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Organic-walled microfossil biostratigraphy and chemostratigraphy of the Ediacaran Volta Basin in Ghana

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Abstract.

A moderately diverse assemblage of Doushantuo-Pertatataka-type (DPA) organic-walled microfossils was recovered for the first time from shales of the Volta Basin of Ghana, West African Craton (WAC). Biostratigraphic and chemostratigraphic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) data for the Kodjari and Pendjari formations were integrated to provide age constraints and establish correlations with other Ediacaran basins. The Kodjari Formation carbonates, developed on a glacial diamictite, have negative carbon isotope values consistent with those for Marinoan cap carbonates. The Pendjari Formation mudstones overlie the Kodjari Formation cap carbonates and have yielded microfossils characteristic of the early Ediacaran, most similar to the assemblages of south-central Australia and Siberia. Carbon and nitrogen isotope values of the Kodjari and Pendjari formations indicate deposition in a shallow-marine, oxygenated environments in a basin with a large nitrate reservoir. The assemblage contains 29 taxa, including diverse acanthomorphs, and it broadly corresponds to the *Tanarium-Schizofusa-Variomargosphaeridium* Zone established in Australia and the *Tanarium conoideum*–*Hocosphaeridium scaberfacium*–*Hocosphaeridium anozos* Zone in China. However, in Ghana, some taxa diagnostic of different eponymous zones in other regions (*Ceratosphaeridium glaberosum*, *Shizofusa zangwenlongii*, *Tanarium conoideum*) appear together throughout the stratigraphic section. Diversity declines at the top of the succession and DPA taxa are replaced by abundant leiosphaerids and budding and flask-shaped

microfossils, which are more characteristic of the post-Shuram anomaly interval. These data establish an early Ediacaran age for the Pendjari Formation and confirm the global distribution and stratigraphic significance of DPA. The Pendjari assemblage further demonstrates a rapid diversification of eukaryotic microbiota following the Marinoan global glaciation.

Keywords:

Ediacaran

Doushantuo-Pertatataka acritarchs

West Africa Craton

Organic-walled microfossils

Chemostratigraphy

Cap carbonate

1. Introduction

The early Ediacaran biosphere, before the rise of widespread macroscopic life (Xiao and Narbonne, 2020), is largely characterised by ornamented, single-celled microfossils commonly referred to as the Doushantuo-Pertatataka acritarchs/microflora (DPA/DPM; Zhou et al., 2001) or Ediacaran Complex Acanthomorph Palynoflora (ECAP; Grey et al., 2003). These microfossils evolved in a period of rapid diversification of complex eukaryotic life in the aftermath of the youngest low-latitude glacial episode of the Cryogenian Period (i.e., the Snowball Earth; Hoffman et al., 2017) and offer insight into pre-macroscopic multicellularity (Cunningham et al., 2017; Agić et al., 2019), but both their global and temporal distributions are still poorly resolved. DPA are organic-walled microfossils (OWM), i.e. soft-bodied, organic remains of a variety of prokaryotic organisms and complex eukaryotic cells/cysts, a fossil group that showcases microbial diversity throughout most of Earth's history (e.g., Agić and Cohen, 2021). DPA rapidly diversified and became widespread in the early Ediacaran, so their fossil record was used in establishing regional biozones and correlation among Australia, Brazil, South China, India, Norway, Greenland, and Russia (Vidal, 1990; Grey, 2005; Zhou et al., 2007; Sergeev et al., 2011; Liu et al., 2014a; Shukla and Tiwari, 2014; Xiao et al., 2014; Liu and Moczyłowska, 2019; Willman et al., 2020; Morais et al., 2021; Vorob'eva and Petrov, 2023; Agić et al., 2024; Xiao et al., 2024; Matos and Silva Caminha, 2025). However, the full extent of their distribution, stratigraphic range, and utility in subdivision of the Ediacaran Period continues to be explored (Anderson et al., 2019; Grazhdankin et al., 2020), while their fossil record can cast light on the biosphere recovery in the aftermath of the Snowball Earth glaciations.

Hitherto, DPA have not been reported from the West Africa Craton (WAC), with the exception of an occurrence of a single acanthomorph in the Nioro Group in Mali (Rossi, 1982), that was tentatively attributed to taxon *Papillomembrana*, otherwise known from the phosphorites of Norway and India (Spjeldnæs, 1963; Shukla and Tiwari, 2014). The Ediacaran strata on the African continent have been mainly explored on the Kalahari Craton, where the Nama Group of Namibia and South Africa played an important role in understanding of the early biomineralization, expansion of bioturbation, and evolutionary dynamics of early macroorganisms (e.g., Penny et al., 2014; Nelson et al., 2022; Bowyer et al., 2023; Darroch et al., 2025). Its scarce Ediacaran OWM record yielded depauperate, but biostratigraphically informative assemblages (Germs et al., 1986; Gaucher et al., 2005; Agić et al., 2022). The West

African and Congo cratons, on the other hand, feature predominantly older units, estimated to be late Mesoproterozoic in age based on biostratigraphy (Couëffé and Vecoli, 2011; Baludikay et al., 2016) as well as the upper Neoproterozoic strata that include glaciogenic deposits. The Volta Basin developed on the West African Craton contains the late Neoproterozoic succession with glaciogenic deposits, assumed to record the Marinoan Snowball Earth glaciation on chemostratigraphic basis (Porter et al., 2004; Nédélec et al., 2007), however, there were no biostratigraphic data to allow for the correlation of the late Neoproterozoic units in the area.

Here, we present results of the combined micropalaeontological and chemostratigraphic study of the Meso- to Neoproterozoic sedimentary succession of the Volta Basin in Ghana, with the focus on the upper Mesoproterozoic Kwahu and upper Neoproterozoic Oti-Pendjari groups based on outcrop material (Fig. 1). Palaeontological exploration was coupled with organic carbon ($\delta^{13}\text{C}_{\text{org}}$) and nitrogen ($\delta^{15}\text{N}$) isotope chemostratigraphy of mudstones and carbonate carbon ($\delta^{13}\text{C}_{\text{carb}}$) and oxygen ($\delta^{18}\text{O}_{\text{carb}}$) isotope chemostratigraphy of carbonates to constrain the age of the units and examine the palaeoenvironmental conditions and the biotic response to the Marinoan glaciation immediately after deposition of cap carbonates. Palynological recovery only revealed minor leiosphaerids in the Poubogou Formation (Kwahu Group) and a diverse and moderately to well-preserved OWM assemblage in the Pendjari Formation, which includes DPA taxa comparable to the early Ediacaran assemblages from Australia, Brazil, China, and Russia. The analysis of palaeoenvironmental conditions indicates deposition in shallow-marine, oxygenated settings in a sedimentary basin that sustained a large dissolved nitrate reservoir. The microfossils provide the first reliable biostratigraphic age constraints for the Volta Basin units and show a rapid diversification in the aftermath of the Marinoan Snowball Earth glaciation.

2. Geological setting

Sedimentary rocks of the Volta Basin are exposed in the NE part of Ghana as well as in parts of Benin, Burkina-Faso, Niger, and Togo, on the WAC (Fig. 1(A)). In Ghana, the Volta Basin strata are divided into three major units: the Mesoproterozoic Kwahu-Bombouaka Group, the Neoproterozoic Oti-Pendjari Group, and the Ordovician-Devonian Tamale-Obosum Group (Fig. 1(B); Kalsbeek, 2008; Kalsbeek and Frei, 2010). The lowermost Kwahu-Bombouaka Group lies unconformably on the Paleoproterozoic crystalline basement, and comprises three siliciclastic units: the Tossiegou, Poubogou, and Panabako formations (Carney et al., 2010). The

approximately 100 m thick Poubogou Formation, investigated herein, contains mudstones and siltstones, and minor sandstones and limestones, representing a shallow-marine to off-shelf setting (Carney et al., 2010; Abu et al., 2019). Analysis of the middle Poubogou Formation shales yielded a Rb/Sr isochron age of 993 ± 65 Ma (Clauer, 1976; Clauer et al., 1982). The overlying Panabako Formation contains feldspathic and quartzitic sandstones, with herringbone cross-stratification indicating a shallow-marine, tidal setting (Affaton et al., 1980; Carney et al., 2010). Detrital zircons from these sandstones set the maximum depositional age at ca. 1.1-1.0 Ga (Akah, 2008; Kalsbeek et al., 2008).

The overlying Oti-Pendjari Group is divided into the Kodjari and Pendjari formations. The Kodjari Formation contains carbonates, cherts, mudstone and argillaceous shale (Fig. 2(A, B)), deposited in shallow-marine, passive continental margin settings (Affaton et al., 1980; Kalsbeek, 2008; Carney et al., 2010; Abu et al., 2022, 2023). In the upper part of the Kodjari Formation, the Darebe Tuff Member contains mudstones and argillaceous shales and is developed locally. It has the maximum depositional age of 601.3 ± 2.0 Ma, based on ID-TIMS U-Pb zircon analyses (Carney et al., 2010). Clast-rich carbonate lenses at the base of the Kodjari Formation contain pebbles of the basement rocks and chert, and were interpreted as glaciogenic diamictites ('mixtites'; Affaton et al., 1980), based on the presence of striated pavement underneath the unit exposed in eastern Burkina Faso (Leprun and Trompette, 1969; Trompette, 1981). Glacial deposits are widespread in the Volta Basin and occur as a part of a triad package of diamictites, carbonates, and siltstones, generally linked to the Marinoan glaciation (Nédélec et al., 2007). In Togo, the Kodjari cap carbonates are overlain by the locally exposed Porga Group, a minor shale and phosphorite deposit where shales have been dated at 660 ± 9 Ma (Rb-Sr isochron age on clay-minerals; Clauer and Deynoux, 1987).

The Pendjari Formation is much thicker, up to 3 km in thickness based on regional correlations (Affaton et al., 1975), and dominated by shales and siltstones (Fig. 2(C, D)) that are occasionally rhythmically bedded and deposited in a marine foreland basin (Affaton et al., 1980; Carney et al., 2010; Abu et al., 2023). These sediments underwent milder diagenesis than the rest of the Volta Basin siliciclastics, based on illite crystallinity (Affaton et al., 1980). Some shale to siltstone sequences are shallowing upwards and have been compared to flysch deposits in a marine foreland basin (Affaton et al., 1980). The youngest unit in the area, the Tamale–Obosum Group, is an undifferentiated succession with red sandstones, mudstones, and conglomerates

(Carney et al., 2010). It was constrained to be “post-Cambrian”, likely Ordovician–Carboniferous in age based on regional correlation (Kalsbeek et al., 2008; Carney et al., 2010; Abu et al., 2023).

Microfossils were reported mainly from the older, Mesoproterozoic strata in the basin. An assemblage of moderate diversity of leiosphaerids, cell aggregates, and photosynthesizing eukaryote *Arctacellularia* occurs in the Abetifi Formation, middle Kwahu Group (Couëffé and Vecoli, 2011). In the Ota-Pendjari Group in Benin, Amard (1992) reported large sphaeromorphs *Chuaria*, which have a long stratigraphic range from Paleoproterozoic to Cambrian (Ye et al., 2015a).

3. Material and methods

3.1. Sampling

Fifty rock samples were collected in outcrops from the Kodjari and Pendjari formations, in addition to five samples from the underlying Poubogou Formation of the Kwahu-Bambuaka Group (AMM and AME sections). Shale and siltstone samples from each horizon were split for micropalaeontological and geochemical ($\delta^{13}\text{C}_{\text{org}}$, TOC, $\delta^{15}\text{N}$, TN) analyses. Carbonate samples from the Kodjari Formation (AMB and AA sections) were analysed for carbonate carbon and oxygen isotope values. Fossiliferous samples from the Pendjari Formation were collected from three continuous sections in the Yendi-Sabare area (AMY) in the northeastern part of the Volta Basin (Fig. 1) and represent the lower part of the formation. The lowest section of grey shales (AMY) sits ~50 m above the Kodjari Formation cap carbonate.

3.2. Palynological acid maceration

Organic-walled microfossils were extracted from the rock matrix using a palynological acetolysis procedure for recovery of large Precambrian microfossils (Grey, 1999, 2005). Shale and siltstone samples were immersed in 30% hydrochloric acid (HCl) for 24h for surficial cleaning and carbonate removal. The samples were then macerated in 48% hydrofluoric acid (HF) for up to 4 days. The resulting residue was cleaned with deionised (DI) water until near neutral, then boiled in 30% HCl for approximately 10 minutes to remove fluorides. The residue was cleaned with DI water again, then filtered through the 25 μm steel mesh whilst agitated by a gentle stream of DI water. Forceful filtering and centrifuging were avoided to minimize the breakage of large fragments of delicate organic microfossils. The filtrate was stored in glass vials

and ethanol and methanol were added to prevent the growth of contaminants. For each sample, a drop of the filtrate was mounted with a pipette onto a glass slide.

3.3. Microscopy and micropalaeontology

The preparates were observed with a transmitted light microscope Zeiss Axioskop 40 and imaged with Leica DM 2700, using Leica LAS EZ4 software. Microfossils were imaged and point-counted on two slides for each sampled horizon to provide an estimate of OWM abundance and diversity (Supplementary Table 1). Taxonomic nomenclature follows the International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code). All illustrated specimens are deposited in the Cork Geological Museum, under designation CKGMF (Supplementary Information).

3.4. Chemostratigraphy

Data are available in Supplementary Table 2 and were analysed using R (R Core Team, 2021), and figures were made using the ggplot2 package (Wickham et al. 2016).

3.4.1. Carbon and oxygen isotope analysis of carbonate samples

Outcrop samples were cut with a diamond saw and polished to obtain fresh surfaces. After rinsing the polished surfaces with deionized (DI) water, least altered portions were micro-drilled with a diamond drill-bit. Carbonate carbon ($\delta^{13}\text{C}_{\text{carb}}$) and oxygen ($\delta^{18}\text{O}_{\text{carb}}$) isotope analysis was carried out at the Stable Isotope Geochemistry Laboratory at the University of California, Riverside, using a Thermo Scientific Gas Bench II device connected to a Delta V Advantage isotope-ratio mass-spectrometer (IRMS) in a continuous-flow mode. The micro-drilled powders were reacted with phosphoric acid in a glass tube at 50°C for 24 h before the analysis. Two international standards, NBS 18 and NBS 19, and one calibrated internal dolomite standard (Tytyri, $\delta^{13}\text{C} = +0.78\text{‰}$ V-PDB and $\delta^{18}\text{O} = -7.07\text{‰}$ V-PDB; Karhu, 1993) were analysed along with the unknown samples to calibrate isotopic data and correct oxygen isotope values for dolostone samples. $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ values are reported in standard delta notation relative to the Vienna Pee Dee Belemnite (V-PDB). Analytical precision was 0.2‰ (1 σ) for $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ based on repeated analyses of standards.

3.4.2. Organic carbon and nitrogen isotope analyses of carbonates and shales

Prior to organic carbon and nitrogen isotope analyses, carbonate and shale samples were powdered using an agate shatterbox and acidified with 6M HCl for three days to dissolve carbonate minerals. The residue was washed with ultrapure water, then dried. Organic carbon ($\delta^{13}\text{C}_{\text{org}}$) and nitrogen ($\delta^{15}\text{N}$) isotope analyses were conducted at the Stable Isotope Geochemistry laboratory of the University of California, Riverside using a Costech ECS 4010 Elemental Analyzer (EA) coupled to a Thermo Scientific Delta V Advantage IRMS. Carbon isotope data were calibrated with a two-point method using international glutamic acid standards (USGS 40 and 41a). A sediment standard (USGS Devonian Ohio shale, SDO-1; $\delta^{13}\text{C}_{\text{org}} = -30.0 \pm 0.1\text{‰}$, $\delta^{15}\text{N} = -0.8 \pm 0.3\text{‰}$; Dennen et al., 2006) and an in-house standard UW-McRae shale ($\delta^{13}\text{C}_{\text{org}} = -37.4\text{‰}$, $\delta^{15}\text{N} = +5.6\text{‰}$; Stüeken et al., 2015) were also analysed with samples, and the replicate analyses of SGR-1b (Dennen et al., 2006) yielded $\delta^{13}\text{C}_{\text{org}}$ values of $-29.5 \pm 0.1\text{‰}$. Obtained $\delta^{13}\text{C}_{\text{org}}$ and total organic carbon (TOC) values were calibrated with standards, and isotope values were normalized to the V-PDB scale. $\delta^{15}\text{N}$ and total nitrogen (TN) data were calibrated with three standard materials: USGS40, USGS41a and SDO-1, and in-house standard UW-McRae, and are reported in standard delta notation relative to air. The mean and standard deviation of UW-McRae among all runs were $+5.66 \pm 0.13\text{‰}$ (1σ ; $n = 18$), which is consistent with the previously reported value of $+5.51 \pm 0.19\text{‰}$ (Stüeken et al., 2015). The analytical precision of each $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}$ measurement was better than 0.2‰ and 0.3‰ , respectively (1σ). Samples exhibiting relatively high $\delta^{13}\text{C}_{\text{org}}$ values were re-treated with HCl at 60°C to confirm that all carbonates were completely removed. Duplicate nitrogen analyses were made on all samples and carbon and nitrogen isotope data are reported in Supplementary Table 2.

