatorial diameter 22.5–(25.5)–28µm; nm: 4; no: 37.
Comparisons. *Echitriporites trianguliformis* Van Hoeken Klinkenberg 1964 is triangular to triangular obtuse-convex and has larger spines (>1µm).

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


*Echitriporites trianguliformis* van Hoeken-Klinkenberg 1964

Plate 7, figs 39–40

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

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

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

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

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


*Echitriporites trianguliformis* var. orbicularis Jaramillo and Dilcher 2001

Plate 7, figs 41–42

**Synonymy.**

*Echitriporites trianguliformis* Forma A Muller et al. 1987

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

**Description.** Monad, radial, amb circular to sub-circular; triporate, pori 2µm wide, annulate, annulus 1–1.5µm thick, 1µm wide, slightly protruding; exine intectate, 0.5–1µm thick; surface ornamentation echinate, echinae spaced 0.5–1µm apart, 0.5µm wide at base, 0.5–2.5µm high.
Dimensions. Equatorial diameter 23.5–(27.5)–31µm; nm: 4; no: 46.


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


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

Type. *Momipites coryloides* Wodehouse 1933

*Momipites cf. africanus* van Hoeken-Klinkenberg 1966

Plate 7, fig. 43

Diagnosis. Triporate, sub-circular, pori annulate and vestibulate, tectate, psilate, equatorial diameter 25µm.

Description. Monad, radial, amb sub-circular; triporate, pore 2µm wide, annulate, annulus 2µm wide, vestibulate; tectate, columellae indistinct, exine 1.5µm thick; surface ornamentation psilate, scabrate around pori.

Dimensions. Equatorial diameter 25µm; nm: 1; no: 9.

Comparisons. *Momipites africanus* van Hoeken-Klinkenberg 1966 is sub-triangular, and each pore has an atrium. *Momipites* sp. 1 Jaramillo and 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-Cheboldaeff 1978

Plate 8, fig. 1

Diagnosis. Triporate, triangular, pori large, tectate, micropitted, equatorial diameter 25µm.
Description. Monad, radial, amb triangular; triporate, pori large, 7µm wide; tectate, columellae indistinct; surface ornamentation micropitted, lumina <0.5µm in size, spaced <0.5µm apart, densely and evenly distributed across the pollen grain surface.

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

Material. Okigwe B4.1 (X60), polar view, specimen folded.


Genus Retitriporites Ramanujam 1966

Type. Retitriporites curvimurati Ramanujam 1966

Retitriporites aff. simplex Van der Kaars 1983

Plate 8, figs 2–3

Diagnosis. Triporate, sub-triangular, pori indistinct, tectate, collumellae indistinct, reticulate, heterobrochate, equatorial diameter 19µm.

Description. Monad, radial, amb sub-triangular; triporate, pori indistinct, possibly due to poor preservation; tectate, collumellae indistinct, exine 1µm thick; surface ornamentation reticulate, heterobrochate, muri 0.5µm wide, lumina 0.5µm–1µm wide and polygonal.

Dimensions. Equatorial diameter 19µm; 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 n. sp.

Plate 8, figs 4–7

Diagnosis. Triporate, triangular and slightly rounded, tectate, reticulate, heterobrochate, equatorial diameter 26µm.

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 4µm wide, borders distinct, pori costate, costae 1µm thick; tectate, collumellae distinct, nexine <0.5µm thick, collumellae 0.5µm thick, tectum very thin <0.5µm thick; surface
ornamentation reticulate, heterobrochate, simplicolumellate, muri 0.5µm wide, slightly curvimurate, lumina 0.5µm–3µm wide and polygonal, lumina of different sizes occur randomly over the surface of the pollen grain.

**Dimensions.** Equatorial diameter 25–(25.5)–26µm; 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 (3.5µm).

**Material.** Holotype Ozuitem 6.1 (H40,4), Plate 8, figs 4–6, polar view; paratype Ozuitem 3.1 (M43), Plate 8, fig 7, polar view, specimen slightly broken.

*Retitriporites “robustus”*

Plate 8, fig. 8–9

**Diagnosis.** Triporate, sub-circular, pori costate, tectate, reticulate–rugulate, heterobrochate, equatorial diameter 21µm.

**Description.** Monad, radial, amb sub-circular; triporate, pori 3µm wide, costate, costae 2µm wide, 1µm thick; tectate, nexine 0.5µm thick, columellae 1µm thick, tectum 0.5µm thick; surface ornamentation reticulate–rugulate, heterobrochate, curvimurate, muri 0.5µm wide, lumina 0.5µm–1µm wide, rugulae 0.5µm wide, 1µm–2µm long.

**Dimensions.** Equatorial diameter 19–(20.5)–22.1µm, 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, figs 10–11

**Diagnosis.** Triporate, sub-triangular, pori annulate, tectate, rugulate, equatorial diameter 29µm.
Description. Monad, radial, amb sub-triangular; triporate, pori 9µm wide, annulate, annulus 1.5µm wide formed by a reduction in the surface ornamentation, pori situated sub-equatorially; tectate, columellae distinct, columellae 1µm wide spaced irregularly 1–3µm apart, nexine 1µm thick, sexine 1µm thick; surface ornamentation rugulate, rugulae 0.5µm wide, 2µm–8µm long, occasional irregularly distributed granulae.