4. Results

4.1. Micropalaeontology

Twenty-nine OWM morphotypes were recovered from 16 fossiliferous shale and siltstone samples from the Volta Basin in Ghana. Over 300 OWM were recorded. The highest abundance of fossils and the highest taxonomic diversity occur in the Pendjari Formation, Ota-Pendjari Group (Fig. 3). The underlying Kodjari Formation carbonates with argillaceous intervals yielded only minor kerogens, but no microfossils. Samples from the underlying Poubogou Formation of the poorly age-constrained upper Mesoproterozoic/lower Tonian Kwahu-Bombouaka Group were

mainly barren, with the exception of two horizons bearing a depauperate leiosphaerid assemblage (Fig. 4; Supplementary Table 1).

The Pendjari Formation OWM are light- to dark-brown in colour and moderately dull. This corresponds to the thermal alteration index (TAI; cf. [Marshall, 1991](#)) of 3-4 (Supplementary Information) and suggests a diagenetic burial temperature corresponding to petroleum generation, consistent with the Rock-Eval pyrolysis data ([Abu et al., 2022](#)). This is higher thermal maturity than that documented for the Pendjari ‘Supergroup’ (=Formation) in neighbouring Benin and Burkina Faso, which was estimated at TAI 2.5 ([Amard, 1992](#)).

OWM taxa in the Pendjari Formation correspond to the Ediacaran Doushantuo-Pertatataka-type acritarchs (DPA; Figs. 5–8) and broadly fall into two distinct assemblages (see Discussion), sharing most similarities to the assemblages from south-central Australia, Siberia, then Baltica (East European Platform and Norway) and central Brazil ([Grey, 2005](#); [Willman et al., 2006](#); [Willman and Moczyłowska, 2008](#); [Vorob’eva et al., 2009](#); [Moczyłowska and Nagovitsin, 2012](#); [Vorob’eva and Petrov, 2023](#); [Matos and Silva Caminha, 2025](#)). Taxonomic composition of the DPA assemblage changes through the Pendjari Formation section (Fig. 3). The OWM abundance and highest species richness are in the lower part of the unit (0–45 m from the base), in the grey shale interval (Supplementary Table 1). Both species richness and abundance decline then and recover in the middle part of the unit (65–69 m stratigraphic height interval) containing green shales. The lower part of the Pendjari Formation contains some taxa from the oldest DPA zones established in Australia (*Appendisphaera anguina*, *Schizofusa zangwenlongii*, *Tanarium tuberosum*), but also taxa with globally younger first appearance datum (FAD) such as *Hocosphaeridium anozos*, *Tanarium conoideum*, and *Multifronsphaeridium ramosum*. The uppermost part of the section (70–100 m) was mostly barren, with few productive horizons with high OWM abundance but low species richness. At this level, DPA taxa are replaced by simple sphaeromorphs *Leiosphaeridia* (Fig. 7). Broadly, this assemblage is similar to that of the Late Ediacaran Leiosphere Palynoflora ‘Zone’ (LELP; [Grey, 2005](#)) characteristic of the post-Shuram Ediacaran interval ([Grey, 2005](#); [Agić et al., 2022](#)). Notably, the upper assemblage also contains budding microfossils *Gemmuloides doncookii* known from Meso- to Neoproterozoic strata, as well as undescribed forms (Fig. 8(A, B)). Based on the present material, we emended *Multifronsphaeridium ramosum*.

Microfossil abundance and species richness covary through most of the Pendjari Formation, except in the upper part. The horizon with the second highest fossil abundance (AMY-18) is of the lowest diversity (6 taxa) and it is dominated by leiosphaerids (Figs. 3, 9; Supplementary Table 1), indicating that the overall diversity decline in the upper unit represents a real signal and not an artefact tied to fossil abundance.

4.2. Carbonate and organic carbon chemostratigraphy

Green shale samples from the Poubogou Formation of the Kwahu-Bombouaka Group (AMM and AME series from the southeastern and central to southern parts of the basin, respectively) contain low TOC content, ranging from 0.08 to 0.028 wt.%, with $\delta^{13}\text{C}_{\text{org}}$ values between -27.9 and -26.2‰ V-PDB (Supplementary Table 2). They contain low TN content (0.09–0.047 wt.%) with a large range of N isotope values from +3.5 to +8.2‰ Air. C/N values are low for AME samples (0.5 to 0.7), but higher for AMM samples (9.9 and 10.5).

Carbonate samples from the lowermost Ediacaran Kodjari Formation are relatively pure dolostones and limestones and show negative $\delta^{13}\text{C}_{\text{carb}}$ values, consistent with their cap carbonate origin, without a clear stratigraphic trend, but with more negative values in the AMB section (-5.8 to -1.9‰ V-PDB) compared to the AA section (-3.8 to -2.0‰ V-PDB; Fig. 10 (A, B); Supplementary Table 2). Oxygen isotope values are also more negative in the AMB section (-9.2 to -3.6‰ V-PDB, most analyses are more negative than -6.0‰ V-PDB) with respect to the AA-section (-14.6 to -3.0‰ V-PDB, most data are more positive than -7.0‰ V-PDB). The carbonates contain very low organic content, ranging from 0.0004 to 0.0125 wt.%, with $\delta^{13}\text{C}_{\text{org}}$ values between -30.3 and -26.5‰ V-PDB, resulting in a fractionation between inorganic and organic carbon of 20.7 to 27.8‰ V-PDB. Samples have low total nitrogen content (0.0002 to 0.0060 wt.%), resulting in molar C/N from 1.2 to 11.7, with $\delta^{15}\text{N}$ values ranging from +1.7 to +5.0‰ Air.

Dark-grey to green shales of the lower Ediacaran Pendjari Formation have low TOC content (0.0005 to 0.0690 wt.%) with C-isotope values ranging from -30.5 to -26.7‰ V-PDB (Fig. 11; Supplementary Table 2). Nitrogen content is low, ranging from 0.0005 to 0.0690 wt.%, resulting in a small range of C/N values of 1.2 to 3.5. Nitrogen isotope range is also small from +5.0 to +6.8‰ Air.

4.3. Systematic palaeontology

Genus ***Appendisphaera*** Moczyłowska, Vidal and Rudavskaya, 1993

Type species: *Appendisphaera grandis* (Moczyłowska et al., 1993).

Appendisphaera anguina Grey, 2005

Fig. 5(A, B)

cf. 2003. *Appendisphaera* sp. - Grey et al., p. 462, fig. 4D.

2005. *Appendisphaera anguina* nov. sp. - Grey, p. 208, fig. 90A–C.

cf. 2009. *Appendisphaera* aff. *anguina* Grey - Vorob'eva et al., p. 175, fig. 9.9.

2014. *Appendisphaera anguina* Grey - Liu et al., p. 10, fig. 6.

non 2016. *Appendisphaera* aff. *anguina* Grey - Prasad and Asher, p. 40, pl. I, figs. 3–4 (= *A. tenuis*).

2019. *Appendisphaera anguina*? Grey - Ouyang et al., p. 180, fig. 8A, B.

2022. *Appendisphaera anguina*? Grey - Ye et al., p. 14, fig. 7D–K.

Holotype: Specimen CPC 36386 at Commonwealth Palaeontological Collection (CPC) at Geoscience Australia, from the Munta 1 drillcore of the Ediacaran Tanana Formation, Australia (Grey, 2005: fig. 92A).

Material: Seven specimens and one fragment from the lower Pendjari Formation.

Occurrence: Ediacaran: Unglolya Group (Officer Basin) and Pertatataka Formation (Amadeus Basin) in Australia (Grey, 2005); upper Member II (Ye et al., 2022) and lower Member III of the Doushantuo Formation in China (Liu et al., 2014a; Ouyang et al., 2019; Liu and Moczyłowska, 2019).

Measurements: The vesicle diameter of the Pendjari specimens ranges 93–120 μm ($\mu = 109 \mu\text{m}$, $\sigma = 8$, $N = 8$). The mean process length is 43 μm ($\sigma = 4$, $N = 30$) and their thickness is around 1–3 μm . The process length is around 40% of the overall specimen diameter (vesicle + processes).

Description: Circular organic-walled vesicles with abundant, long, thin, contorted and highly flexible processes. The processes have slightly wide bases separate from one another, but are narrow and homomorphic and hollow inside. The processes are distributed densely across the vesicle surface. Where unbroken, the process termini taper slightly and are contorted.

Remarks: Grey (2005) emended the diagnosis of the genus *Appendisphaera* to state that the processes are solid or “nearly solid”, but also noted that, in the Australian material, it was

“difficult to determine if they are solid or hollow” in *A. anguina* (p. 207). However, some paratypes do show that the broad bases of the processes are in open communication with the vesicle interior (Grey, 2005: fig. 30B). Upon re-examining the type material, Moczyłowska (2005) mentioned that the processes are likely open, but no new illustrations were provided and the taxon was not formally emended. The open nature of the processes is confirmed by observations on our material, as well as the specimens tentatively identified as *A. anguina*? from South China (Ouyang et al., 2019; Ye et al., 2022).

The Pendjari specimens are slightly smaller than the Australian type material (ranging 118–224 µm, measured including the processes; Grey, 2005) and the Chinese specimens (250–600 µm; Liu et al., 2014a), but if process length is included in the overall diameter, there is an overlap in sizes. The length and shape of the processes and the ratio of process size to overall diameter of the vesicle (40%) is consistent with the type material.

Genus ***Asseserium*** Moczyłowska and Nagovitsin, 2012

Type species: *Asseserium diversum* from the lower Ediacaran Ura Formation in Patom Uplift, Russia (Moczyłowska and Nagovitsin 2012).

Asseserium fusulentum Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, 2012 Fig. 5(D)

1992. *Leiofusa bicornuta* Sin and Liu - Zang and Walter, p. 286, pl. 7, fig. K.

1996. *Dactylofusa verilera* Cocchio - Brocke, p. 355, pl. 2, fig. 7.

cf. 2009. *Galeasphaeridium bicorporis* nov. sp. - Vorob’eva et al., fig. 10.6–10.10.

2012. *Asseserium fusulentum* nov. sp. - Moczyłowska and Nagovitsin, p. 13, fig. 5E, F.

2019. *Asseserium fusulentum* Nagovitsin and Moczyłowska - Liu and Moczyłowska, p. 65, fig. 31C.

2021 *Asseserium fusulentum* Nagovitsin and Moczyłowska - Morais et al., fig. 5B.

cf. 2024. *Asseserium* cf. *fusulentum* Nagovitsin and Moczyłowska - Agić et al., fig. 4B.

cf. 2025. *Asseserium* cf. *diversum* Nagovitsin and Moczyłowska - Matos and Silva Caminha, p.7, pl. 1, fig. C.

2025. *Asseserium fusulentum* Nagovitsin and Moczyłowska - Matos and Silva Caminha, p. 7, pl. 1, fig. D.

Holotype: Specimen PN8/4-17/3-5 from the Ura Formation, Russia (Moczyłowska and Nagovitsin, 2012: fig. 5G).

Material: Three specimens and a fragment from the Pendjari Formation.

Occurrence: Lower–middle Ediacaran Ura Formation in Siberia (Moczyłowska and Nagovitsin, 2012), lower Ediacaran Doushantuo Formation in China (Liu and Moczyłowska, 2019), Ediacaran Bocaina Formation (Morais et al., 2021) and Araras Group (Matos and Silva Caminha, 2025) in Brazil. Very similar microfossils also occur in the lower Ediacaran of Norway (Agić et al., 2024).

Description: Ovoid to ellipsoidal vesicles with elongated ends. On the poles, the vesicles bear conical extensions with dull tips, giving the vesicle a bipolar symmetry. The processes are stubby and 8–18 μm long ($\mu = 13.8 \mu\text{m}$, $\sigma = 4.3 \mu\text{m}$, $N = 5$). Along the long axis, the diameter of the Pendjari Formation vesicles is 88–102 μm long ($\mu = 93.3 \mu\text{m}$, $\sigma = 7.6 \mu\text{m}$, $N = 3$).

Remarks: The Pendjari specimens are poorly preserved, and the vesicles have a chagrinated texture and scars from mineral growth (Fig. 5(F)). However, they fall in the size range and morphology of *A. fusulentum* (Moczyłowska and Nagovitsin, 2012) and contain only a single tip on both poles, so we include them into this taxon. Similar poorly-to-moderately preserved specimens were reported from the Araras Group in Mato Grosso, Brazil and identified as *Asseserium* cf. *diversum* (Matos and Silva Caminha, 2025). Although the Araras specimens do not have well-preserved extensions to distinguish between *A. fusulentum* (single extension on each pole) and *A. diversum* (uneven number of polar extensions), they are symmetrical, similar to the Pendjari specimens. This is more characteristic of *A. fusulentum* vesicles (Moczyłowska and Nagovitsin, 2012: fig. 5C) as opposed to *A. diversum* vesicles that tend to be wider on the pole that contains multiple extensions (Moczyłowska and Nagovitsin, 2012: fig. 5C). Despite the poor preservation, both occurrences indicate a cosmopolitan distribution of *Asseserium* in the early Ediacaran.

Genus ***Blastanosphaira*** Javaux and Knoll, 2017

Type species: *Blastanosphaira kokkoda* from the Mesoproterozoic Roper Group, Australia (Javaux and Knoll, 2017).

Blastanosphaira kokkoda Javaux and Knoll, 2017

Fig. 8(F, G)

2005. ?‘*Vanvarataenia*’ string of spheroids - Grey, p. 352, fig. 275A, B.

2017. *Blastanosphaira kokkoda* nov. sp. - Javaux and Knoll, p. 203, fig. 1.1–1.11.

cf. 2020. Unknown sp. 2 - Arvestål and Willman, fig. 5D.

2025. Unnamed colonial form A - Matos and Silva Caminha, p. 22, fig. 8A, B.

2026. *Blastanosphaira kokkoda* Javaux and Knoll - Cruz et al., p. 7, fig. 6A–J.

Holotype: Specimen on slide U5 569.1 m, from the Mainoru Formation, Roper Group (Javaux and Knoll, 2017: fig. 2.1).

Material: Three specimens from the Pendjari Formation.

Occurrence: Mesoproterozoic Roper Group, Australia (Javaux and Knoll, 2017); lower Ediacaran Pertatataka Formation in Amadeus Basin and the upper? Ediacaran Tanana Formation in Officer Basin, Australia (Grey, 2005); lower Ediacaran Araras Group, Brazil (Cruz et al., 2026); herein.

Measurements: Vesicle diameter ranges 67–105 μm ($\mu = 89.3 \mu\text{m}$, $\sigma = 12.7 \mu\text{m}$, $N = 9$), measured on three colonies. The diameter of the largest cell in all colonies is uniform, 98–105 μm ($\mu = 101.6 \mu\text{m}$, $\sigma = 3.5 \mu\text{m}$, $N = 3$), in the size range of the type material.

Description: Circular cells with a thin chagrinate wall. Vesicles are connected with septa-like joints. Smaller cells are budding out of a larger cell.

Remarks: Similar OWM in fragmented chains occur in lower Ediacaran strata of the Amadeus Basin, as well as in the LELP-horizons in the Officer Basin in Australia (Grey, 2005: fig. 275A). Both the original material and the Ediacaran material from Australia and Brazil show size heterogeneity of the connected vesicles, similar to the jointed cells in the Pendjari Formation (Fig. 8(F)).

Genus *Calyxia* Willman in Willman and Moczyłowska, 2008

Type species: *Calyxia xandaros* from the Ediacaran Tanana Formation, Australia (Willman and Moczyłowska, 2008).

?*Calyxia xandaros* Willman in Willman and Moczyłowska, 2008

Fig. 5(G)

419 cf. 2008. *Calyxia xandaros* nov. sp. - Willman in Willman and Moczyłowska, p. 521, figs. 4A–
420 F, 5A, B.

421 **Holotype:** Specimen J56/1 from the lower Tanana Formation in Australia, Giles 1 drillcore at a
422 depth of 481.15 m (Willman and Moczyłowska, 2008: fig. 4A).

423 **Material:** Two fragments from the Pendjari Formation.

424 **Occurrence:** *C. xandaros* occurs in the Ediacaran Tanana Formation in the Officer Basin,
425 Australia (Willman and Moczyłowska, 2008) and the Doushantuo Formation in South China
426 (Liu and Moczyłowska, 2019).

427 **Description:** Vesicle fragments appear to be torn. At the open end, the vesicle ends in long,
428 tapering, ribbon-like extensions aligned in one direction.

429 **Remarks:** Willman and Moczyłowska (2008) concluded that the shape of the ribbon-
430 extensions, when closed, would encompass a rounded-to-elongate vesicle. Thus, the extensions
431 are likely remnants of the vesicle wall after it has been torn apart during excystment. This is a
432 unique opening type compared to other more common split-excystment whereby the vesicle tends
433 to open in two halves (e.g. *Schizofusa rizzoria*). The Pendjari Formation material is mainly
434 fragmented and the extensions appear to have been torn from the main vesicle during transport,
435 so here we tentatively include those specimens into *Calyxia*.