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


Material. Ozuitem 6.1 (V48,1), polar view.

Genus Triporotetradites van Hoeken-Klinkenberg 1964

Type. Triporotetradites cf. scabratus van Hoeken-Klinkenberg 1964

Triporotetradites cf. scabratus van Hoeken-Klinkenberg 1964

Plate 8, fig. 12

Diagnosis. Decussate tetrad, monad amb sub-circular, triporate, pori annulate, intectate, scabrate, tetrad equatorial diameter 32µm, monad equatorial diameter 18µm.

Description. Decussate tetrad, monad amb sub-circular; triporate, pori 1µm wide, annulate, annulus 1µm wide; intectate, exine 0.5µm thick; surface ornamentation scabrate, sculptural elements spaced 1µm–2µm apart.

Dimensions. Tetrad 26–(31.5)–37µm in diameter, equatorial diameter of monads 13–(18)–23µm; nm: 3; no: 14

Comparisons. Triporotetradites scabratus van Hoeken-Klinkenberg 1964 is larger (tetrad 40µm x 50µm, monads 32µm x 22µm).


Heterocolpate Pollen

Genus Heterocolpites Van der Hammen 1956

Type. Heterocolpites incomptus Van der Hammen 1956
**Heterocolpites cf. laevigatus** Salard-Cheboldaeff 1978

Plate 8, fig. 13

**Diagnosis.** Heterocolpate, circular, atectate, psilate, equatorial diameter 11µm.

**Description.** Monad, radial, amb circular; heterocolpate with three colpi and three pseudocolpi, colpi 3µm wide, borders straight and slightly diffuse, covered by a thin (<0.5µm) colpus membrane at the equator, pseudocolpi 1.5µm wide, borders straight and slightly diffuse; atectate, exine 0.5µm thick; surface ornamentation psilate.

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

**Comparisons.** *Heterocolpites laevigatus* Salard-Cheboldaeff 1978 is tectate (nexine 0.5µm thick and sexine 0.5µm thick) and slightly larger (14–22µm).

**Material.** Ozuitem 6.1 (P55,1), oblique view.

**Botanical affinity.** Combretaceae (Salard-Cheboldaeff 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 sowunmiae** Jan du Chêne et al. 1978

Plate 8, fig. 14

**Diagnosis.** Syncolporate, triangular, colpi marginate, pori costate, intectate, scabrate, equatorial diameter 36µm.

**Description.** Monad, radial, amb triangular and slightly convex; syncolporate (3 colpi), colpi 20µm long, 2µm wide, colpi marginate, margo 2.5µm wide, thickened by 1µm, pori costate, costae 1.5µm thick; intectate, exine 0.5µm thick, exine thickened to 1µm in mesocolpium; surface ornamentation scabrate.

**Dimensions.** Equatorial diameter 36µm; nm: 1; no: 3.

**Material.** Ozuitem 6.1 (V45), polar view.

**Syncolporites marginatus** van Hoeken Klinkenberg 1964

Plate 8, figs 15–18
**Diagnosis.** Syncolporate, sub-circular, pori costate, tectate, reticulate, homobrochate, equatorial diameter 29µm.

**Description.** Monad, radial, amb sub-circular; syncolporate, colpi narrow (0.5µm wide), borders straight, colpi marginate, margines 1.5µm wide, formed by thickening of the sexine and a slight coarsening of the reticulum, endoapertures indistinct and costate, costae 1.5µm thick and 1.5µm wide; tectate, columellae distinct, exine 1µm thick, nexine <0.5µm, sexine 0.5–0.7µm; surface ornamentation reticulate, homobrochate, lumina rounded and 0.5µm wide, spaced densely and evenly over the surface of the pollen grain, lumina on margines 0.5–0.7µm wide, muri 0.5µm.

**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 27–30µm but the specimens examined here cover a larger size range.

**Material.** Ozuitem 3.1 (J37,4), oblique view; Ozuitem 6.1 (T40), oblique view.

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**Syncolporites angusticolpatus** n. sp.

Plate 8, figs 19–20.

**Diagnosis.** Parasyncolporate, sub-circular, pori annulate, tectate, columellae indistinct, exine 1µm thick, micropitted, equatorial diameter 27µm.

**Etymology.** After the narrow colpi.

**Description.** Monad, radial, amb sub-circular; parasyncolporate, pori rounded, 4µm wide, annulate, annulus 1µm wide, 1µm thick and slightly protuberant, large apocolpial field demarcated by prominent slightly curved colpi 15µm long and 0.5µm wide, each colpus is separate and there is no division of a single colpus into two branches: exine tectate, 1µm thick, thickened very slightly around the pori, columellae indistinct; surface ornamentation micropitted.

**Dimensions.** Equatorial diameter 26–(26.5)–27.1µm, 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 apoporium 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, fig. 19, polar view; paratype Ozuiem 3.1 (P62,3), Plate 8, fig. 20, polar view.

**Syncolporites rostro n. sp.**
Plate 8, figs 21–23

**Diagnosis.** Syncolporate, amb triangular, colpi marginate, pori costate, tectate, reticulate, homobrochate, equatorial diameter 28µm.