436

437 Genus ***Cavaspina*** Moczyłowska, Vidal and Rudavskaya, 1993

438 **Type species:** *Cavaspina acuminata* (Kolosova, 1991) from the Ediacaran Torgo Formation,
439 Torgo G-2 borehole, Siberian Platform, Russia (Moczyłowska et al., 1993).

440 **Remarks:** One of the defining characteristics of *Cavaspina* are short processes <10% of the
441 vesicle diameter. While this is broadly the case for many taxa with short processes in the Pendjari
442 Formation, *Cavaspina* differs from specimens of *Gyalosphaeridium* in having broader process
443 bases connected with the vesicle interior.

444

445 *Cavaspina uria* Nagovitsin and Faizullin in Nagovitsin et al., 2004 recomb. Nagovitsin and
446 Moczyłowska, 2012

447 Fig. 5(C)

448 2004. *Goniosphaeridium urium* nov. sp. - Nagovitsin and Faizullin in Nagovitsin et al., p. 13, pl.
449 2, fig. 1

2006. *Cavaspina* sp. - Veis et al., pl. 1, fig. 7, pl. 2, figs. 3–5.
 2011. *Gyalosphaeridium minutum* Nagovitsin and Faizullin- Sergeev et al., p. 1004, fig. 7.7.
 2012. *Cavaspina uria* nov. comb. - Nagovitsin and Moczyłowska in Moczyłowska and
 Nagovitsin, 2012, p. 12, fig. 4G, H.
 2022. *Cavaspina uria* Nagovitsin and Moczyłowska - Shi et al., fig. 7I–M.
 2024. *Cavaspina uria* Nagovitsin and Moczyłowska - Ouyang et al., p. 20, fig. 10.2, 10.3.
 2024. *Cavaspina* sp. - Palacios, p. 674, fig. 6c.
Holotype: Specimen 2 on prepare no. 673, 8/17-2 from the Baikal Horizon, Ura Formation,
 Patom Uplift, Russia (Nagovitsin et al., 2004: pl. 2, fig. 4).
Material: Four specimens and a fragment in the lower Pendjari Formation.
Occurrence: Lower Ediacaran Ura Formation, Siberia (Nagovitsin et al., 2004; Moczyłowska
 and Nagovitsin, 2012) and Vychegda Formation, East European Platform/Baltica (Veis et al.,
 2006) in Russia; lower Ediacaran Doushantuo Formation in the Hunan Province in China (Shi et
 al., 2022; Ouyang et al., 2024); herein.
Measurements: Vesicle diameter ranges 82–95 μm ($\mu = 88 \mu\text{m}$, $\sigma = 6 \mu\text{m}$, $N = 4$) in size. The
 processes are 15–22 μm long ($\mu = 17 \mu\text{m}$, $\sigma = 2 \mu\text{m}$, $N = 20$), overlapping in size with the type
 material (Nagovitsin et al., 2004).
Description: Oval to circular vesicles with spaced out short, conical processes that make up ~10–
 15% of the vesicle diameter. The bases of the processes are wide and the processes narrow
 outwards in a rigid, triangular shape. The termini are sharp. The bases are separate from one
 another. The processes appear to be open to the vesicle cavity.
 Genus *Ceratosphaeridium* Grey, 2005
Type species: *Ceratosphaeridium mirabile* from the lower Ediacaran Tanana Formation in the
 Officer Basin, Australia (Grey, 2005: fig. 125A, B).
Ceratosphaeridium glaberosum Grey, 2005
 Fig. 5(E)
 2005. *Ceratosphaeridium glaberosum* nov. sp. - Grey; p. 237–241, figs. 134A–F, 135A–G.
 2006. *Ceratosphaeridium glaberosum* Grey - Willman et al., pl. 2, figs. 1, 2.
 2008. *Ceratosphaeridium glaberosum* Grey - Mikuláš et al., p. 343, fig. 3D.

481 2010. *Ceratosphaeridium* cf. *C. glaberosum* Grey - Golubkova et al., p. 370, pl. 4, fig. 1.
 482 2011. *Ceratosphaeridium glaberosum* Grey - Willman and Moczyłowska, p. 25, pl. 2, fig. 4.
 483 2011. *Ceratosphaeridium glaberosum* Grey - Yin et al., p. 292, fig. 6g.
 484 2012. *Ceratosphaeridium glaberosum* Grey - Liu et al., p. 197, fig. 2A–E.
 485 cf. 2012. *Ceratosphaeridium* cf. *glaberosum* Grey - Moczyłowska and Nagovitsin, p. 12, fig.
 486 4D.
 487 2014. *Ceratosphaeridium glaberosum* Grey - Liu et al., p. 33, fig. 28.1–28.7.
 488 2016. *Ceratosphaeridium glaberosum* Grey - Prasad and Asher, p. 46, pl. 4, figs. 9, 10.
 489 2017. *Ceratosphaeridium glaberosum* Grey - Asher et al., p. 151, pl. 2, fig. 2.
 490 2020. *Ceratosphaeridium glaberosum* Grey - Grazhdankin et al., p. 711, fig. 4G.
 491 2021. *Ceratosphaeridium glaberosum* Grey - Prasad and Asher, p. 119, pl. 2, figs. 10, 11.
 492 2024. ?*Ceratosphaeridium glaberosum* Grey - Agić et al., fig. 4A.
 493 2025. *Ceratosphaeridium glaberosum* Grey - Matos and Silva Caminha, p. 9, pl. 2, fig. C.
 494 **Holotype:** Specimen CPC 36431 repositied at Commonwealth Palaeontological Collection, from
 495 the Ediacaran Tanana Formation, Observatory Hill 1 drillcore, Officer Basin, Australia (Grey,
 496 2005: fig. 134A).
 497 **Material:** Seven specimens from the Pendjari Formation.
 498 **Occurrence:** Lower Ediacaran: Tanana, Karlaya Limestone, and Pertatataka formations in south-
 499 central Australia (Grey, 2005; Willman et al., 2006; Willman and Moczyłowska, 2008); Khorip
 500 Group (Lower Vindhyan) and Chambal Valley in Rajasthan, India (Prasad and Asher, 2016;
 501 Asher et al., 2017); Doushantuo Formation, south China (Liu et al., 2013); Nobres Formation,
 502 Brazil (Matos and Silva Caminha, 2025); similar forms occur in the Ura Formation in Siberia,
 503 Russia (Golubkova et al., 2010) and Nyborg Formation in Norway (Agić et al., 2024).
 504 **Measurements:** The Pendjari vesicles range 62–80 μm ($\mu = 70 \mu\text{m}$, $\sigma = 6.4 \mu\text{m}$, $N = 6$) in
 505 diameter. The processes are 22–27 μm long ($\mu = 24.2 \mu\text{m}$, $\sigma = 2.2 \mu\text{m}$, $N = 6$).
 506 **Description:** Smooth-walled vesicles with a single process. The vesicles are circular in outline,
 507 and bear compression folds. The process has a rounded tip and slightly tapers distally.
 508 **Remarks:** The Pendjari Formation specimens overlap with the smaller size end of the type
 509 material from Australia (64–118 μm ; Grey, 2005). *C. glaberosum* is a diagnostic taxon of the
 510 eponymous *Tanarium pycnacanthum-Ceratosphaeridium glaberosum* Assemblage Zone
 511 recognized in south China. This is the uppermost of the four DPA/ECAP assemblage zones

established in the Doushantuo Formation (Liu and Moczydłowska, 2019), also equivalent of the *Tanarium conoideum*-*Hocosphaeridium scaberfacium*-*Hocosphaeridium anozos* Zone established by previous workers (Liu et al., 2013). This is the only DPA/ECAP Zone established in Member III of the Doushantuo Formation, above the strata recording the EN3 carbon isotope excursion (also correlated with the Shuram CIE). In Australia, *C. glaberosum* is present throughout the sequences bearing DPA/ECAP taxa, but is more abundant and more common in the upper two assemblage zones: the eponymous *Tanarium irregulare*-*Ceratosphaeridium glaberosum*-*Multifronsphaeridium pelorium* Zone and the younger *Ceratosphaeridium mirabile*-*Distosphaera australica*-*Apodastoides verobturatus* Zone (Grey, 2005; Grey and Calver, 2007). In both instances, *C. glaberosum* is more common in the upper range of the regional DPA/ECAP distribution. In the present material, *C. glaberosum* is relatively low in abundance and first appears in the lower Pendjari Formation, approximately 50 m above the Marinoan cap carbonate. Here it co-occurs with taxa indicative of older DPA zones (e.g., *Appendisphaera*). Its rarity in the present material fits its distribution pattern in Australia, where the taxon is less abundant and less common in older zones (Grey, 2005). However, the same pattern of co-occurrences of *C. glaberosum* with older taxa like *Appendisphaera* was also observed in the Siberian material (Grazhdankin et al., 2020).

Specimens assigned to *Ceratosphaeridium* sp. were also reported from the Ediacaran Tentudía Formation in Spain (Palacios, 2024: fig. 5C, D), but are characterised by a single neck-like protrusion rather than a thin tail/process present in the type material (Grey, 2005: p. 232-238), so we do not include those specimens in the stratigraphic distribution of *Ceratosphaeridium*.

Genus ***Cymatiosphaeroides*** Knoll, 1984, emend. Knoll, Swett and Mark, 1991, emend. Shang et al., 2019

Type species: *Cymatiosphaeroides kullingii* Knoll, 1984, emend. Knoll et al., 1991, emend. Butterfield et al., 1994, emend. Shang et al., 2019, from the Tonian Hunnberg Formation, Svalbard.

Cymatiosphaeroides kullingii Knoll, 1984, emend. Knoll et al., 1991, emend. Butterfield et al., 1994, emend. Shang et al., 2019

Fig. 5(F)

1984. *Cymatiosphaeroides kullingii* nov. sp. - Knoll, p. 153, fig. 9A–C.

1989. *Cymatiosphaeroides kullingii* Knoll - Allison and Awramik, p. 287, fig. 11.1–11.3.

1991. *Cymatiosphaeroides kullingii* emend. - Knoll et al., p. 557, fig. 4.4, 4.6.

1993. *Cymatiosphaeroides kullingii* Knoll - Maithy and Babu, pl. 1, fig. 2.

1994. *Cymatiosphaeroides kullingii* emend. - Butterfield et al., 1994, p. 36, fig. 15A–E.

1995. *Cymatiosphaeroides kullingii* Knoll - Zang, p. 163, fig. 24H–K.

2014. *Cymatiosphaeroides kullingii* Knoll - Singh and Sharma, p. 97, pl/ 4, figs. 9–11.

2014. *Shuiyougousphaeridium echinulatum* nov. sp. - Singh and Sharma, p. 94, 96, pl. 2, figs. 1–3, pl. 3, figs. 1–9, pl. 4, fig. 4, pl. 5, figs. 1, 4.

2015. *Cymatiosphaeroides kullingii* Knoll - Butterfield, p. 861, fig. 2I.

2015b. *Cymatiosphaeroides kullingii* Knoll - Ye et al., p. 48, pl. 1, figs. 1, 2.

2019. *Cymatiosphaeroides kullingii* Knoll - Liu and Moczyłowska, p. 85, fig. 42A–D.

2019. *Cymatiosphaeroides kullingii* Knoll - Shang et al., p. 13, fig. 10D–K.

Holotype: Specimen in Knoll (1984: fig. 9A, B), thin section K2023-1J, Harvard University Paleobotanical Collection n° 60598., from the Tonian Hunnberg Formation, Svalbard.

Material: Two specimens and two wall fragments from the lower Pendjari Formation.

Occurrence: Mesoproterozoic Chitrakut Formation (Singh and Sharma, 2014) and Neoproterozoic Bhander Group (Maithy and Babu, 1993) in India; Tonian Hunnberg (Knoll, 1984), Draken (Knoll et al., 1991), and Svanbergfjellet formations (Butterfield et al., 1994) of Svalbard; Neoproterozoic upper Tindir Group, Canada (Allison and Awramik, 1989); Tonian Fifteen Mile Group, Canada (Butterfield, 2015); lower Ediacaran Doushantuo Formation, China (Liu and Moczyłowska, 2019; Shang et al., 2019); herein.

Measurements: Vesicle diameter ranges 92–105 μm ($\mu = 98 \mu\text{m}$, $\sigma = 9 \mu\text{m}$, $N = 3$). Length of the membrane-bound processes is 16–25 μm ($\mu = 21 \mu\text{m}$, $\sigma = 3 \mu\text{m}$, $N = 10$).

Description: Round double-walled vesicles bearing processes encased in the outer envelope. The processes have conical bases, but are mostly straight and end in round termini. The processes appear to be open to the vesicle cavity and are encased in a membranous outer wall.

Remarks: The outer wall is supported by the processes. The Pendjari Formation specimens are relatively poorly preserved, so the outer wall is partially torn in a few places (Fig. 5(F)).

Moczyłowska (2016: pl. 1, fig. 11) illustrated a similar-sized double-walled vesicle from the

Ura Formation, with scarce processes encased in an outer membrane, but re-examination of the Ura material is needed to confirm the presence of *Cymatiosphaeroides*. *C. kulingii* is a long-ranging morphotype more common to the Tonian strata, but its rare occurrence was recorded in Ediacaran cherts from Australia and China (Zang et al., 1992) and, for the first time, in the shales in Ghana (this study).

Genus ***Densisphaera*** Nagovitsin and Moczyłowska, 2012, emend. Moczyłowska, 2016

Type species: *Densisphaera arista* Nagovitsin and Moczyłowska, 2012, from the lower Ediacaran Ura Formation, Siberia, Russia (Moczyłowska and Nagovitsin, 2012).

Densisphaera fistulosa Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, 2012 emend. Moczyłowska, 2016

Fig. 5(J)

2012. *Densisphaera fistulosa* nov. sp. - Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, p. 16, fig. 6H, I.

2016. *Densisphaera fistulosa* Nagovitsin and Moczyłowska - Moczyłowska, p. 7, pl. 1, figs. 9, 10.

2016. *Densisphaera fistulosa* Nagovitsin and Moczyłowska - Prasad and Asher, p. 51, pl. 6, figs. 1, 2.

Material: Two specimens from the Pendjari Formation.

Occurrence: Lower-middle Ediacaran Ura Formation, Russia (Sergeev et al., 2011; Moczyłowska and Nagovitsin, 2012); lower Ediacaran Larawan and Khorip subgroups, Semri Group, India (Prasad and Asher, 2016); herein.

Measurements: Overall vesicle diameter ranges 121–130 μm ($\mu = 125 \mu\text{m}$, $N = 2$). The central vesicle diameter is 85–88 μm ($\mu = 86.5 \mu\text{m}$, $N = 2$). The process-like extensions of the outer vesicle are 31–40 μm long ($\mu = 35.2 \mu\text{m}$, $\sigma = 3.8 \mu\text{m}$, $N = 5$) and 20–29 μm wide ($\mu = 25.2 \mu\text{m}$, $\sigma = 3.5 \mu\text{m}$, $N = 5$).

Description: Vesicles with a central internal body surrounded by an external membrane that forms broad and heteromorphic process-like extensions. The outer membrane and the extensions are of lower opacity than (i.e., thinner) than the central vesicle. The extensions are tubular and

randomly distributed on the vesicle surface. The extensions terminate in blunt tips and freely communicate with the cavity of the outer vesicle.

Remarks: In the type material, some portions of the vesicle, the outer vesicle wall may be attached to the internal body wall or it may be separated by a substantial void, and in some portions the outer vesicle might appear torn (Moczyłowska and Nagovitsin, 2012). The latter is the case on one Pendjari specimen (Fig. 5(K)). Moczyłowska (2016) argued that a prominent central body in the genus *Densisphaera* and some other DPA taxa represents a developmental stage of zygotic cysts of green algae. While that remains a possibility, *D. fistulosa* also shares similarities with other protists. The heteromorphic and plastic nature of the extensions surrounding an internal body occurs in vegetative feeding stage (trophozoite) of a modern amoebozoan parasite *Entamoeba histolytica* (Abdel-Hafeez et al., 2012: fig. 1).

Densisphaera sp.

Fig. 5(I)

cf. 2012. *Densisphaera arista* Nagovitsin and Moczyłowska - Moczyłowska and Nagovitsin, p. 16, fig. 6A–F.

cf. 2012. *Densisphaera fistulosa* Nagovitsin and Moczyłowska - Moczyłowska and Nagovitsin, p. 16, fig. 6H, I.

cf. 2016. *Densisphaera fistulosa* Nagovitsin and Moczyłowska - Moczyłowska, p. 7, pl. 1, figs. 9, 10.

Material: Four specimens and a fragment from the Pendjari Formation.

Occurrence: *Densisphaera* occurs in the lower–middle Ediacaran Ura Formation, Russia (Sergeev et al., 2011; Moczyłowska and Nagovitsin, 2012); herein.

Measurements: Overall vesicle diameter ranges 98–128 μm ($\mu = 115 \mu\text{m}$, $\sigma = 12 \mu\text{m}$, $N = 4$). The central vesicle diameter ranges 60–72 μm ($\mu = 66 \mu\text{m}$, $\sigma = 4.5 \mu\text{m}$, $N = 4$).

Description: Circular to oval double-walled vesicle consisting of a central vesicle surrounded by a thin, translucent layer that forms process-like extensions. The internal body is optically dense (thick) and evenly outlined. The outer vesicle is uneven in outline.

Remarks: The Pendjari Formation specimens are on the smaller end of the diameter range of *Densisphaera fistulosa* type material from Siberia, and are smaller than the *D. arista* type material (Moczyłowska and Nagovitsin, 2012). The outer vesicle does not form obvious

heteromorphic processes as in some specimens in the type material. However, the uneven outline of the outer vesicle with process-like extensions (Figs. 5(I, J)) strongly resembles the outer vesicle of type specimens of *D. fistulosa* (Moczyłowska, 2016: pl. 1, fig. 8.). The thin process-like extensions of the outer vesicle in some specimens (Fig. 5(J)) also resemble the thin ‘processes’ growing out of the outer vesicle of *D. arista* (Moczyłowska and Nagovitsin, 2012: fig. 6A–D). Based on that, we tentatively identify these Pendjari specimens as *Densisphaera* sp.

Genus ***Gemmuloides*** Samuelsson and Butterfield, 2001

Type species: *Gemmuloides doncookii* from the Neoproterozoic Lone Land Formation, Canada (Samuelsson and Butterfield, 2001).

Gemmuloides doncookii Samuelsson and Butterfield, 2001

Fig. 8(A)

2001. *Gemmuloides doncookii* nov. sp. - Samuelsson and Butterfield, p. 245, fig. 7D–G.

cf. 2001. ?*Gemmuloides* sp. - Samuelsson and Butterfield, p. 245, fig. 7F.

2007. “small spherical vesicle with two ellipsoid projections” - Kochnev et al., p. 936, fig. 2.8.

2007. ?*Gemmuloides* sp. - Hidalgo, pl. 9, figs. 121, 122.

cf. 2011. *Leiosphaeridia* div. sp. - Willman and Moczyłowska, pl. 6, fig. 11.

2017. *Gemmuloides doncookii* Samuelsson and Butterfield - Adam et al., p. 388, fig. 2H.

2023. unnamed forms - Środoń et al., fig. 6F.

cf. 2025. *Coneosphaera inaequalis* Luo - Matos and Silva Caminha, p. 9, pl. 2, figs. E, F.

Holotype: Specimen GSC 117042 from the lower Neoproterozoic Lone Land Formation, British Columbia, Canada (Samuelsson and Butterfield, 2001: fig. 7D).

Material: Four specimens from the Pendjari Formation.

Occurrence: Mesoproterozoic Greyson Formation, Belt Supergroup, USA (Adam et al., 2017); Tonian Lone Land Formation, Canada (Samuelsson and Butterfield, 2001); Tonian–Cryogenian Terina Formation, Russia (Kochnev et al., 2007); upper Ediacaran Nagoryany Formation in the Podillya-Moldova area, Ukraine (Środoń et al., 2023); potential occurrence in the Ediacaran Guia Formation, Brazil (Hidalgo, 2007).

Measurements: Overall vesicle diameter ranges 105–139 μm ($\mu = 122 \mu\text{m}$, $\sigma = 14 \mu\text{m}$, $N = 4$).

The diameter of individual buds is 20–38 μm ($\mu = 29 \mu\text{m}$, $\sigma = 5 \mu\text{m}$, $N = 12$).

Description: Circular to elongate vesicles with bud-like, circular protrusions. The main vesicle has a slightly higher opacity than the smaller, budding cells. The buds make up to 24% of the overall main vesicle diameter, within the size-range of the type material from Canada (Samuelsson and Butterfield, 2001). In the present material, a single vesicle contains up to three buds.

Remarks: Although *Gemmuloides* is predominantly found in Mesoproterozoic–Neoproterozoic strata, younger occurrences of very similar budding forms were reported within a DPA/ECAP assemblages from the lower Ediacaran (Hidalgo, 2007; Kochnev et al., 2007; Willman and Moczyłowska, 2011). Thus, its presence in the Ediacaran strata of the Volta Basin is not anomalous, and it further expands the record of “budding” OWM to the Ediacaran (Grey, 2005: fig. 275A, B). Similar OWM assigned to *Coneosphaera inaequalis* occur in the Ediacaran Araras Group in Brazil (Matos and Silva Caminha, 2025).

Genus ***Gyalosphaeridium*** Zang in Zang and Walter, 1992 emend. Grey, 2005

Type species: *Gyalosphaeridium pulchrum* from the Pertatataka Formation, Amadeus Basin, Australia (Zang and Walter, 1992).

?*Gyalosphaeridium pulchrum* Zang in Zang and Walter, 1992 emend. Grey, 2005
Fig. 8(H)

Holotype: Specimen CPC 27770, slide 87ZW15-2, from 48.38–48.68 m in Rodinga 4, Pertatataka Formation, Amadeus Basin, Australia (Zang and Walter, 1992: fig. 43E, F).

Material: Four specimens from the lower Pendjari Formation grey shales.

Occurrence: *G. pulchrum* occurs in the Pertatataka Formation and the Ungoolya Group in Australia (Grey, 2005), the upper Doushantuo Formation in China (Liu et al., 2013), and in the Lower Vindhyan Group in India (Prasad and Asher, 2016).

Measurements: Vesicle diameter ranges 93–100 μm ($\mu = 96 \mu\text{m}$, $\sigma = 3.5 \mu\text{m}$, $N = 3$). Mean process length is 7 μm ($\sigma = 1.5 \mu\text{m}$, $N = 12$).

Description: Circular to ovoid vesicles bearing short thorny processes. The vesicles are optically dense / dark in colour. The processes are rigid, thin and slightly conical. They have broader conical bases and taper toward the tip, but do not exceed 9 μm in length.

Remarks: The Pendjari Formation specimens are poorly preserved, so the bases of the processes could not be thoroughly observed and we only tentatively recognize the specimens as ?*Gyalosphaeridium*. Based on the vesicle size and process length, these specimens fit the type material of *G. pulchrum* from Australia. The type specimens are also relatively optically dense compared to other microfossils within the assemblage. However, similarly preserved, ‘dark’ specimens also occur within the *G. pulchrum* type material itself (Grey and Willman, 2009: fig. 12C). The Pendjari specimens differ from other DPA taxa with short processes like *Echinosphaeridium triangulum* Zang and Walter, 1992 in having longer and less triangular processes, and from the species within *Ericiasphaera* Vidal, 1990 in having thicker and more rigid processes. Thus, despite not being able to verify whether the processes are open to the vesicle interior (a feature of *Gyalosphaeridium*) or closed (a feature of *Ericiasphaera*), based on overall similarity, we assign them to ?*G. pulchrum*. In Australia, *G. pulchrum* is rare but an eponymous species in the oldest ECAP biozone (Ab/Am/Gp) and occurs in both Tc/Sr/Vl and Ti/Cg/Mp zones (Grey and Calver, 2007). In Ghana, it is only present in the lower part of the Pendjari Formation. *G. pulchrum* was interpreted to be a eukaryotic alga, based on the presence of a four-layered wall ultrastructure observed via TEM (Willman and Moczyłowska, 2007).

Genus ***Hocosphaeridium*** Zang in Zang and Walter, 1992, emend. Xiao et al., 2014.

Type species: *Hocosphaeridium scaberfacium* Zang in Zang and Walter, 1992, emend. Liu et al., 2014a from Ediacaran Tanana Formation in the Giles 1 borehole, Australia.

Hocosphaeridium anozos (Willman in Willman and Moczyłowska, 2008), Xiao et al., 2014 Fig. 5(K)

1992. *Hocosphaeridium scaberfacium* Zang - Zang and Walter, fig. 45 G (not 45A–F).

2003. *Tanarium conoideum* Kolosova - Grey et al., p. 462, fig. 4C.

2005. *Tanarium irregulare?* Moczyłowska, Vidal, and Rudavskaya - Grey, p. 309, fig. 225.

cf. 2006. *Tanarium conoideum* Kolosova - Willman et al., p. 34, pl. 6, figs. 1, 2.

2008. *Tanarium anozos* nov. sp. - Willman in Willman and Moczyłowska, p. 526, fig. 13A–F.

2010. *Tanarium conoideum* Kolosova - Golubkova et al., p. 367, pl. 3, fig. 7.

2011. *Tanarium anozos* Willman - Yin C. et al., fig. 6d.

2012. *Tanarium anozos* Willman - Liu et al., fig. 3A–C.

2013. *Tanarium anozos* Willman - Liu et al., fig. 11B.
 2014. *Hocosphaeridium anozos* comb. nov. - Xiao et al., p. 28, fig. 16.
 2014a. *Hocosphaeridium anozos* (Willman) - Liu et al., p. 75, figs. 37, 38, 39.1.
 2014b. *Hocosphaeridium anozos* (Willman) - Liu et al., p., 208, figs. 8A, B.
 non 2016.. *Tanarium anozos* Willman - Prasad and Asher, p. 54, pl. 7, figs. 6, 7.
 2017. *Hocosphaeridium anozos* (Willman) - Hawkins et al., fig. 7E, F.
 2019. *Hocosphaeridium anozos* (Willman) - Liu and Moczyłowska, p. 113, fig. 60.
 partim 2022. *Hocosphaeridium anozos* (Willman) - Shi et al., fig. 8G–K.
 2024. *Hocosphaeridium anozos* (Willman) - Ouyang et al., p. 27, fig. 14.1–14.14.
Holotype: Specimen CPC 39635, repositied at Commonwealth Palaeontological Collection
 (CPC) at Geoscience Australia, from the Ediacaran Tanana Formation of the Giles 1 drillhole in
 Officer and Amadeus basins, South Australia ([Willman and Moczyłowska, 2008](#); fig. 13A).
Material: Five specimens from the lower Pendjari Formation.
Occurrence: Lower Ediacaran Pertatataka, Tanana, and Karlaya Limestone formations, Officer
 Basin, Australia ([Zang and Walter, 1992](#); [Grey, 2005](#); [Willman and Moczyłowska, 2008](#)); lower
 Ediacaran Ura Formation, east Siberia, Russia ([Golubkova et al., 2010](#), [Moczyłowska and](#)
[Nagovitsin, 2012](#)); lower Ediacaran Doushantuo Formation in the Weng'an area ([Xiao et al.,](#)
[2014](#)) and Hebei and Hunan provinces, China ([Liu et al., 2014a,b](#); [Hawkins et al., 2017](#); [Ouyang](#)
[et al., 2024](#)); herein.
Measurements: Vesicle diameter ranges 90–112 μm ($\mu = 99 \mu\text{m}$, $\sigma = 9 \mu\text{m}$, $N = 5$). The average
 process length is 19.5 μm ($\sigma = 3 \mu\text{m}$, $N = 22$).
Description: Spheroidal vesicles bearing process with hooked termini. The processes are evenly
 distributed on the vesicle surface. Their bases are conical, but the processes are narrow and taper
 slightly towards the distal end which has a hooked appearance.
Remarks: Since the defining feature of *H. anozos* are the curved process tips and many
 acanthomorphs from the Pendjari Formation do not have well preserved process tips, the
 abundance of *H. anozos* may be higher than observed.
 Genus ***Labruscasphaeridium*** Grey, 2005
Type species: *Labruscasphaeridium intertextum* from the Ediacaran Wilari Dolomite Member,
 Tanana Formation, Officer Basin, Australia ([Grey, 2005](#)).

?*Labruscasphaeridium intertextum* Grey, 2005

Fig. 8(I)

cf. 2005. *Labruscasphaeridium intertextum* nov. sp. - Grey, pp. 278, 280, figs. 185A–C, 186A–F.

cf. 2006. *Labruscasphaeridium intertextum* Grey - Willman et al., pl. 1, fig. 6.

cf. 2012. *Labruscasphaeridium* sp. - Moczyłowska and Nagovitsin, p. 14, fig. 4J, K.

Holotype: Specimen CPC 36489 from the Tanana Formation in the Observatory 1 drillcore, Officer Basin, Australia (Grey, 2005: fig. 185B, C).

Material: Two specimens and a fragment in the Pendjari Formation.

Occurrence: Ediacaran Tanana Formation (Grey, 2005) and Karlaya Limestone (Willman et al., 2006) in the Officer Basin, Australia; Ura Formation, Siberia, Russia (Moczyłowska and Nagovitsin, 2012); herein.

Measurements: Vesicle diameter is 68–89 μm ($\mu = 77 \mu\text{m}$, $\sigma = 10 \mu\text{m}$, $N = 3$).

Description: Circular to ovoid vesicles with slender and flexible processes that curve and loop. Some processes are folded in and are enveloping the vesicle surface. The tips are twisted and curved. Processes are of variable length, likely broken.

Remarks: *L. intertextum* differs from other taxa with curved processes like *Hocosphaeridium anozos* (e.g., Fig. 5(K)) and *H. scaberfacium* in its long and flexible processes. *H. anozos* processes are generally straight, with curved termini, whereas the processes of *L. intertextum* and these Pendjari specimens are uneven, very flexible and crumpled, and often hugging the vesicle closely (Grey, 2005: fig. 186). Processes in our material are of variable length, some are short and curved while some, on the upper side of the fossil (Fig. 8(F)), curve around the vesicle. This could be attributed to preservation: long and delicate processes are likely to break during transport as well as processing. Both the Pendjari Formation vesicles and the type material from Australia have processes that are broadly reminiscent to those of *Tanarium irregulare*. With that, these specimens and *Labruscasphaeridium* in general could represent *Tanarium* taphomorphs with particularly folded processes. However, specimens of *T. irregulare* observed here tend to have more rigid processes than those of *L. intertextum*, so we identify these few specimens as ?*L. intertextum*, following the arguments by Grey (2005).

Genus ***Leiosphaeridia*** Eisenack, 1958 emend. Downie and Sarjeant, 1963 emend. Jankauskas et al., 1989

Type species: *Leiosphaeridia baltica* from the Ordovician Ostsee kalk glacial erratics (Eisenack, 1958).

Remarks. Genus *Leiosphaeridia* is a polyphyletic group of form-species of smooth-walled vesicles, with stratigraphic range as far back as the Mesoarchean (Sugitani et al., 2026). Here, we follow the classification established by Butterfield et al. (1994) that recognizes individual species based on their size range and colour/opacity of the vesicle wall. Sphaeromorphs <70 µm are classified as *L. crassa* (thick-walled with lanceolate folds) and *L. minutissima* (thin-walled), and those >70 µm belong to *L. jacutica* (thick-walled) and *L. tenuissima* (thin-walled). Additional morphotypes are present in the Pendjari Formation: *L. anquiensis* bearing a polar opening, as well as leiosphaerids with a pliant wall without lanceolate folds (Fig. 7(D, F)). Similar leiosphaerids were also reported from the lower Ediacaran Las Ventanas Formation in Uruguay (Gaucher et al., 2008).

Leiosphaeridia anquiensis (Yin, 1991) Yin and Guan, 1999

Figs. 5(H), 8(E)

1989. ‘an acritarch with opening’ - Morad and Vidal, figs. 3, 4.

1991. *Eoaperturilites anquiensis* nov. sp. - Yin, p. pl. 2, figs. 4, 8, 9, 11–13.

1999. *Leiosphaeridia anquiensis* Yin - Yin and Guan, p. 129, fig. 4.1, 4.8, 4.13.

cf. 1999. *Leiosphaeridia kulgunica* Jankauskas - Yin and Guan, p. 129, figs. 3, 11, 14.

Holotype: Specimen P14D14BF1-1 from the Neoproterozoic Dongjiazhuang Formation, Anhui, China (Yin, 1991: pl. 2, fig. 11).

Material: Six specimens from the lower Pendjari Formation.

Occurrence: Neoproterozoic Dongjiazhuang and Dongjia formations, China (Yin and Guan, 1999); Tonian Visingsö Group, Sweden (Morad and Vidal, 1989); herein.

Measurements: Vesicle diameter ranges 36–74 µm ($\mu = 56 \mu\text{m}$, $\sigma = 17 \mu\text{m}$, $N = 6$).

Description: Slightly ovoid vesicles with a single circular opening on one pole. The wall texture is smooth.

Remarks: *L. anquiensis* is distinguished from other species with a circular pylome like *L. kulgunica*, in the location of the opening on a pole of the ovoid vesicle and a larger opening diameter in relation to the vesicle diameter.

Leiosphaeridia crassa Naumova, 1949 emend. Jankauskas in Jankauskas et al., 1989
Figs. 4(A), 7(A, D, F)

Holotype: Jankauskas et al. (1989) designated a specimen of *Leiotriletes simplicissimus* from the type material (Naumova, 1949: pl. 1, fig. 3) as lectotype.

Material: Seven specimens from the Mesoproterozoic Poubogou Formation. Over 70 specimens from the Ediacaran Pendjari Formation.

Occurrence: Common occurrence through Proterozoic and Phanerozoic. Present in nearly all fossiliferous horizons in the Pendjari Formation.