**Etymology.** After the beak-like appearance of each aperture.

**Description.** Monad, radial, amb triangular; syncolporate, colpi narrow (1µm wide), marginate, margo 1µm 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 1.5µm thick and 1.5µm wide; tectate, columellae distinct, exine 1µm thick; surface ornamentation reticulate, homobrochate, lumina rounded and 0.5µm wide, spaced densely and evenly over the surface of the pollen grain.

**Dimensions.** Equatorial diameter 28µm, nm: 1; no: 1.

**Comparisons.** *Cupanieidites acuminatus* Boltenhaegen 1967 is syncolpate.

**Material.** Holotype Ozuiem 3.1 (X36,1), Plate 8, figs 21–23, polar view.

**Syncolporites sp.**
Plate 8, figs 24–25

**Diagnosis.** Parasyncolporate, sub-circular, colpi marginate, tectate, striate, equatorial diameter 34µm.

**Description.** Monad, radial, amb sub-circular; parasyncolporate, colpi 14µm long, 1µm wide, marginate, margo variable in width (0.5µm–1.5µm), apocolpium distinguished by a triangle with sides 3.5µm long, pori 6µm wide, pore borders irregular; tectate, columellae distinct, exine 1µm thick; surface ornamentation striate, muri 1µm wide and spaced <0.5µm apart, striae anastomosing.

**Dimensions.** Equatorial diameter 34µm; nm: 1; no: 6.
Comparisons. *Syncolporites subtilis* Boltenhagen 1976 is triangular in polar view. *Striasyncolpites zwaardi* 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, fig. 26

**Synonymy.**

*Stephanocolpites costatus* van Hoeken Klinkenberg 1964

**Diagnosis.** Stephanocolpate, circular, tectate, columellae indistinct, rugulate, rugulae pronounced in mesocolpium, equatorial diameter 41µm.

**Description.** Monad, radial, amb circular; stephanocolpate (6 colpi), colpi 2µm wide; tectate, columellae indistinct, exine 0.5µm thick, thickened in the mesocolpium to form rugulae; surface ornamentation rugulate, rugulae 3µm wide.

**Dimensions.** Equatorial diameter 41µm; nm 1; no: 4.


**Botanical affinity.** Ctenolophonaceae (by comparison to *Ctenolophon engleri* (Morley 2000)).

*Ctenolophonidites aff. costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966

Plate 8, fig. 27

**Diagnosis.** Stephanocolpate, circular, tectate, columellae indistinct, rugulate, rugulae pronounced in mesocolpium, equatorial diameter 25µm.
**Description.** Monad, radial, amb circular; stephanocolpate, colpi 1.5µm wide, exine thickened in the mesocolpium to form rugulae; tectate, columellae indistinct, exine 0.5µm thick; surface ornamentation rugulate, rugulae 2.5µm wide, rugulae anastomose in apocolpial region.

**Dimensions.** Equatorial diameter 25µm; nm 1; no: 3.

**Comparisons.** *Ctenolophonidites costatus* (van Hoeken-Klinkenberg 1964) van Hoeken-Klinkenberg 1966 is larger (35–70µm).

**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, fig. 28

**Diagnosis.** Tricolpate, angular, three pseudocolpi, colpi and pseudocolpi costate, apocolpium distinct and circular, tectate, reticulate, heterobrochate, equatorial diameter 29µm.

**Description.** Monad, radial, amb angular; tricolpate, colpi 7µm long, 12µm wide, colpi costate, colpi costae 2µm wide, three pseudocolpi, pseudocolpi 7µm long, 12µm wide, pseudocolpi costae 2µm wide, pseudocolpi infilled with a quantity of thin exine, equator protrudes 2µm beyond this quantity of thin exine, apocolpium defined by a circular region of thin exine 4µm in diameter; tectate, columellae distinct, exine 0.5µm thick, and 1.5µm thick in thickened areas; surface ornamentation reticulate, heterobrochate, muri 0.5µm thick, lumina 0.5–1µm wide.

**Dimensions.** Equatorial diameter 29µm; nm 1; no: 3.

**Comparisons.** No other species of *Ctenolophonidites* van Hoeken-Klinkenberg 1966 have pseudocolpi. *Margocolporites rauvolfii* Salard-Cheboldaeff 1978 is tricolporate, with a slightly coarser heterobrochate reticulum (lumina up to 3µm).

**Material.** Okigwe A7.1 (R46,2), polar view.

*Ctenolophonidites? “echicolpatus”*
Plate 8, fig. 29
**Diagnosis.** Stephanocolpate with three colpi and three pseudocolpi, colpi and pseudocolpi marginate, sub-circular, tectate, scabrate and echinate, equatorial diameter 37µm.

**Description.** Monad, radial, amb sub-circular; stephanocolpate, three colpi, three pseudocolpi, colpi 13µm wide, pseudocolpi 5µm wide, colpi and pseudocolpi marginate (1µm wide), borders of margo irregular, edges of colpi lined with echinæ 1µm high; exine intectate, 0.5µm thick; surface ornamentation scabrate and echinate.