Measurements: The Poubogou Formation specimens range 22–48 μm in diameter ($\mu = 34.3 \mu\text{m}$, $\sigma = 10.1 \mu\text{m}$, $N = 6$) and the Pendjari Formation specimens are 35–70 μm in diameter ($\mu = 48 \mu\text{m}$, $\sigma = 8 \mu\text{m}$, $N = 50$).

Description: Smooth-walled vesicles, circular to ellipsoidal in outline. Some vesicles contain an internal body (Fig. 7(A)). Lanceolate compression folds are common.

Remarks: *L. crassa* is the main constituent of the depauperate Poubogou assemblage. Differences in the vesicle colour/TAI indicate that some specimens may have been reworked. The Poubogou *L. crassa* are better preserved than the Pendjari leiosphaerids with chagrinated vesicle walls. Some specimens in the Pendjari Formation have exceptionally pliant walls, seen in the uneven vesicle shape (Fig. 8(D, F)).

Leiosphaeridia jacutica Timofeev, 1966 emend. Mikhailova and Jankauskas in Jankauskas et al., 1989
Fig. 8(C)

Holotype: Preparation 452/1 from the upper Mesoproterozoic Lakhanda Group, Russia (Timofeev, 1966: pl. 7, fig. 2).

Material: Four full specimens and 16 wall fragments in the Pendjari Formation.

Occurrence: Common in Mesoproterozoic to Phanerozoic OWM assemblages worldwide.

Measurements: Vesicles range in diameter of 102–190 μm ($\mu = 155 \mu\text{m}$, $\sigma = 33 \mu\text{m}$, $N = 8$).

Description: Large, spherical, smooth-walled vesicles, circular to ellipsoidal in outline. The vesicle wall has moderate to high opacity and bears lanceolate compression folds.

Leiosphaeridia minutissima (Naumova, 1949) Jankauskas et al., 1989

Figs. 4(B), 7(E)

Lectotype: No holotype was designated in the original description. Jankauskas et al. (1989: p. 80) designated *Leiotriletes minutissimus* (Naumova, 1949: pl. 1, fig. 1) as lectotype.

Material: Four specimens from the Poubogou Formation and seventeen specimens from the Pendjari Formation.

Occurrence: Common in Mesoproterozoic to Phanerozoic OWM assemblages.

Measurements: The Poubogou Formation vesicles are 17–33 μm in diameter ($\mu = 24 \mu\text{m}$, $\sigma = 7 \mu\text{m}$, $N = 4$). The Pendjari Formation vesicles range 18–45 μm in diameter ($\mu = 27 \mu\text{m}$, $\sigma = 7.4 \mu\text{m}$, $N = 17$).

Description: Small, spheroidal vesicles with a smooth wall of low-opacity.

Genus *Multifronsphaeridium* Zang, 1992 emend. Grey, 2005

Type species: *Multifronsphaeridium pelorium* from the Ediacaran Pertatataka Formation in the Ooraminna 1 borehole, Amadeus Basin, Australia (Zang and Walter, 1992).

Multifronsphaeridium ramosum Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, 2012 emend. Moczyłowska, 2016 emended
Fig. 6(A–C)

2008. *Dicrospinasphaera* sp. - Vorob'eva et al., fig. 2e, j.

2010. *Dicrospinasphaera virgata* Grey - Golubkova et al., pl. 4, fig. 8.

partim 2010. *Multifronsphaeridium pelorium* Zang - Golubkova et al., pl. 4, fig. 9a, b.

2011. *Dicrospinasphaera virgata* Grey - Sergeev et al., p. 1004–1005, fig. 8.1–5.

2012. *Multifronsphaeridium ramosum* nov. sp. - Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, p. 17, fig. 7A–C.

2016. *Multifronsphaeridium ramosum* Nagovitsin and Moczyłowska - Moczyłowska, p. 10, pl. 2, figs. 1–7.

2024. ?*Multifronsphaeridium ramosum* Nagovitsin and Moczyłowska - Agić et al., p. 7, fig. 4I.

Holotype: Specimen PN8/4-17/8-1 reposit at Museum of Evolution, Uppsala University, from the early Ediacaran Ura Formation, 3–15 m above a base of the section, on the bank of the Ura River, Siberia, Russia (Moczyłowska and Nagovitsin, 2012: fig. 7A).

Material: Fourteen specimens from the lower part of the Pendjari Formation.

Occurrence: Ediacaran Ura Formation, Siberia, Russia (Golubkova et al., 2010; Moczyłowska and Nagovitsin, 2012); Doushantuo Member III in Hubei Province, China (Liu and Moczyłowska, 2019), herein. Few poorly preserved specimens with characteristic *M. ramosum* processes occur in Arctic Norway (Agić et al., 2024).

Measurements: The diameter of the Pendjari vesicles (including processes) ranges 90–120 μm in size ($\mu = 102.4 \mu\text{m}$, $\sigma = 9.2 \mu\text{m}$, $N = 14$). Processes ranges 28–41 μm in length ($\mu = 35 \mu\text{m}$, $\sigma = 3.5 \mu\text{m}$, $N = 40$). The length of the second order branches (Fig. 6(A1)) ranges 9–16 μm in length ($\mu = 12.7 \mu\text{m}$, $\sigma = 2 \mu\text{m}$, $N = 35$).

Emended diagnosis: Circular to oval in outline vesicles with robust, conical, distally divided processes. The processes are spread out from one another and relatively unevenly distributed on the vesicle surface. The processes are robust, hollow, and freely communicate with the vesicle cavity. Their shape is conical to cylindrical, with broad bases and they range in length between the specimens. The processes branch distally into up to five branches. Distal, second order branches bifurcate or multi-radiate. Remnants of a thin membrane may be present between the second order process branches. Length of the processes, as well as the second order branches, are uniform on a single specimen and proportional to the vesicle size. Internal body may be present inside the vesicle. No excystment opening is seen.

Description: As diagnosis. Most Pendjari specimens have bifurcated processes, but some spread out into up to six second-order branches (Fig. 6(A1)).

Remarks: We emend the diagnosis of *M. ramosum* to include specimens with robust and long process trunks and radially-branching process tips that can have up to six second-order branches, with remnants of a membrane between them (Fig. 6(B)). The membrane remnants are likely a preservational feature, suggesting that the vesicle of *M. ramosum* was covered in a translucent membrane at some point during its development, similar to Paleo–Mesoproterozoic acanthomorphs (Agić et al., 2017: fig. 14M). In the initial emendation, Moczyłowska (2016: p. 9) noted that *M. ramosum* bears short (10–26 μm), heteromorphic processes. Based on the present and previously published material, we note that well-developed processes can be

considerably longer, up to 46 μm (Fig. 6(B)). Process length is usually proportional to the vesicle size, which is an indicator of growth. Some specimens in the Pendjari Formation have particularly long and robust processes with well-developed second-order branching, generally longer than in *Multifronsphaeridium* species described so far (Fig. 12). We include those morphotypes into *M. ramosum* based on overall processes shape, distribution and the presence of radial termini. These differences in process length are more likely ontogenetic or ecophenotypic (Mertens et al., 2009) instead of a true phylogenetic difference.

Overall, the Pendjari *M. ramosum*, as well as many other *Multifronsphaeridium* species like *M. pelorium*, are quite similar to another common DPA genus *Variomargosphaeridium*. Our material differs from *Variomargosphaeridium floridum* with large and distally-branched processes (Moczyłowska and Nagovitsin, 2012) in the overall shape of the processes. While *V. floridum* processes broaden outwards (Moczyłowska and Nagovitsin, 2012: fig. 9A–I), the processes of *M. ramosum* are defined by broad bases and slightly tapering termini with radial branches. The Pendjari material is also slightly smaller than the *V. floridum* type material from Siberia. Our material further differs from *M. pelorium* type material from Australia (Grey, 2005: fig. 189A–D) in having longer and more robust processes. *M. pelorium* is also characterised by planoconvex shape of the vesicle, which is not always obvious in compressed OWM, not even in the type material itself (Grey 2005). Furthermore, there are only minor differences in the type material between *Multifronsphaeridium* specimens and *Variomargosphaeridium litoschum*, one distinction being the generally narrower and shorter processes in *V. litoschum* (Grey, 2005: figs. 189, 257). However, some *V. litoschum* specimens bear broad, *M. pelorium*-like processes (Grey, 2005: fig. 257C). Our comparison of vesicle diameter and process length between the species of *Multifronsphaeridium* and *Variomargosphaeridium* shows quite an overlap in the sizes of several taxa across genera, excluding the >900 μm specimen from Australia (Fig. 12).

Considering this, the differences between these two genera are minor and probably preservational, and a revision of the type material is necessary. Based on the strong similarity and within-assemblage and across-assemblage variations, those morphotypes belong to the same genus and *Multifronsphaeridium* holds the nomenclatural seniority (as discussed by Xiao et al., 2014: p. 57). Re-examination of the type material from Australia is needed to confidently synonymize them, because both taxa were used to establish biozones in south-central Australia (Grey, 2005; Grey and Calver, 2007). However, the effects of synonymy on biostratigraphic

divisions would be minimal, because most species within both genera have overlapping stratigraphic ranges. In Australia, *M. pelorium* occurs through the Tc/Sr/Vl Zone and its eponymous Ti/Cg/Mp Zone, and *V. litoschum* occurs through its eponymous Tc/Sr/Vl Zone as well as through most of the overlying Ti/Cg/Mp Zone (Grey and Calver, 2007: fig. 8). In Siberia, *M. pelorium* and *M. ramosum* have a slightly longer stratigraphic range than specimens identified as ?*V. litoschum*, but the age-ranges of both taxa overlap for the most part (Golubkova et al., 2010: fig. 4). In South China, *V. lithoschum* occurs in Doushantuo Formation Member III, and *M. pelorium* in upper Member II. *M. ramosum* is also found in Member III (Liu and Moczyłowska, 2019). Both in China and Siberia, *Multifronsphaeridium* has a slightly longer range and appears earlier than *Variomargosphaeridium*, despite *V. lithoschum* being the older eponymous zone in Australia. This pattern illustrates the need to revise the biozones subdivision of south-central Australia.

Genus ***Schizofusa*** Yan, 1982

Type species: *Schizofusa sinica*, from the Paleoproterozoic Chuanlinggou Formation in China (Yan, 1982).

Schizofusa risoria Grey, 2005

Fig. 7(B)

2005. *Schizofusa risoria* nov. sp. - Grey, p. 187–188, figs. 68A–E, 69A–C.

2006. *Schizofusa risoria* Grey - Willman et al., pl. 4, fig. 4.

2008. *Schizofusa risoria* Grey - Willman and Moczyłowska, fig. 11A, B.

2008. *Schizofusa risoria* Grey - Mikuláš et al., p. 343, fig. 3B.

2016. *Schizofusa* sp. - Joshi and Tiwari, fig. 6D.

Holotype: Specimen CPC 36347 from the Karlaya Limestone of the Lake Maurice West 1 drillcore, Officer Basin, South Australia (Grey, 2005: fig. 68A).

Material: Six specimens in the Pendjari Formation.

Occurrence: Occurs in the lower Ediacaran strata from Australia (Grey, 2005; Willman et al., 2006, Willman and Moczyłowska, 2011), China (Xiao et al., 2014), Czech Republic (Mikuláš et al., 2008), and India (Prasad and Asher, 2016) and is an eponymous component of *T. conoideum*-*S. risoria*-*V. litoschum* Zone established in South-Central Australia.

972 **Measurements:** Vesicle length in the Pendjari material ranges from 64–90 μm ($\mu = 75 \mu\text{m}$,
973 $\sigma = 9.2 \mu\text{m}$, $N = 6$) and the width of each half ranges 15–25 μm ($\mu = 19.9 \mu\text{m}$, $\sigma = 3.3 \mu\text{m}$,
974 $N = 12$).

975 **Description:** Large, elongate, fusiform, smooth-walled vesicles split in two hemispheres and
976 attached on through a narrow hinge on one end. The vesicle wall is thin, indicated by its low
977 opacity. Both halves of the vesicle are fusiform and narrow, indicating an original ellipsoidal
978 shape of the vesicle. The length to width ratio of both halves is 3.7.

979 **Remarks:** Grey (2005) documented abundant *S. rizzoria* in the Officer and Amadeus basins. Due
980 to its frequency and unique shape, it was used to establish the *T. conoideum*-*S. rizzoria*-*V.*
981 *litoschum* Zone subdividing the pre-Shuram early Ediacaran interval (Grey and Calver, 2007;
982 Xiao and Narbonne, 2020). However, *S. rizzoria* is relatively rare in other contemporaneous units
983 on other palaeocontinents. Notably, it is absent from DPA-rich units in south China. This is likely
984 an issue of microfossil preservation in different lithologies; a thin-walled split *S. rizzoria* might
985 not be easily observed in chert or phosphorite material. Regardless, due to its rarity in the
986 Tc/Sr/Vl Zone established in Australia, it does not hold a global biostratigraphic potential (also
987 discussed by Liu et al., 2014a). In our material, *S. rizzoria* is more common and abundant in the
988 lower part of the Pendjari Formation, unlike *S. zangwenlongii* which is present throughout the
989 unit.

990

991 *Schizofusa zangwenlongii* Grey, 2005
992 Fig. 7(H)
993 cf. 1989. *Tasmanites* sp. - Baudet et al., pl. 2, fig. 17.
994 partim 1992. *Schizofusa* sp. - Zang and Walter, p. 96, fig. 71C, E, G; non *Schizofusa* sp.; p. 96,
995 figs. 71I.
996 2005. *Schizofusa zangwenlongii* nov. sp. - Grey, p. 190, fig. 71A–D.
997 2011. *Schizofusa zangwenlongii* Grey - Sergeev et al., p. 132, fig. 9.8.
998 2013. *Schizofusa zangwenlongii* Grey - Liu et al., fig. 11M.
999 2014a. *Schizofusa zangwenlongii* Grey - Liu et al., p. 117, fig. 108.1–108.6.
1000 2014b. *Schizofusa zangwenlongii* Grey - Liu et al., p. 209, fig. 9D.
1001 2024. *Schizofusa zangwenlongii* Grey - Xiao et al., p. 50, fig. 30.5, 30.6.
1002 2024. *Schizofusa zangwenlongii* Grey - Agić et al., fig. 4G.

2024. *Schizofusa zangwenlongii* Grey - Palacios, p. 676, fig. 8a, b.

Holotype: Specimen CPC 36355 from the Dey Dey Mudstone in the Observatory Hill 1 drillcore, Officer Basin, South Australia, (Grey, 2005: fig. 71A).

Material: 27 specimens from the Pendjari Formation.

Occurrence: Lower Ediacaran strata in Amadeus and Officer basins, Australia (Grey, 2005); Doushantuo Formation, South China (Liu et al., 2013, 2014a,b); Krol A Formation in India (Xiao et al., 2024); Dal’nyaya Taiga Group (Vorob’eva and Petrov, 2023) and the Ura Formation (Sergeev et al., 2011) in Siberia, Russia; Nyborg Formation in northern Norway (Agić et al., 2024); Tentudía Formation, south-central Spain (Palacios, 2024).

Measurements: The vesicles in this material are 172–240 µm long ($\mu = 206.4$ µm, $\sigma = 21.3$, $N = 26$), and halves are on average 91 µm thick ($\sigma = 15$, $N = 50$).

Description: Oval to fusiform vesicles with a large median-split opening. The Pendjari Formation vesicles are chagrinata and have a high opacity, indicating a thick wall. The median split is large, and the two halves of the vesicle are connected on one end. The length to width ratio of both halves is 2.3, smaller than the long and narrow halves of *S. risoria*.

Remarks: *S. zangwenlongii* is a more widely distributed species of *Schizofusa* within Ediacaran strata, and more common than *S. risoria* outside of Australia. *S. zangwenlongii* is a key taxon of the *Tanarium tuberosum*-*Schizofusa zangwenlongii* third zone recognized in the Member II of the Doushantuo Formation, the age of which is estimated to ca. 620 Ma (Liu and Moczyłowska, 2019). However, in Ghana, *S. zangwenlongii* occurs throughout the Pendjari Formation in outcrop, and it co-occurs with eponymous taxa of other zones (Fig. 3).

Genus **Simia** Mikhailova and Jankauskas in Jankauskas et al., 1989

Type species: *Simia simica* (Jankauskas, 1980) Jankauskas et al., 1989, from the upper Riphean (= Tonian) Podinzersk Formation in the Urals, Russia.

Simia annulare (Timofeev, 1969) Mikhailova in Jankauskas et al. 1989

Fig. 7(G)

2014. “ceratophyton” - Jachowicz-Zdanowska, pl. 2, fig. 14.

2022. *Simia annulare* (Timofeev) - Agić et al., fig. 6f.

2025. *Simia annulare* (Timofeev) - Matos and Silva Caminha, p. 17, fig. 6D.

Holotype: Preparete 147/4 of Biostratigraphy Laboratory of the USSR Academy of Sciences, from the Neoproterozoic Kildinskoye Formation (Timofeev, 1969: pl. 3, fig. 9).

Material: Four specimens in the lower Pendjari Formation grey shales.

Occurrence: Common occurrence in Paleoproterozoic to lower Neoproterozoic strata. Rare occurrence in the post-Cryogenian strata, including: lower Ediacaran Nobres Formation in Brazil (Matos and Silva Caminha, 2025); Ediacaran strata from the Małopolska Block in Poland (Jachowicz-Zdanowska, 2014); upper Ediacaran Nama Group in Namibia (Agić et al., 2022).

Measurements: The diameter of the Pendjari vesicles ranges from 87–141 μm ($\mu = 113 \mu\text{m}$, $\sigma = 20.9$, $N = 4$).

Description: Circular vesicles with a spheroidal central body surrounded by a narrow equatorial flange. The flange is on average 12% of the diameter of the central body.

Remarks: “*Simia* sp.” was reported from the upper Ediacaran drill-hole material of the Małopolska Block corresponding to diagnosis of *S. annulare* (Jachowicz-Zdanowska, 2014: fig. 2.14), but mislabelled in the figure caption as *Ceratophyton*, which is illustrated instead in fig. 2.15. *S. annulare* is a common and long-ranging Proterozoic taxon (Agić et al., 2017; Agić and Cohen, 2021), but rare in the Ediacaran. Moczyłowska (2008) suggested that it went extinct in the Snowball Earth interval. Recent reports of *S. annulare* in the ECAP/DPA assemblages (Matos and Silva Caminha, 2025; herein) show that the stratigraphic range of this morphotype extends to the terminal Proterozoic, although this simple form could represent multiple biological species through time.

Genus *Tanarium* Kolosova 1991, emend. Moczyłowska et al., 1993

Type species: *Tanarium conoideum* Kolosova, 1991, emend. Moczyłowska, Vidal and Rudavskaya, 1993; from the Ediacaran Kursov Formation, Siberian Platform, Russia.

Remarks: Housing over 20 described species, *Tanarium* is one of the most specious genera in the Proterozoic, owing in part to its broad definition (Moczyłowska et al., 1993). Grey (2005) emended the genus to include acanthomorphic acritarchs with processes longer >20% of the vesicle diameter. Despite that, numerous species have been described over the years on the basis of subtle differences in process shape and length, although such morphological plasticity could also be caused by ecology or ontogeny (Mertens et al., 2009; Delabroye et al., 2012). In the last decade, many species were lumped into fewer senior synonyms based on the lack of clear size

divisions between the species. For example, *T. araithecum*, *T. muntense*, *T. paucispinosum* and *T. pluriprotensum* were considered potentially synonymous with *T. conoideum*, and *T. mattoides* and *T. pycnacanthum* synonymous with *T. irregulare* (Moczyłowska, 2016). A biostratigraphically important taxon occurring in South Australia, South China, and Siberia, *Tanarium anozos*, was transferred into the genus *Hocosphaeridium* (= *H. anozos*) on the basis of distally curved processes (Xiao et al., 2014), which are generally straight in the genus *Tanarium* (Kolossova, 1991).

Tanarium conoideum Kolossova 1991, emend. Moczyłowska, Vidal and Rudavskaya 1993
Fig. 6(D–F)

1985. *Baltisphaeridium primarium* Jankauskas – Pyatiletov et al. pl. 1, figs. 1–4.

1991. *Tanarium conoideum* nov. sp. - Kolossova, p. 57, fig. 5.1–5.3.

1993. *Tanarium conoideum* Kolossova - Moczyłowska et al., p. 514, fig. 10D.

2005. *Tanarium muttense* nov. sp. - Grey, p. 317, fig. 234E, F.

2005. *Tanarium plutipotensum* nov. sp. - Grey, p. 321, fig. 240A–D.

cf. 2008. *Tanarium pluripotensum* Grey - Willman and Moczyłowska, fig. 14D–F.

2011. *Tanarium conoideum* Kolossova - Sergeev et al., fig. 6.1, 6.2.

2012. *Tanarium muttense* Grey - Moczyłowska and Nagovitsin, p. 19, fig. 8L, M.

2014a. *Tanarium conoideum* Kolossova - Liu et al., p. 109, figs. 76.2, 77.1–77.6.

2014. *Tanarium conoideum* Kolossova - Xiao et al., p. 51, fig. 33.1–33.6.

2015. *Tanarium conoideum* Kolossova - Golubkova et al., p. 550, fig. 2c.

2019. *Tanarium conoideum* Kolossova - Shang et al., p. 26, fig. 16A–E.

2020. *Tanarium conoideum* Kolossova - Vorob'eva and Petrov, p. 374, 375, pl. 1, fig. 15.

2020. *Tanarium conoideum* Kolossova - Grazhdankin et al., fig. 4K.

2022. *Tanarium conoideum* Kolossova - Ye et al., p. 61, fig. 42.

cf. 2024. *Tanarium* cf. *T. conoideum* Kolossova - Xiao et al., p. 199, fig. 26.1–26.5.

2024. *Tanarium conoideum* Kolossova - Wu et al., p. 319, figs. 7.1–7.6.

2026 *Tanarium conoideum* Kolossova - Shang et al., p. 6, fig. 5L.

Holotype: Specimen YIGS 87-115 from the Byuk drill-hole, Ediacaran Kursov Formation, Siberia, Russia (Kolossova, 1991: fig. 5.1.).

Material: 29 specimens and a fragment in the Pendjari Formation.

Occurrence: Lower Ediacaran strata in south-central Australia (Grey, 2005; Willman et al., 2006; Willman and Moczyłowska, 2008); Siberia, Russia (Moczyłowska et al., 1993; Golubkova et al., 2015; Vorob'eva and Petrov, 2020), upper Ediacaran Oppokun Formation in Siberia (Grazhdankin et al., 2020); Member III of the Doushantuo Formation in the Yangtze Gorges area and members II and III at the Weng'an section of the Doushantuo Formation in China (Liu et al., 2014a; Ye et al., 2022; Wu et al., 2024); similar morphotypes also occur in the Krol A Formation in India (Xiao et al., 2024).

Measurements: Vesicle diameter in the Pendjari Formation specimens ranges broadly from 45–97 μm ($\mu = 75 \mu\text{m}$, $\sigma = 11.6$, $N = 28$), although only two small outliers were observed (Fig. 6(F)) and most specimens have vesicles $>72 \mu\text{m}$ in diameter. Processes are 15–35 μm long ($\mu = 23.9 \mu\text{m}$, $\sigma = 6$, $N = 75$).

Description: Spheroidal vesicles with long, conical processes. The bases of processes are broad and conical, and the processes narrow and taper outwards and are mostly rigid. The processes are hollow and communicate with the vesicle interior. They are evenly spread around the vesicle surface and spaced by 10–15 μm from one another. Process length is proportional to the vesicle size (Fig. 6(E, F)).

Remarks: Smaller specimens with vesicles of about 45 μm in diameter occur in the same horizons as larger *T. conoideum* ($>70 \mu\text{m}$, corresponding to the size of the type material), which could be a result of ontogeny. Some *T. conoideum* specimens with very even and rigid processes (Fig. 7(C)) are similar to a newly erected species *T. uniformum* from the Doushantuo Formation (Liu and Moczyłowska, 2019: fig. 87). However, the diagnosis of *T. uniformum* being a vesicle with even and uniform processes, corresponds to the original description and is likely a well-preserved form, so here we use the senior name.

Tanarium irregulare Moczyłowska, Vidal, and Rudavskaya, 1993

Fig. 7(G–I)

1993. *Tanarium irregulare* nov. sp. - Moczyłowska et al., pl. 7, figs. 1, 2.

2005. *Tanarium irregulare* Moczyłowska - Grey, p. 306, figs. 220A–F, 221A–D.

2006. *Tanarium irregulare* Moczyłowska - Willman et al., pl. 7, figs. 1, 2.

2011. *Tanarium irregulare* Moczyłowska - Yin et al., fig. 3A–D, L.

2013. *Tanarium irregulare* Moczyłowska - Liu et al., p. 39, fig. 11L.

1127 cf. 2020. *Tanarium pycnacanthum* Moczyłowska - Vorob'eva and Petrov, pl. 1, figs. 10–12.
 1128 2024. *Tanarium irregulare* Moczyłowska - Agić et al., p. 7, fig. 4J.

1129 **Holotype:** Specimen PMU-Sib.2-J/57/1 from 1887–1894 m depth in the drill-hole Zapad 742,
 1130 Khamaka Formation (Moczyłowska et al., 1993).

1131 **Material:** 16 specimens from the middle Pendjari Formation.

1132 **Occurrence:** Upper Neoproterozoic Khamaka Formation (Moczyłowska et al., 1993) and
 1133 potential occurrence in the lower Ediacaran Barakun Formation in Siberia, Russia (Vorob'eva
 1134 and Petrov, 2020); lower Ediacaran Karlaya Limestone, Australia (Grey, 2005; Willman et al.,
 1135 2006); Ediacaran Doushantuo Formation, China (Yin et al., 2011), Ediacaran Nyborg Formation,
 1136 Norway (Agić et al., 2024).

1137 **Measurements:** Vesicle diameter ranges 80–102 μm ($\mu = 88.8 \mu\text{m}$, $\sigma = 7$, $N = 12$). Processes are
 1138 30–40 μm long ($\mu = 34 \mu\text{m}$, $\sigma = 3$, $N = 30$).

1139 **Description:** Circular to ovoid vesicles bearing long, hollow, thin and flexible processes with
 1140 conical bases. Processes are heteromorphic, mainly straight, but can also be bifurcated (Fig.
 1141 6(G)).

1142 **Remarks:** Many *T. irregulare* vesicles in the Pendjari assemblage appear shrivelled or torn (Fig.
 1143 6(G, H)) and are generally more poorly preserved than other *Tanarium* species in the same
 1144 samples. This suggests a different, more pliant nature of the vesicle and the processes. *T.*
 1145 *irregulare* is common in Australian strata, where it is the eponymous species of the third biozone
 1146 Ti/Cg/Mp, but it is scarce in assemblages on other cratons. Since this is a rare taxon, its presence
 1147 in Ghana suggests a close proximity of WAC and South-Central Australia.

1148

1149 *Tanarium paucispinosum* Grey, 2005
 1150 Fig. 6(J)

1151 partim 1992. *Hocosphaeridium scaberfacium* nov. sp. - Zang and Walter, p. 61, fig. 45H.
 1152 2005. *Tanarium paucispinosum* nov. sp. - Grey, pp. 318–320, fig. 237A–E.

1153 cf. 2009. *Tanarium* sp. - Vorob'eva et al., p. 169, fig. 7.5.

1154 2019. *Tanarium paucispinosum* Grey - Liu and Moczyłowska, p. 150, fig. 83A–H.

1155 2022. *Tanarium paucispinosum* Grey - Ye et al., p. 66, fig. 44E, F.

1156 2024. *Tanarium paucispinosum* Grey - Ouyang et al., p.39, fig. 20.4–20.7.

1157 **Holotype:** CPC 36552 reposit at Commonwealth Palaeontological Collection (CPC) at
 1158 Geoscience Australia, Canberra, from the Ediacaran Wilari Dolomite Member of Observatory
 1159 Hill 1 drill core, South Australia (Grey, 2005: fig. 237D).

1160 **Material:** Four specimens from the lower Pendjari Formation.

1161 **Occurrence:** Lower Ediacaran Wilari Dolomite Member and Tanana Formation, South Australia
 1162 (Grey, 2005); Doushantuo Formation in Hubei and Hunan provinces, China (Ye et al. 2022;
 1163 Ouyang et al., 2024).

1164 **Measurements:** Vesicles are 93–104 μm in size ($\mu = 97.7 \mu\text{m}$, $\sigma = 4$, $N = 4$). Processes are 10–
 1165 21 μm long ($\mu = 17.5 \mu\text{m}$, $\sigma = 2.8$, $N = 15$).

1166 **Description:** Spheroidal to ovoid vesicles with a small number of sparsely distributed narrow
 1167 and conical processes. The processes are straight, but have slightly conical bases. Each vesicle
 1168 has up to four processes. Some processes are truncated due to poor preservation.

1169 **Remarks:** The Pendjari Formation specimens have the same size range as the Australian type
 1170 material, and both are smaller than the Doushantuo specimens (ranging from ~150 to 200 μm ;
 1171 Ouyang et al., 2024). However, all fall into the diagnosis of *T. paucispinosum* characterised by
 1172 sparse processes.

1173

1174 *Tanarium tuberosum* Moczyłowska, Vidal and Rudavskaya, 1993, emend. Moczyłowska, 2016
 1175 Fig. 6(K)

1176 1993. *Tanarum tuberosum* nov. sp. - Moczyłowska et al., pp. 516–518, text-fig. 15A–D.

1177 1998. *Tanarium tuberosum* Moczyłowska et al. - Faizullin, pl. 2, fig. 1.

1178 2004. *Tanarium stellatum* Nagovitsin and Faizullin - Nagovitsin et al., p. 14, pl. 2, figs. 16–18.

1179 2005. *Tanarium tuberosum* Moczyłowska et al. - Moczyłowska, p. 303, fig. 7B–D.

1180 2008. *Tanarium tuberosum* Moczyłowska et al. - Willman and Moczyłowska, p. 527, fig. 12F.

1181 2009. *Tanarium tuberosum* Moczyłowska et al. - Vorob'eva et al., 2009, p. 182, fig. 6.7, 6.8.

1182 2010. *Tanarium tuberosum* Moczyłowska et al. - Golubkova et al., p. 367, pl. 3, fig. 11.

1183 2011. *Tanarium tuberosum* Moczyłowska et al. - Sergeev et al., p. 1006, fig. 6.3.

1184 2012. *Tanarium tuberosum* Moczyłowska et al. - Moczyłowska and Nagovitsin, p. 19, fig. 8G,
 1185 H.

1186 2016. *Tanarium tuberosum* Moczyłowska et al. - Moczyłowska, p. 34., pl. 3.

1187 2017. *Tanarium tuberosum* Moczyłowska et al. – Asher et al., p. 151, pl. 2, figs. 4, 5.

1188 2019. *Tanarium tuberosum* Moczyłowska et al. - Shang et al., p. 21, fig. 18A.
 1189 cf. 2021. *Tanarium* sp. - Morais et al., p. 8, fig. 5P.
 1190 2024. *Tanarium tuberosum* Moczyłowska et al. - Ouyang et al., fig. 22.4.
 1191 cf. 2024. *Tanarium* sp. - Palacios, p. 676, fig. 8e.
 1192 2024. *Tanarium tuberosum* Moczyłowska et al. - Wu et al., p. 320, fig. 8.3, 8.4.
 1193 **Holotype:** Specimen PMU-Sib.4-J/30/3 reposit at Uppsala University, from the Ediacaran
 1194 Khamaka Formation, Siberia, Russia (Moczyłowska et al., 1993: fig. 15A).
 1195 **Material:** Five specimens from the middle Pendjari Formation.
 1196 **Occurrence:** Lower Ediacaran Kamakha and Ura formations in Siberia (Moczyłowska et al.,
 1197 1993; Golubkova et al., 2010; Moczyłowska and Nagovitsin, 2012); lower Ediacaran Vychegda
 1198 Formation on Baltica, Russia (Vorob'eva et al., 2009); lower Ediacaran Doushantuo Formation in
 1199 Guizhou and Hunan provinces, China (Shang et al., 2019; Ouyang et al., 2024); Ediacaran of
 1200 Chambal Valley, Rajasthan, India (Asher et al., 2017); potential occurrence in the upper Ediacaran
 1201 Bocaina Formation, Brazil (Morais et al., 2021); herein.
 1202 **Measurements:** Vesicle diameter ranges 93–112 μm ($\mu = 77 \mu\text{m}$, $\sigma = 8$, $N = 5$). Processes are
 1203 25–36 μm long ($\mu = 30 \mu\text{m}$, $\sigma = 3.4$, $N = 16$). Process bases are 30–52 μm wide ($\mu = 35.6 \mu\text{m}$,
 1204 $\sigma = 4.7$, $N = 34$), within the range of the type material from Siberia (Moczyłowska et al., 1993).
 1205 Terminal width of the processes ranges 7–15 μm ($\mu = 8.7 \mu\text{m}$, $\sigma = 1.9$, $N = 34$).
 1206 **Description:** Circular to oval vesicles, with sparse processes with wide bases. The processes are
 1207 conical and taper outwards in a triangular appearance, and they are hollow and open to the vesicle
 1208 interior. The tips are rounded. There are only a few processes on the vesicle, irregularly
 1209 distributed on the surface.
 1210 **Remarks:** In the Pendari Formation, *T. tuberosum* have a lower opacity than other *Tanarium*
 1211 specimens in the assemblage, suggesting a thinner vesicle wall.
 1212
 1213 Unnamed Form A
 1214 Fig. 8(B)
 1215 **Material:** Four specimens in the Pendjari Formation.
 1216 **Measurements:** Elongated vesicles are 99–118 μm long ($\mu = 107 \mu\text{m}$, $\sigma = 9.5$, $N = 3$). Bud-like
 1217 protrusions are 30–35 μm long and 29–32 μm wide.
 1218 **Description:** Elongated, ovoid to ellipsoidal vesicles with a broad, bud-like extension.