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

**Comparisons.** No other species of *Ctenolophonidites* van Hoeken-Klinkenberg 1966 have pseudocolpi.

**Material.** Okigwe B7.1 (J50,4), polar view.

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**Genus Echistephanocolpites Wijmstra 1971**

**Type.** *Echistephanocolpites echinatus* Wijmstra 1971

*Echistephanocolpites echinatus* Wijmstra 1971  
Plate 8, fig. 30

**Diagnosis.** Stephanocolpate, colpi simple, tectate, echinate, equatorial diameter 53.5µm

**Description.** Monad, radial, amb sub-circular; stephanocolpate (5 colpi), colpi simple, 15µm long; exine tectate, collumellae distinct, exine 2.5µm thick, nexine 1µm thick, sexine 1.5µm thick; nexine characterised by a loose infrareticulum, muri 1µm wide, lumina 1.5–2.5µm wide and polygonal, sometimes disconnected; surface ornamentation echinate, echinæ 1–2µm high, 1µm wide at base.

**Dimensions.** Equatorial diameter 53.5µm; nm 1; no: 1.

**Material.** Okigwe B7.1 (D37,1), polar view.

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**Genus Foveostephanocolpites Leidelmeyer 1966**

**Type.** *Foveostephanocolpites typicus* Leidelmeyer 1966

*Foveostephanocolpites sp. 1*  
Plate 8, fig. 31
**Diagnosis.** Stephanocolpate (4 colpi), sub-circular, tectate, foveoreticulate, lumina 1µm in apocolpial region, 0.5µm in mesocolpial region, equatorial diameter 44µm.

**Description.** Monad, radial, amb sub-circular; stephanocolpate (4 colpi), colpi 4µm wide, 14µm long; exine tectate, nexine 1µm thick, columellae 0.5µm thick, 1µm wide and spaced 0.5µm apart, tectum 0.5µm thick; surface ornamentation foveoreticulate, heterobrochate, lumina irregularly shaped, lumina 1µm in apocolpial region, 0.5µm in mesocolpial region.

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

**Comparisons.** *Foveostephanocolpites typicus* Leidelmeyer 1966 has seven costate colpi and is 25µm in size. *Foveostephanocolpites perfectus* Leidelmeyer 1966 has six marginate colpi and is 29µm in size.

**Material.** Ameke 1.1 (K55,2), polar view.

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**Foveostephanocolpites sp. 2**  
Plate 8, fig. 32

**Diagnosis.** Stephanocolpate (5 colpi), circular, tectate, foveolate, lumina 0.5µm, equatorial diameter 30µm.

**Description.** Monad, radial, amb circular; stephanocolpate (5 colpi), colpi 4µm wide, 10µm long; exine tectate, columellae distinct, columellae 0.5µm wide, spaced 1µm apart, nexine 1.5µm, sexine 0.5µm; surface ornamentation foveolate, lumina 0.5µm wide, spaced 1-2µm apart.

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

**Comparisons.** *Foveostephanocolpites typicus* Leidelmeyer 1966 has seven costate colpi and is 25µm in size. *Foveostephanocolpites perfectus* Leidelmeyer 1966 has marginate colpi.

**Material.** Ozuitem 3.1 (Q62), polar view.

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**Genus Psilastephanocolpites** Leidelmeyer 1966

**Type.** *Psilastephanocolpites maia* Leidelmeyer 1966

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**Psilastephanocolpites sp.**  
Plate 8, fig. 33
Diagnosis. Stephanocolpate, sub-circular, colpi marginate, tectate, psilate, equatorial diameter 38µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (5 colpi), colpi 10µm long, borders straight, ends slightly curved, marginate, margo 1–1.5µm wide; tectate, nexine 0.5µm thick, columellae 0.5 µm thick, 0.5µm wide and spaced 1µm apart, tectum 0.5–1µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 38µm; nm: 1; no: 3.


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, fig. 34

Diagnosis. Stephanocolpate, sub-circular, tectate, reticulate, homobrochate, equatorial diameter 29µm.

Description. Monad, radial, amb sub-circular; stephanocolpate (five–six colpi), colpi 8µm long 3µm wide, colpi simple, borders straight, ends pointed; tectate, exine 1µm thick, nexine 0.5µm, sexine 0.5µm; surface ornamentation reticulate, homobrochate, lumina 1µm in diameter and rounded, muri 1µm wide.

Dimensions. Equatorial diameter 25–(28.5)–32.5µm; 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 24.5µm 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, fig. 35

**Diagnosis.** Stephanocolpate, polygonal, tectate, reticulate, heterobrochate, equatorial diameter 37µm.

**Description.** Monad, radial, amb polygonal; stephanocolpate (six colpi), colpi 12µm long and 2µm wide, ends pointed; tectate, collumellae distinct, spaced 2µm apart, exine 1µm thick, nexine 0.5µm, sexine 0.5µm; surface ornamentation reticulate, lumina 0.5µm–1µm in diameter, spaced densely and evenly over the surface of the grain, muri 0.5µm wide.

**Dimensions.** Equatorial diameter 35–(36.5)–38µm; nm: 2; no: 7.

**Comparisons.** *Jandufouria seamrogiformis* Germeraad et al. 1968 is larger (40–57µm) and micropitted.

**Material.** Ozuitem 3.1 (S42,4), polar view.

**Botanical affinity.** Ctenolophonaceae (by comparison to *Ctenolophon parvifolius* (Germeraad et al. 1968; Morley 2000)).

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**Genus Scabrastephanocolpites** Van der Hammen and Garcia 1966

**Type.** *Scabrastephanocolpites scabratus* Van der Hammen and Garcia 1966

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**Scabrastephanocolpites vanegensis** Van der Hammen and Garcia 1966

Plate 8, fig. 36

**Diagnosis.** Stephanocolpate, sub-circular, colpi marginate, tectate, collumellae indistinct, scabrate, equatorial diameter 33µm.

**Description.** Monad, radial, amb sub-circular; stephanocolpate (4 colpi), colpi long (16µm), 9µm wide, borders well defined, ends rounded, marginate, margo 0.5µm wide, margo produced by slight thickening of the sexine; tectate, collumellae indistinct; surface ornamentation scabrate, sculptural elements spaced 0.5–2µm over the pollen surface.

**Dimensions.** Equatorial diameter 31–(33)–35µm; 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, fig. 37

Diagnosis. Stephanocolpate (4 colpi), circular, colpi margins irregular, tectate, columellae indistinct, scabrate, equatorial diameter 27µm.

Description. Monad, radial, amb circular; stephanocolpate (4 colpi), colpi 7µm long, 6µm wide, margins irregular, ends pointed; tectate, columellae indistinct, exine 0.5µm thick; surface ornamentation scabrate, sculptural elements distributed densely and evenly over the surface of the pollen grain.

Dimensions. Equatorial diameter 27µm; nm: 1; no: 3.

Comparisons. Scabrastephanocolpites scabratus Van der Hammen and García 1966 has 5 colpi and is larger (37µm). S. guadensis Van der Hammen 1954 has a thicker exine (2µm) and shorter colpi. S. vanegensis Van de Hammen and García 1966 has marginate colpi and S. sp. 1 Jaramillo and Dilcher 2001 has shorter marginate colpi.

Material. Okigwe A5.1 (U50,1), polar view.

Stephanocolporate Pollen

Genus Tetracolporites Couper 1953 emend. Pocknall and Mildenhall 1984

Type. Tetracolporites oamaruensis Couper 1953

Tetracolporites cf. spectabilis Pocknall and Mildenhall 1984
Plate 8, fig. 38

Diagnosis. Stephanocolporate, circular, colpi short and costate, tectate, psilate, equatorial diameter 27µm.

Description. Monad, radial, amb circular; stephanocolporate (5 colpi), colpi 5µm long, 2.5µm wide, borders straight, ends rounded, costate, costae 1.5µm wide, pore lalongate indistinct; tectate, nexine 0.5µm thick, columellae 0.5µm thick but indistinct, tectum 0.5µm thick; surface ornamentation psilate.

Dimensions. Equatorial diameter 27µm; nm: 1; no: 3.

**Material.** Ozuiten 3.1 (M35), polar view.

Stephanoporate Pollen

**Genus Echistephanoporites Leidelmeyer 1966**

**Type.** *Echistephanoporites alfonsi* Leidelmeyer 1966

*Echistephanoporites alfonsi* Leidelmeyer 1966

Plate 8, fig. 39

**Diagnosis.** Stephanoporate, pori annulate, tectate, columellae indistinct, echinate, equatorial diameter 27.5µm.

**Description.** Monad, radial, amb sub-circular; stephanoporate, pori annulate, annulus 2.5µm wide; tectate, collumellae indistinct, exine 1µm thick; surface ornamentation echinate, echinae spaced 1–2µm and 1µm apart.

**Dimensions.** Equatorial diameter 27.5µm; nm: 1; no: 2.

**Material.** Okigwe B7.1 (N40,1), polar view.

**Genus Pachydermites Germeraad et al. 1968**

**Type.** *Pachydermites diederixi* Germeraad et al. 1968

*Pachydermites diederixi* Germeraad et al. 1968

Plate 8, fig. 40

**Diagnosis.** Stephanoporate, sub-circular, pore margins irregular, tectate, psilate, equatorial diameter 43µm.

**Description.** Monad, radial, amb sub-circular; stephanoporate (6 pori), pori sub-circular, margins irregular, 4µm wide; tectate, exine 4.5µm thick; surface ornamentation psilate, micropitted around pori.

**Dimensions.** Equatorial diameter 43µm; 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, fig. 41

**Diagnosis.** Stephanoporate, sub-circular, pori annulate, tectate, reticulate, homobrochate, equatorial diameter 18µm.

**Description.** Monad, radial, amb sub-circular; stephanoporate (four pori), pori 1.5µm wide, annulate, annulus 1.5µm wide, 1µm high; tectate, columellae indistinct, exine 1µm thick; surface ornamentation reticulate, homobrochate, lumina 0.5µm wide.