Remarks: These vesicles resemble and fall into the size-range of a Meso–Neoproterozoic taxa *Majasphaeridium* and *Itirindia*, ovoid vesicles that bear up to three bud-like extensions (Hermann and Podkovyrov, 2002: pl. 1), interpreted as polyps or fungal sporangia (Shuvalova et al., 2021). However, the Pendjari Formation specimens lack multiple ‘buds’ and the pear-like vesicle shape common to *Majasphaeridium*, so we retain them in open nomenclature. In any case, the presence of a single broad protrusion from the vesicle wall indicates a flexible cell wall common among heterotrophic eukaryotes (Javaux, 2007). Similarly to other budding OWM *Gemmuloides doncooki* co-occurring in the same horizons, these vesicles likely reproduced via asexual budding.

Unnamed Form B

Fig. 8(C)

Material: Five specimens from the upper part of the Pendjari Formation section.

Measurements: Vesicle length is 99–132 μm ($\mu = 115 \mu\text{m}$, $\sigma = 14.3$, $N = 5$) and the width of the ‘neck’ structure is 23–36 μm ($\mu = 29 \mu\text{m}$, $\sigma = 15.2$, $N = 5$).

Description: Oval to elongate vesicle with a neck-like protrusion. The neck is broad and open distally.

Remarks: These vesicles are similar to some morphotypes of flask-shaped microfossil *Lagoenaforma collaris* (Agić et al., 2022: fig. 5b–d). *Lagoenaforma* occurs in upper Ediacaran (post Shuram–CIE) strata worldwide. We retain these specimens in open nomenclature because their ‘necks’ are broader and shorter than those of *L. collaris* and their overall vesicle is larger.

Unnamed Form C

Fig. 8(D)

Material: One specimen from the Pendjari Formation.

Measurements: Vesicle diameter is 69 μm .

Description: Circular vesicles with broad and sparsely distributed processes. The processes are uneven and bifurcate distally. Remnants of a thin membrane are visible between the tips of the processes. Only one side of the vesicle bears processes, while the other part of the vesicle has scars/holes.

Remarks: This specimen are similar to some specimens of *Alicesphaeridium medusoideum* where the processes are broad and occur on one pole of the vesicle (Willman and Moczyłowska, 2008: figs. 6A, B). However, its size is generally smaller than large, >100 µm in diameter *Alicesphaeridium* from Australia. This vesicle could also represent poorly preserved *Multifronsphaeridium* with truncated processes, consistent with the process scars on the other part of the vesicle.

Unnamed Form D

Fig. 8(J)

Material: Two specimens from the middle Pendjari Formation.

Measurements: Vesicle diameter is 67–75 µm in size (N = 2).

Description: Circular vesicles with thorn-like processes encased in an outer membrane. The processes are short and conical. The outer membrane is thin and translucent.

Remarks: The vesicles are similar to double-walled OWM *Distosphaera australica* (Grey, 2005: figs. 148A–D). However, both morphotypes are poorly preserved, so we cannot determine if the processes are solid like in *D. australica* or open to the vesicle cavity, and we leave them in open nomenclature.

5. Discussion

5.1. Biodiversity of the Poubogou and Pendjari formations

Previous micropalaeontological investigations of the WAC drill-hole material reported a moderately diverse OWM assemblage of prokaryotes and eukaryotes from the Abetifi Formation, middle Kwahu Group in the southern Volta Basin (Couëffé and Vecoli, 2011), estimated to be the latest Mesoproterozoic in age based on the U/Pb dates of detrital zircons (ca. 1100 Ma; Kalsbeek et al., 2008) and broad biostratigraphic correlation (Couëffé and Vecoli, 2011). Additionally, carbonaceous compressions *Chuarina circularis* (Mesoproterozoic–Cambrian age range) were reported from the Oti-Pendjari Group correlative strata in Benin and Burkina Faso (Amard, 1992, 1997). The late Mesoproterozoic / early Tonian Poubogou Formation assemblage studied here contains only non-age-diagnostic leiosphaerids (Fig. 4). This lower diversity as well as poorer preservation could be a result of preservational difference between drill-hole and outcrop material, or an indicator of a different palaeoenvironment. Nitrogen isotopes indicate that

the Poubogou shales were deposited in an oxygenated basin with a significant nitrate reservoir (Supplementary Table 2). The Poubogou shales postdate and represent a deep-marine environment compared to the shallow marine Abetifi Formation.

Eukaryotic OWM dominate the Pendjari Formation assemblage, comprising 25 taxa and 50.5% of the overall microfossil abundance (Fig. 9(A)). Simple sphaeromorphs (leiosphaerids) are abundant (61% of microfossil abundance, 27% of taxa; Figs. 7, 9(B)) throughout the unit, but the bulk diversity consists of acanthomorphs (17 taxa, 35% of microfossil abundance; Figs. 5, 6, 9). This is characteristic of the early Ediacaran, pre-Shuram carbon isotope excursion (CIE; cf. Rooney et al., 2020) interval deposits. Overall, DPA forms make up 31% of the overall assemblage, indicating a thriving community of microeukaryotes. These include four species of *Tanarium* (Fig. 6(D–K)), one of the most speciose Proterozoic genera. Partly, its diverse nature can be attributed to minor differences in process size and shape that were used as a basis for establishing myriad species (Xiao et al., 2024), which potentially led to oversplitting. This morphological variability within *Tanarium* is considerably greater than that seen in most older Proterozoic acanthomorphic acritarchs until the Ediacaran Period, and it thus indicates a real increase in OWM disparity in the aftermath of the Cryogenian glaciations. However, such variability in the shape of processes is also common among younger palynomorphs and modern protists like dinoflagellates. In those cases, short-term and local environmental factors such as fluctuations in salinity and temperature can lead to differences in the number of processes and their length (e.g., Kokinos and Anderson, 1995; Mertens et al., 2009). This indicates that the early Ediacaran microeukaryotes likely experienced stronger selective pressure or environmental stressors than the long-ranging OWM taxa common throughout most of the Proterozoic.

Microfossil diversity declined in the uppermost part of the Pendjari Formation section, and acanthomorphs were replaced by leiosphaerids, which comprise 88% of OWM abundance (Figs. 3, 9). This overturn in the assemblage composition is seemingly independent of regional palaeoenvironmental changes (Fig. 11). The shales and siltstones of the lower Pendjari Formation exhibit shallowing-upward trend in the upper part of the outcrop section, so the biotic shift could reflect water-depth changes. The depositional environment shifted from grey shales deposited below fair-weather wave-base, to the green shales with siltier intervals and cross laminations, and into the rippled sandstones representing a tidal environment (Fig. 3). Generally, simple sphaeromorphs like leiosphaerids tend to be a dominant component of deep-water assemblages

(Lei et al., 2012), but they are also characteristic of the late Ediacaran interval. On the other hand, DPA have been found in deposits representing a range of water depths (Ouyang et al., 2017; Morais et al., 2021; Agić et al., 2024). Moreover, in the Dal'nyaya Taiga Group of Siberia, DPA are considerably more diverse and abundant in the shallower parts of the unit than in the distal inner or outer ramp settings (Vorob'eva and Petrov, 2023: fig. 1). Thus, the presence of leiosphaerids and the absence of DPA in the middle, shallow-marine part of the studied sequence suggests that factors other than water depth variations played a role in OWM distribution.

Geochemical proxies broadly indicate deposition in a well-oxygenated basin for the Pendjari Formation (Fig. 11), so the oscillations in redox conditions are also unlikely to have influenced the observed taxonomic shift. The most diverse DPA occur in the horizons with the highest organic C and N content, indicating that productivity and nutrient availability support the diversity of DPA to some extent. There is also a positive correlation ($\rho = 0.66$) between high taxonomic richness and $\delta^{13}\text{C}_{\text{org}}$ value per horizon. We can mostly exclude taphonomic bias as a control on this taxonomic shift, as large, unweathered samples were collected in the recently mined quarries and their outer surfaces were trimmed in the lab and cleaned with HCl prior to maceration to further minimize recent weathering impacts. Our preferred interpretation is thus that these co-variations reflect nutrient-rich conditions in the water column, conducive to higher primary and secondary biological productivity.

Globally, DPA taxa largely went into a decline after the mid-Ediacaran glaciation(s) and the Shuram CIE (Grey and Calver, 2007; Agić et al., 2022, 2024; Ye et al., 2023), with only few exceptions (Grazhdankin et al., 2020). Although the section in Ghana lacks strata that record a negative CIE, perhaps due to missing sedimentary record, the shift in the composition of the microfossil assemblage in the upper part of the sequence is indicative of the late Ediacaran. This depauperate assemblage also includes budding vesicles (*Gemmuloides*, *Blastanosphaira*, Unnamed Form A; Fig. 8(A, B, F–G)) and flask-shaped microfossils (Fig. 8(C)). Similar microfossils with budding or fungi-like features have recently been described from upper Ediacaran successions on Baltica (Golubkova et al., 2022; Środoń et al., 2023). Branching and budding microfossils are also present in the upper Ediacaran strata in Brazil (Denezine et al., 2024). Together with mixotrophic flask-shaped microfossils widely distributed at this time (Agić et al., 2022), such microfossils suggest a rise of heterotrophic microeukaryotes in the late Ediacaran following the decline of DPA. This interval broadly coincides with the 'Kotlinian

Crisis' that marks the first extinction event of macroscopic (Ediacaran) biota (Kolesnikov et al., 2015). In the Pendjari Formation, this interval of taxonomic overturn is weakly correlated with a minor decline in N nutrient availability (Fig. 11), suggesting that DPA were outcompeted by generalists and mixotrophs.

5.2. Biostratigraphic constraints on the depositional age of the Pendjari Formation and its correlation with other Ediacaran units

The base of the Pendjari Formation shales in the outcrop is approximately 50 m above the uppermost Kodjari Formation carbonates, which contains highly negative $\delta^{13}\text{C}_{\text{carb}}$ values (Fig. 10), consistent with the Marinoan cap carbonate that marks the base of the Ediacaran (Kennedy, 1996; Halverson et al., 2005; Xiao and Narbonne, 2020). The OWM recovered from the Pendjari Formation shales further affirm the early Ediacaran, post-Marinoan glaciation depositional age of the unit. With the exception of leiosphaerids and few taxa like *Gemmuloides* and *Simia* that have very long stratigraphic ranges through the Mesoproterozoic and Neoproterozoic, the bulk of the diversity is made up of DPA characteristic of the lower Ediacaran strata worldwide (Table 1).

The Pendjari assemblage shares the most taxa with assemblages from the basins of south-central Australia (19 taxa), Siberian Platform (15 taxa), and South China (13 taxa; Grey, 2005; Willman et al., 2006; Moczyłowska and Nagovitsin, 2012; Liu and Moczyłowska, 2019; Vorob'eva and Petrov, 2023; Table 1). The Australian strata have been divided into four distinct zones based on microfossil distribution (Grey, 2005; Grey and Calver, 2007; Willman and Moczyłowska, 2008). In Ghana, however, these zones are not clearly recognised/separated, despite the overall assemblage composition being similar between the two areas. The main similarity is the absence of *Tanarium irregulare* and *Tanarium tuberosum* in the lower part and their occurrence in the upper part of the sequence (40–72 m stratigraphic height), similarly to their distribution in the upper zones of Australia. However, unlike in Australia, in Ghana they postdate the FAD and LAD of rare *Hocosphaeridium anozos*.

A number of taxa with a well-established local stratigraphic distribution on other cratons have a unique distribution in the Pendjari Formation. For example, some eponymous taxa from separate zones established in Australia and China appear throughout most of the studied Pendjari Formation: *Schizofusa zangwenlongii*, *Tanarium conoideum*, *Multifronsphaeridium*. The lower Pendjari Formation also contains co-occurring species from different biozones in Australia that

are otherwise not found together. *Appendisphaera anguina* is a component of the two lowermost ECAP zones in Australia: the *Appendisphaera barbata*-*Alicesphaeridium medusoideum*-*Gyalosphaeridium pulchrum* (Ab/Am/Gp) and *Tanarium conoideum*-*Schizofusa risoria*-*Variomargosphaeridium litoschum* (Tc/Sr/Vl) zones (Grey, 2005; Grey and Calver, 2007). However, in the lower Pendjari Formation, it co-occurs with *Hocosphaeridium anozos*, which is known from younger zones in Australia (reported as *T. anozos*; Willman and Moczyłowska, 2008). Instead, the distribution of these two taxa in Ghana is more similar to that of South China, where *H. anozos* is found predominantly in the *Tanarium pycnacathum*-*Ceratosphaeridium glaberosum* and *Tanarium conoideum*-*Hocosphaeridium scaberfacium*-*Hocosphaeridium anozos* zones of the Doushantuo Member III (Liu et al., 2014a; Liu and Moczyłowska, 2019), but also co-occurs with specimens reported as *Appendisphaera anguina*? in the upper Member II (Lianhuacun section; Ye et al., 2022). Their co-occurrence was previously also reported on the Siberian Platform, in the Dal’nyaya Taiga Group (Vorob’eva and Petrov, 2023) below the Shuram-equivalent negative CIE in the Zhuya Group (Melezhik et al., 2009), as well as in the Oppokun Formation, inferred to be late Ediacaran in age (Grazhdankin et al., 2020). Taken together with the DPA record from Siberia and China, the Pendjari Formation assemblage suggests that the temporal distribution of key taxa relevant for the Ediacaran subdivision is still not fully resolved globally, and will benefit from continued micropalaeontological work.

Tanarium conoideum is a prominent component of our assemblage and it occurs nearly throughout the DPA-bearing strata of the Pendjari Formation (2–69 m stratigraphic interval). In South China, it is mainly constrained to a relatively narrow stratigraphic interval of a few meters in Doushantuo Member III (in Baiougouyuan, Niuping, and Wagfenggang sections; Liu and Moczyłowska, 2019), but it was also found over a longer stratigraphic interval (ca. 20 m) in Doushantuo Member II in the Lianhuacun section (Ye et al., 2022). *T. conoideum* is more abundant in the lower part of the Pendjari Formation, and its distribution with co-occurring taxa is comparable to that of the *Tanarium conoideum*-*Cavaspina basionica* Zone (3rd zone; Liu and Moczyłowska, 2019; Ye et al., 2022). However, in the Pendjari Formation this assemblage lies below the first and last appearance of *Tanarium tuberosum* (60–69 m), which is more indicative of the *Tanarium tuberosum*-*Schizofusa zangwenglongii* Zone, the second zone of South China (Liu and Moczyłowska, 2019). In that, the distribution of these *Tanarium* species in Ghana is more similar to Australia. There, *T. conoideum* is eponymous to a lower, second zone (*Tanarium*-

conoideum-*Schizofusa risoria*-*Variomargosphaeridium litoschum* (Tc/Sr/Vl) Zone), but *T. tuberosum* is rare, occurring in a single horizon of the Dey Dey Mudstone in the Tc/Sr/Vl Zone and in the Wilari Dolomite Member of the Tanana Formation, in the Cm/Da/Av Zone (Willman and Moczyłowska, 2008). Further deviations from the established biostratigraphic patterns on other cratons include *Schizofusa risoria*, the eponymous species of the Tc/Sr/Vl Zone in Australia (Grey, 2005). It is rare in the Pendjari Formation and mostly occurs in the lower part of the unit, co-occurring with both *T. conoideum* and *Multifronsphaeridium ramosum*, as well as *H. anozos*. *Schizofusa zangwenlongii*, eponymous species of the second biozone established in the Doushantuo Formation in China (*Tanarium tuberosum*-*Schizofusa zangwenlongii*; Liu and Moczyłowska, 2019), is present throughout most of the Pendjari Formation, but is less common in the horizons that contain *T. tuberosum* (Fig. 3; Supplementary Table 1).

Another global taxon *Ceratosphaeridium glaberosum* occurs sporadically through the lower and middle parts of the Pendjari Formation. While it is a common and eponymous species of the upper biozones established both in Australia (*Tanarium irregulare*-*Ceratosphaeridium glaberosum*-*Multifronsphaeridium pelorium* (Ti/Cg/Mp) Zone and *Ceratosphaeridium mirabile*-*Distosphaera australica*-*Apodastoides verobturatus* (Cm/Da/Av) Zone) and China (*Tanarium pycnachantum*-*Ceratosphaeridium glaberosum* Zone), Grey and Calver (2007) reported its presence throughout the DPA-bearing strata in Australia and noted that it is present in older zones but in much lower abundance. *C. glaberosum* is also very rare in the pre-Shuram CIE Ura Formation in Siberia (Moczyłowska and Nagovitsin, 2012), co-occurring with *Assesserium fusulentum*, *Densisphaera fistulosa*, *Hocosphaeridium anozos*, *Tanarium conoideum* and *T. tuberosum*, as in Ghana. Its infrequent occurrence and low abundance in the Pendjari strata corresponds to its distribution patterns in the older DPA zones elsewhere.