**Dimensions.** Equatorial diameter 18µm; nm: 1; no: 10.

**Comparisons.** *Retistephanoporites minutiporus* Jaramillo and Dilcher 2001 has distinct columellae.

**Material.** Ameke 1.1 (M44,2), polar view.

Pantoporate Pollen

**Genus Chenopodipollis** Krutzsch 1966

**Type.** *Chenopodipollis multiplex* (Weyland and Pflug 1957) Krutzsch 1966

*Chenopodipollis multiplex* (Weyland and Pflug 1957) Krutzsch 1966

Plate 8, fig. 42

**Synonymy.**

*Periporopollenites multiplex* Weyland and Pflug 1957

**Diagnosis.** Pantoporate, circular, tectate, columellae indistinct, scabrate, equatorial diameter 23µm.

**Description.** Monad, radial, amb circular; pantoporate (>46 pori), pori circular, annulate, and 1.5µm in diameter; tectate, columellae indistinct, exine 1.5µm thick; surface ornamentation scabrate.
Dimensions. Equatorial diameter 23µm; nm: 1; no: 4.


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, figs 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, 2–4µm in diameter; exine intectate, 2µm thick; surface ornamentation clavate, clavae 1.5µm high, 1–1.5µm wide, triangular in plan view, arranged in a Croton pattern, clavae bases connect in the nexine to form a heterobrochate infrareticulum, muri 1µm wide, lumina 1–1.5µm wide and polygonal.

Dimensions. Equatorial diameter 34–(39)–44µm; 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 pore is annulate.

Material. Amaogugu 1.1 (E48,4), oblique view.

Genus *Echiperiporites* Van der Hammen and Wymstra 1964

Type. *Echiperiporites akanthos* Van der Hammen and Wymstra 1964


**Echiperiporites aff. scabrannulatus** Jaramillo et al. 2010

Plate 8, fig. 45

**Diagnosis.** Pantoporate, pori annulate, intectate, echinate, equatorial diameter 25µm.

**Description.** Monad, radial, amb sub-circular; pantoporate, pori spaced 2–7µm apart, pori annulate, annulus 1.5µm wide; exine intectate, 1µm thick; surface ornamentation echinate, echinae spaced 1.5–3.5µm apart, 1µm wide at base, 2–3.5µm high, ornamentation elsewhere scabrate.

**Dimensions.** Equatorial diameter 25µm; nm 1; no: 3.

**Comparisons.** *Echiperiporites scabrannulatus* Jaramillo et al. 2010 is larger (67 µm). *Echiperiporites "psilatus"* is larger (35µm–44µm) (Jaramillo and Rueda 2023). *Echiperiporites akanthos* Van der Hammen and Wymstra 1964 is tectate and more densely distributed echinae.

**Material.** Okigwe B6.1 (M57).

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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 Ameki Formations, and this is illustrated by comparing *Longapertites proxapertitoides var. proxapertoides* (Plate 3, fig. 2, from sample Okigwe A5.1), *Longapertites proxapertitoides var. reticuloides* (Plate 3, fig. 3, from sample Amaogugu 1.1), and *Longapertites proxapertitoides var. reticuloides* (Plate 3, fig. 4, from sample Ozuitem 3.1). It has been shown that the Paleocene–Eocene thermal maximum (PETM) in the Bighorn Basin, USA, is characterised by extensive reworking of Cretaceous palynomorphs in samples from the PETM (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 *Foveotriletes margaritae* (Van der Hammen 1954) Germeraad et al. 1968 (Germeraad et al. 1968) and the presence of *Retimonocolpites pluribaculatus* Salard-Cheboldaefff 1978 (Salard-Cheboldaefff 1990). All of these diagnostic taxa are absent from the samples we have examined apart from a single well-preserved specimen of *Foveotriletes margaritae* (Van der Hammen 1954) Germeraad et al. 1968 in the sample Amaogugu 7.1 (Plate 1, fig. 19) (Fig. 2), and this suggests that reworking of pollen and spores from the Cretaceous is unlikely. However, as noted by Salard-Cheboldaefff (1990, p. 6) “many forms are common to the Upper Maastrichtian, Paleocene and Eocene” (see Fig. 2) and it is possible that taxa other than these zone fossils that are found in both the Maastrichtian and Paleocene 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) (Fig. 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) (Fig. 2). The samples from the Imo and Ameki Formations contain both *Striatopollis catatumbus* and *Lanagiopollis erassa* (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) (Fig. 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 Paleocene (Upper Nsukka Formation and Imo Formation) have a lower average richness compared to the Eocene (Ameki Formation), the difference being significant ($t$-test, $p=0.003$, df=6.337, Paleocene=37.4, Eocene=54.7) (Table 1). If the ages tentatively assigned to these formations is correct (Fig. 1) then this may suggest an increase in Eocene diversity but this will be tested in further work. Samples from Okigwe A and B (Paleocene Upper Nsukka Formation) are dominated by pollen with botanical affinities to the Arecaceae (palms) including *Longapertites* spp., *Monocolpolpollenites ovatus*, *Mauritiidites franciscoi* var. *franciscoi* and *Mauritiidites crassibaculatus* which both closely resemble the pollen of extant *Mauritia*, together with *Proxapertites operculatus* and *P. cursus* (Araceae (arums) (Zetter et al. 2001)) (Fig. 3a). This assemblage is very similar to the Paleocene 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. Instead, samples from these three sections contain more spores such as *Polypodiisporites spectios* (Polypodiaceae) and *Laevigatosporites ovatus* (Marattiaceae), together with tricolpate pollen such as *Striatopollis catatumbus* (Fabaceae) and *Foveatricolpites simplex* (Euphorbiaceae) (Fig. 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 (Fig. 3a). The lithology (Table 1) and palynofacies (Oboh-Ikuenobe et al. 2005) of the samples studied here is 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 (Fig. 3b). Samples are 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 Ameki Formation plot close to each other despite being from two different sections (Ameke and Amaogugu) (Fig. 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 from the other samples taken from the Upper Nsukka Formation (Fig. 3b) and is dominated by *Monoporopollenites annulatus* (Van der Hammen 1954) Jaramillo and Dilcher 2001 (48%, Plate 4 fig. 8, Poaceae) and *Luminidites microreticulatus* n. sp. (24%, Plate 3 figs 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 (Fig. 3) palm swamps in the West African Paleocene.

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 *Proxaperites 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 Ameki formations (Table 1) may represent the *Retibrevitricolpites triangulatus* Atlantic Zone of Germeraad et al. (1968).
The richness of each sample ranges from 29 (Okigwe B4.1) to 76 (Amaogugu 1.1), and when compared at 150 specimens following rarefaction (Table 1), samples from the Paleocene (Upper Nsukka and Imo formations) have an average richness of 37.4, while samples from the Eocene Ameki Formation have an average richness of 54.7.

The top-ranked taxa in samples from the Okigwe A and Okigwe B sections are dominated by pollen with botanical affinities to the Arecaceae (palms) and Araceae (arums), while the number of top-ranked taxa with botanical affinities to palms is lower in samples from the Ozuitem, Ameke and Amaogugu sections (Fig. 3a). The general vegetation type represented by the palynoflora as a whole consists of palm-dominated swamps, perhaps with mangroves.

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References


Frederiksen NO. 1980. Sporomorphs from the Jackson Group (Upper Eocene) and adjacent strata of Mississippi and western Alabama. USGS Professional Paper. 1084:1–75.


Figure 1. Map and stratigraphy of the rock succession under investigation modified from Oboh-Ikuenobe et al. (2005). The towns Okigwe (Imo State) and Umuahia (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 Reyment (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 Paleocene–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.
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 Paleocene–Eocene boundary is placed between the Imo and Ameki Formations following Nawajide (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).
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).
Table Caption
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. $S_{ob}$ = number of species observed, $S(100)$ number of species expected at 100 individuals, $S(150)$ number of species expected at 150 individuals.

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PLATE 1

4. Laevigatosporites aff. catanejensis Muller et al. 1987, Amaogugu 1.1 (X68,3).
5. Laevigatosporites ovatus Wilson and Webster 1946, Okigwe B4.1 (D44).
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).
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.
17. Distaverrusporites margaritatus Muller 1968, Okigwe B4.1 (V56), low focal plane.
23. Microreticulatisporites cf. uniformis Singh 1964, Okigwe B1.1 (Y63,1), high focal plane.
PLATE 2

1. *Psilatriletes brevilaesurus* n. sp., 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.
7. *Punctatisporites interfoveolatus* n. sp., Okigwe B1.1 (R33,4), holotype, low focal plane.
17. *Inaperturopollenites fossulatus* n. sp., Ozuitem 3.1 (W34,2), high focal plane.
18. *Inaperturopollenites fossulatus* n. sp., 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).
PLATE 3


7. *Longapertites crassireticuloides* n. sp., Okigwe A5.1 (M33,4), holotype.

8. *Longapertites crassireticuloides* n. sp., Okigwe A5.1 (G33,3), paratype.


26. *Luminidites microreticulatus* n. sp., Okigwe B4.1 (F48), paratype, high focal plane.
27. *Luminidites microreticulatus* n. sp., Okigwe B4.1 (F48), paratype, low focal plane.
29. *Luminidites microreticulatus* n. sp., Okigwe B4.1 (P52,2), paratype, mid focal plane showing columellae tips.


**PLATE 4**


9. *Retimonoporites heterobrochatus* n. sp., Okigwe B3.1 (G33), holotype, high focal plane.

10. *Retimonoporites heterobrochatus* n. sp., Okigwe B3.1 (G33), holotype, low focal plane.

11. *Retimonoporites heterobrochatus* n. sp., Okigwe B3.1 (F40,2), paratype, high focal plane.

12. *Retimonoporites heterobrochatus* n. sp., Okigwe B3.1 (F40,2), paratype, low focal plane.


15. *Bacubrevitricolpites* sp., Amaogugu 1.1 (P56,4), low focal plane.


18. *Crototricolpites* “superatus”, Okigwe A7.1 (W37,3).


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).
PLATE 5

13. *Retitrescolpites* sp. 1, Ozuitem 6.1 (K60,3).
15. *Retitrescolpites* sp. 2, Ozuitem 6.1 (J42,4), low focal plane.
17. *Retitrescolpites* sp. 4, Ozuitem 3.1 (Q35,2).
32. *Tricolpites multiornamentus* n. sp., Okigwe B1.1 (M46), paratype, high focal plane, an air bubble rests over the specimen.
33. *Tricolpites multiornamentus* n. sp., Okigwe B1.1 (M46), paratype, low focal plane, an air bubble rests over the specimen.
34. *Tricolpites brevicolpatus* n. sp., Okigwe B1.1 (W56), holotype, high focal plane.
35. *Tricolpites brevicolpatus* n. sp., Okigwe B1.1 (W56), holotype, low focal plane.
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, Ozuiem 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, Ozuiem 6.1 (T32,2), high focal plane.
43. *Tricolpites* sp. 4, Ozuiem 6.1 (T32,2), low focal plane.
PLATE 6

2. Bombacacidites “pluricolumellatus”, Okigwe B4.1 (H45,2).
3. **Fillaeopsidites cf. reticulatus** (Guinet and Salard-Chaeboldaeff 1975) Salard-Chaeboldaeff 1978, Okigwe A5.1 (E45,4), high focal plane.


5. **Foveotricolporites cf. crassiexinus** van Hoeken-Klinkenberg 1966, Ameke 1.1 (H31,3), high 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.


11. **Lanagiopollis crassa** (Van der Hammen and Wymstra 1964) Frederiksen 1988, Ozuitem 6.1 (S35,2), tetracolporate specimen, high focal plane.

12. **Lanagiopollis crassa** (Van der Hammen and Wymstra 1964) Frederiksen 1988, Ozuitem 6.1 (S35,2), tetracolporate specimen, low focal plane.

13. **Lanagiopollis crassa** (Van der Hammen and Wymstra 1964) Frederiksen 1988, Ozuitem 3.1 (W59,3), high focal plane.


15. **Margocolporites cf. mandjicus** Boltenhagen 1976, Okigwe B6.1 (M46,2).

16. **Margocolporites cf. rauvolfi** Salard-Cheboldaeff 1979, Ameke 1.1 (H43,2).


20. **Psilabrevitricolporites porolatus** n. sp., Amaogugu 1.1 (T60), holotype, high focal plane.
21. *Psilabrevitricolporites porolatus* n. sp., Amaogugu 1.1 (T60), holotype, low focal plane.
22. *Psilabrevitricolporites porolatus* n. sp., Amaogugu 1.1 (M48,1), paratype, high focal plane.
23. *Psilabrevitricolporites porolatus* n. sp., Amaogugu 1.1 (M48,1), paratype, low focal plane.
27. *Rugutricolporites cumulus* n. sp., Ozuitem 3.1 (V40,4), paratype, low focal plane.
34. *Tricolporites torus* n. sp., Amaogugu 1.1 (W67,1), holotype, high focal plane.
35. *Tricolporites torus* n. sp., Amaogugu 1.1 (W67,1), holotype, mid focal plane.
36. *Tricolporites torus* n. sp., Amaogugu 1.1 (W67,1), holotype, low focal plane.
37. *Tricolporites torus* n. sp., Okigwe A1.1 (F66), paratype, high focal plane.
38. *Tricolporites torus* n. sp., Okigwe A1.1 (F66), paratype, mid focal plane.
41. *Tricolporites densus* n. sp., Okigwe B3.1 (S46), paratype, high focal plane.
42. *Tricolporites densus* n. sp., Okigwe B3.1 (S46), paratype, low focal plane.
PLATE 7

1. *Tricolporites “reticulomargites”*, Ozuitem 6.1 (H36), high 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.
18. *Casuarinidites foveolatus* n. sp., Ameke 11.1 (N52,1), holotype, high focal plane.
22. *Clavatriciporites dispersiclavatus* n. sp., Okigwe B1.1 (K48,4), paratype.
23. *Clavatriciporites spicatus* n. sp., Okigwe B6.1 (S47,4), holotype.
24. *Clavatriciporites spicatus* n. sp., Okigwe B6.1 (S47,4), paratype, high focal plane.
25. *Clavatriciporites spicatus* n. sp., Okigwe B6.1 (S47,4), paratype, low focal plane.
29. *Corsinipollenites “striatus”*, Ozuitem 3.1 (X58,2), high focal plane.
30. *Corsinipollenites “striatus”*, Ozuitem 3.1 (X58,2), low focal plane.


PLATE 8


5. *Retitriporites irregularis* n. sp., Ozuitem 6.1 (H40,4), holotype, mid focal plane.
7. *Retitriporites irregularis* n. sp., Ozuitem 3.1 (M43), paratype, low focal plane.
8. *Retitriporites* “*robustus*”, Ameke 1.1 (M65,1), high focal plane.
17. *Syncolporites marginatus* van Hoeken Klinkenberg 1964, Ozuitem 6.1 (T40), high focal plane.
21. *Syncolporites rostro* n. sp., Ozuitem 3.1 (X36,1), holotype, high focal plane.
22. *Syncolporites rostro* n. sp., Ozuitem 3.1 (X36,1), holotype, mid focal plane.
23. *Syncolporites rostro* n. sp., Ozuitem 3.1 (X36,1), holotype, low focal plane.
25. *Syncolporites* sp., Amaogugu 1.1 (L39,2), mid focal plane showing details of the exine.
31. *Foveostephanocolpites* sp. 1, Ameke 1.1 (K55,2).
32. *Foveostephanocolpites* sp. 2, Ozuitem 3.1 (Q62).
37. *Scabrastephanocolpites “irregularis”, Okigwe A5.1 (U50,1).
41. *Retistephanoporites* sp., Ameke 1.1 (M44,2).
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.