The lowermost horizons in the Pendjari Formation succession (0–40 m height) are characterized by the first and last appearances of *Appendisphaera anguina*, *Cavaspina uria*, *Hocosphaeridium anozos*, and *Cymatiosphaeroides kullingii* (Figs. 3, 5). This interval also includes ?*Gyalosphaeridium pulchrum*, *Simia annulare*, and abundant *Tanarium conoideum* and *T. paucispinosum*, but no other *Tanarium* species (Figs. 3, 7). *Multifronsphaeridium ramosum* (Fig. 6(A–C)) is also abundant in the lower part of the section and occurs only in a single horizon in the upper part of the section (at 67 m height). Genera *Multifronsphaeridium* and *Variomargosphaeridium* have been used to subdivide the lower Ediacaran strata in Australia

(Grey, 2005), but due to the similarity in vesicle size and processes, as well as their stratigraphic overlap in Australia and Siberia (Grey and Calver, 2007; Golubkova et al., 2010; Vorob'eva and Petrov, 2023), they likely belong to the same genus, where *Multifronsphaeridium* holds seniority (see Systematics). Only *M. ramosum* morphotype is present in the Pendjari Formation.

Overall, the lower part of the Pendjari Formation (0–40 m above the base) broadly corresponds to the second biozone (Tc/Sr/VI) of Australia (Grey and Calver, 2007), the *Tanarium conoideum*–*Hocosphaeridium scaberfacium*–*Hocosphaeridium anozos* Zone of South China (Liu et al., 2013; Hawkins et al., 2017) or *Tanarium conoideum*–*Cavaspina basionica* Zone (Liu and Moczyłowska, 2019), and the upper part of the Ura Formation in Siberia (Vorob'eva and Petrov, 2023). On the other hand, *Tanarium irregulare*, *T. tuberosum*, ?*Labruscasphaeridium intertextum*, and poorly preserved microfossils similar to *Distosphaera* first appear in the middle part of the Pendjari Formation (40–72 m height), which hosts overall lower species richness (Fig. 3; Supplementary Table 1). Thus, the middle part of the unit broadly corresponds to the Ti/Cg/Mp Zone of south-central Australia (Grey and Calver, 2007) and *Tanarium tuberosum*–*Schizofusa zangwenlongii* Zone in South China (Liu et al., 2014a,b; Liu and Moczyłowska, 2019). In contrast to Australia and China, both the lowermost horizons and green shales from the middle part of the Pendjari Formation contain some co-occurring taxa from Australian and Chinese assemblages, and in that, this assemblage is more similar to the pre-Shuram CIE assemblage of the Dal'nyaya Taiga Group of Siberia. The age of these Siberian units was broadly constrained to the early Ediacaran based on the carbonate Pb–Pb isochron dates of 581 ± 16 and 575 ± 20 Ma (Rud'ko et al., 2021) and the stratigraphic position of DPA-bearing strata >800 m above the Marinoan glacial diamictites (Chumakov et al. 2011; Moczyłowska and Nagovitsin, 2012). In contrast, the upper part of the Pendjari Formation (73–92 m above the base) is marked by a decline of DPA taxa and contains a depauperate leiosphaerid assemblage as well as flask-shaped microfossils and budding forms (Fig. 8(A–C, F, G)) that are more characteristic of the upper Ediacaran (post-Shuram) strata globally (Grey and Calver, 2007; Agić et al., 2022, 2024; Ye et al., 2023; Golubkova et al., 2023; Śrdoń et al., 2023). Although the Pendjari assemblage shares 13 taxa with the Doushantuo Formation, South China houses overall much higher diversity of DPA (>100 taxa), so we consider the Pendjari assemblage more similar to the Siberian Ura assemblage (sharing 15 of 28 eukaryotic taxa in the Dal'nyaya Taiga Group).

The similarities among assemblages from the Volta Basin on the WAC and those from south-central Australia and Siberia call for a tantalizing possibility that these three cratons were in a closer proximity during the early Ediacaran than the current palaeogeographic reconstructions suggest (Merdith et al., 2017), or at the very least were in close proximity together and further away from South China, which has a higher OWM diversity and endemism (Liu et al., 2014a; Table 1).

5.3. Palaeoenvironmental context

The studied units were episodically deposited in shallow-marine environments in the intracratonic Volta Basin, from the late Mesoproterozoic/early Tonian to the early Ediacaran. These environments were characterized by low biological productivity based on low TOC content and moderately preserved microfossils (Figs. 10, 11; Supplementary Tables 1, 2). High to moderate positive nitrogen isotope values indicate deposition in the basin with a large dissolved nitrate reservoir and oxygenated water-column (Stüeken et al., 2016). Oxidic setting at the depositional site is further supported by the lack of highly negative $\delta^{13}\text{C}_{\text{org}}$ values and resultant moderate $\Delta\delta^{13}\text{C}$ values, arguing against significant contribution from secondary biological productivity associated with methanotrophy and sulphur oxidation (Karhu and Bekker, 2020), and low C/N values, indicating significant organic matter remineralization (Fig. 11). Carbon and oxygen isotope values of carbonates from the Kodjari Formation argue for a good preservation of original seawater C isotope signature and deposition of the Kodjari and Pendjari formations in the immediate aftermath of the Marinoan glaciation (Fig. 10). Taken together, our geochemical data imply persistently oxygenated, shallow-marine, intracratonic depositional setting at the Mesoproterozoic/Neoproterozoic transition and in the late Neoproterozoic, in which the DPA taxa became abundant in the early Ediacaran.

While regional redox conditions did not affect the OWM diversity and distribution as discussed above, there are weakly positive co-variations between species richness and TOC ($r = +0.51$) and TN ($r = +0.53$) contents, indicating that the highest species richness was associated with more nutrient-rich, productive water column conditions. Interestingly, organic carbon and nitrogen isotope composition of the Pendjari shales corresponds to the values in the DPA-bearing Doushantuo Formation Member III (Cañadas et al., 2022). Our geochemical data also indicate that the taxonomic turnover from DPA to leiosphere- and budding microfossil-

dominated assemblage in the upper part of the Pendjari Formation (70–92 m) coincides with only a slightly reduced nutrient availability (TN) (Figs. 3, 11), where DPA were outcompeted by generalists and mixotrophs. However, since no significant geochemical shifts were observed, the environmental changes only played a minor role in the post-Snowball diversification of DPA on WAC. Our study thus emphasizes that biological innovation and nutrient availability, rather than large scale environmental changes, such as persistent oxygenation of shallow-marine environments, controlled the emergence and expansion of the complex DPA taxa in the early Ediacaran of the Volta Basin.

6. Conclusions

Moderately preserved Doushantuo-Pertatataka type organic-walled microfossils were recovered from the Pendjari Formation in the Volta Basin in Ghana, which establish the early Ediacaran age for the unit. The biostratigraphic inference is also consistent with previous correlations of the underlying Kodjari Formation carbonates with the post-Marinoan cap carbonate. The OWM assemblage comprises 29 taxa. Microfossil diversity declines in the upper part of the formation and a DPA-dominant assemblage is replaced by an assemblage of sphaeromorphs (leiosphaerids) and budding taxa. As palaeoenvironmental conditions during that interval did not significantly change, this suggests global rather than basinal control on DPA diversity decline in the Volta Basin. The observed DPA taxa are shared predominantly with assemblages from south-central Australia, Siberia and South China, as well as south-central Brazil, Baltica, and India. However, some eponymous species from zones established in other regions appear throughout most of the Pendjari Formation (*Schizofusa zangwenlongii*, *Tanarium conoideum*, *Multifronsphaeridium*). Furthermore, the lower Pendjari Formation contains taxa found in distinct biozones in Australia and China (*Appendisphaera anguina*, *Hocosphaeridium anozos*) and co-occurrence of these taxa was also reported from the Ediacaran Oppokun Formation in Siberia and Doushantuo members II and III in China. This might indicate that the Pendjari Formation is a condensed succession, in comparison to those in the Amadeus and Officer basins.

The Pendjari assemblage is diverse and changes over approximately 90 m of stratigraphy, allowing the recognition of three successive assemblages: 1) diverse community with abundant *Tanarium conoideum* and *Multifronsphaeridium ramosum*, as well as *Appendisphaera anguina*

and *Hocosphaeridium anozos*, which compositionally broadly corresponds to the 2nd zone (Tc/Sr/Vl) of Australia, the *Tanarium conoideum*–*Hocosphaeridium scaberfacium*–*Hocosphaeridium anozos* Zone in South China and the upper part of the Ura Formation in Siberia; 2) less diverse community characterised by the first appearances within the unit of *Tanarium irregulare* and *Tanarium tuberosum*, broadly corresponding to the Ti/Cg/Mp Zone of south-central Australia and *Tanarium tuberosum*–*Schizofusa zangwenlongii* Zone in South China; and 3) depauperate leiosphaerid assemblage with budding forms, more characteristic of the upper Ediacaran strata globally.

Many of the Pendjari Formation taxa, reported here for the first time on the WAC, are known from assemblages in Australia, South China, Brazil, Baltica and Siberia, which confirms a cosmopolitan distribution of DPA. Overall, the high species richness in strata overlying the post-Marinoan cap carbonate of the Kodjari Formation and a widespread distribution of those taxa, indicates a relatively rapid, global diversification of marine microeukaryotes in the aftermath of the Snowball Earth glaciation.

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Figure captions

Fig. 1. A. Geological map of the Volta Basin, based on units established by Affaton (1980) and modified from Kalsbeek (2008). Sampled sections are marked by red stars. **B.** The area in (A) shown on the map of Africa. **C.** Schematic stratigraphy of the Volta Basin exposed in outcrop. Material in this study comes from the Poubogou, Kodjari, and Pendjari formations. Age estimates are based on: (i) ID-TIMS U-Pb zircon depositional age of 601.3 ± 2.0 Ma in the discontinuous Darebe Tuff member in the upper Kodjari Formation (Carney et al., 2010), marked in orange line; (ii) detrital zircon depositional age of 1.1-1.0 Ga from the Panabako Formation (Kalsbeek et al., 2008); (iii) Rb/Sr isochron age of 993 ± 65 Ma from the Poubogou Formation (Clauer, 1976).

Fig. 2. Representative late Neoproterozoic strata of the Volta Basin in outcrop. **A, B.** Carbonates of the Kodjari Formation near Buipe. **C, D.** Mudstones of the Ediacaran fossiliferous Pendjari Formation near Yendi.

Fig. 3. Distribution of organic-walled microfossils through the composite stratigraphy of the studied Oti-Pendjari Group. Organic-walled microfossils occur throughout the outcrop section of the Pendjari Formation. Doushantuo-Pertatataka acanthomorph acritarch taxa are abundant in the lower part of the Pendjari Formation, but are replaced by sphaeromorphs and budding taxa in the upper part of the unit.

Fig. 4. Sphaeromorphs from the latest Mesoproterozoic / early Tonian Poubogou Formation. **A.** *Leiosphaeridia crassa* (Naumova, 1949) Jankauskas et al., 1989; AMM001-1 81x11. **B.** Two overlapping cells of *Leiosphaeridia minutissima* (Naumova, 1949) Jankauskas et al., 1989. AMM003-1 80x19. Scale bars: 15 μ m.

Fig. 5. Organic-walled microfossils from the Pendjari Formation. **A, B.** *Appendisphaera anguina* Grey, 2005; A: AMY-3-1 111x8; B: AMY-3 102x12. **C.** *Cavaspina uria* Nagovitsin and Moczyłowska, 2012; AMY-6-1 80x7. **D.** *Assesserium fusulentum* Nagovitsin and Moczyłowska, 2012; AMY11-1. **E.** *Ceratosphaeridium glaberosum* Grey, 2005; AMY-3-2 89x9. **F.** *Cymatiosphaeroides kullingii* Knoll, 1984 emend. Shang et al., 2019; AMY-11-1 90x9. Arrows indicate processes that support the outer membrane. **G.** ?*Calyxia xandaros*

Willman and Moczyłowska, 2008; AMY-11-1 75x19. **H.** *Leiosphaeridia anquiensis* (Yin, 1991) Yin and Guan, 1999; AMY-3-1 111x12 20x. **I.** *Densisphaera* sp.; AMY-9-1 105x12. Arrows are showing thin ‘process-like extensions’ on the outer vesicle. **J.** *Densisphaera fistulosa* Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, 2012 emend. Moczyłowska, 2016; AMY-3-2 124x18. Arrows are showing heteromorphic processes of the outer vesicle. **K.** *Hocosphaeridium anozos* (Willman and Moczyłowska, 2008) Xiao et al., 2014. Scale bars: 30 µm.

Fig. 6. A–C. *Multifronsphaeridium ramosum* Nagovitsin and Moczyłowska in Moczyłowska and Nagovitsin, 2012. **A:** Two specimens of *Multifronsphaeridium ramosum*, AMY-3 102,5x12; **A1:** Higher magnification of prominent trunk-like processes with multifurcated termini on the lower left side of the specimen; **B:** Processes terminate in radially spreading second-order branches. AMY-1 124x14; **C:** Specimen with bifurcating termini, AMY-3 119x15. **D–F.** *Tanarium conoideum* Kolosova, 1991, emend. Moczyłowska, Vidal, Rudavskaya, 1993; **D:** AMY-11-1 80x13; **E:** AMY-6-1 77x19; **F:** AMY-6-1 76x17. **G–I.** *Tanarium irregulare* Moczyłowska, Vidal, Rudavskaya, 1993; **G:** Specimen with a few bifurcated processes; AMY-9-1 120x4; **H:** Fragmented collapsed vesicle, taphomorph *Tanarium pycnacanthum*; AMY-9-1 79x9; **I:** AMY-11-2 82x5 20x. **J.** *Tanarium paucispinosum* Grey, 2005. AMY-3 104x9. **K.** *Tanarium tuberosum* Moczyłowska, Vidal, Rudavskaya, 1993. AMY-9-1 114x11. Scale bars: 30 µm (single bar), 15 µm (double bar).

Fig. 7. Sphaeromorphs and ellipsoid OWM from the Pendjari Formation. **A.** *Leiosphaeridia crassa* (Naumova, 1949) Jankauskas et al., 1989; AMY-9-1 120x4. **B.** *Schizofusa risoria* Grey, 2005; AMY-9-1 120x6. **C.** Fragment of a large vesicle *Leiosphaeridia jacutica* (Timofeev, 1966) Jankauskas et al., 1989; AMY-3-2 101x15. **D.** A leiosphaerid with a pliant vesicle wall; AMY-9-1 88.5x14. **E.** Two specimens of *Leiosphaeridia minutissima* (Naumova, 1949) Jankauskas et al., 1989; AMY-14-1 77x11. **F.** Leiosphaerid with a pliant wall; AMY-3-2 120x16. **G.** *Simia annulare* (Timofeev, 1969) Mikhailova in Jankauskas et al. 1989; AMY-3-2 128x14. **H.** *Schizofusa zangwenlongii* Grey, 2005; AMY-3-2 125x12. Scale bar: 25 µm.

Fig. 8. Budding OWM and problematica from the Pendjari Formation. **A.** *Gemmuloides doncookii* Samuelsson and Butterfield, 2001; AMY-9-2 79x12. **B.** Unnamed Form A, a budding vesicle. AMY-3-1 103x10. **C.** Unnamed Form B, vesicle with a neck-like protrusion. AMY-18-1 88x16. **D.** Vesicle with short, thin processes (bottom) and Unnamed Form C—an acanthomorph with thick, sparse processes (top); AMY3-1 123x15. **E.** Ovoid vesicle with a polar opening (indicated by an arrow), *L. anquiensis* (Yin, 1991) Yin and Guan, 1999; AMY-3-2 85x9. **F, G.** Budding vesicles with septate joints, *Blastanosphaera kokkoda* Javaux and Knoll, 2017; F: AMY-14-1 100x11, arrows indicate joints between the cells; G: AMY-5 108x10. **H.** ?*Gyalosphaeridium pulchrum* Zang in Zang and Walter, 1992 emend. Grey, 2005; AMY-3-2 128x14; arrows indicate short processes characteristic of *Gyalosphaeridium*. **I.** Acanthomorph with processes wrapped around the vesicle, ?*Labruscasphaeridium intertextum* Grey, 2005. AMY-9-1 119x15. **J.** Unnamed Form D, acanthomorph vesicle with a spongy, uneven envelope, similar to *Distosphaera*. AMY-20-1 89x18. Scale bars: 35 μm (single bar), 25 μm (double bar).

Fig. 9. A. Abundance of OWM taxa in the Ediacaran Pendjari Formation. **B.** Taxonomic richness and abundance of different OWM morphology types in the Pendjari Formation.

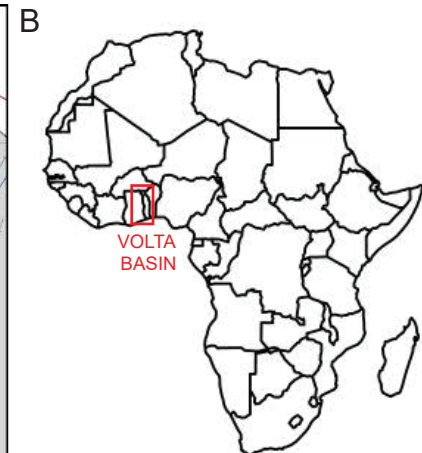
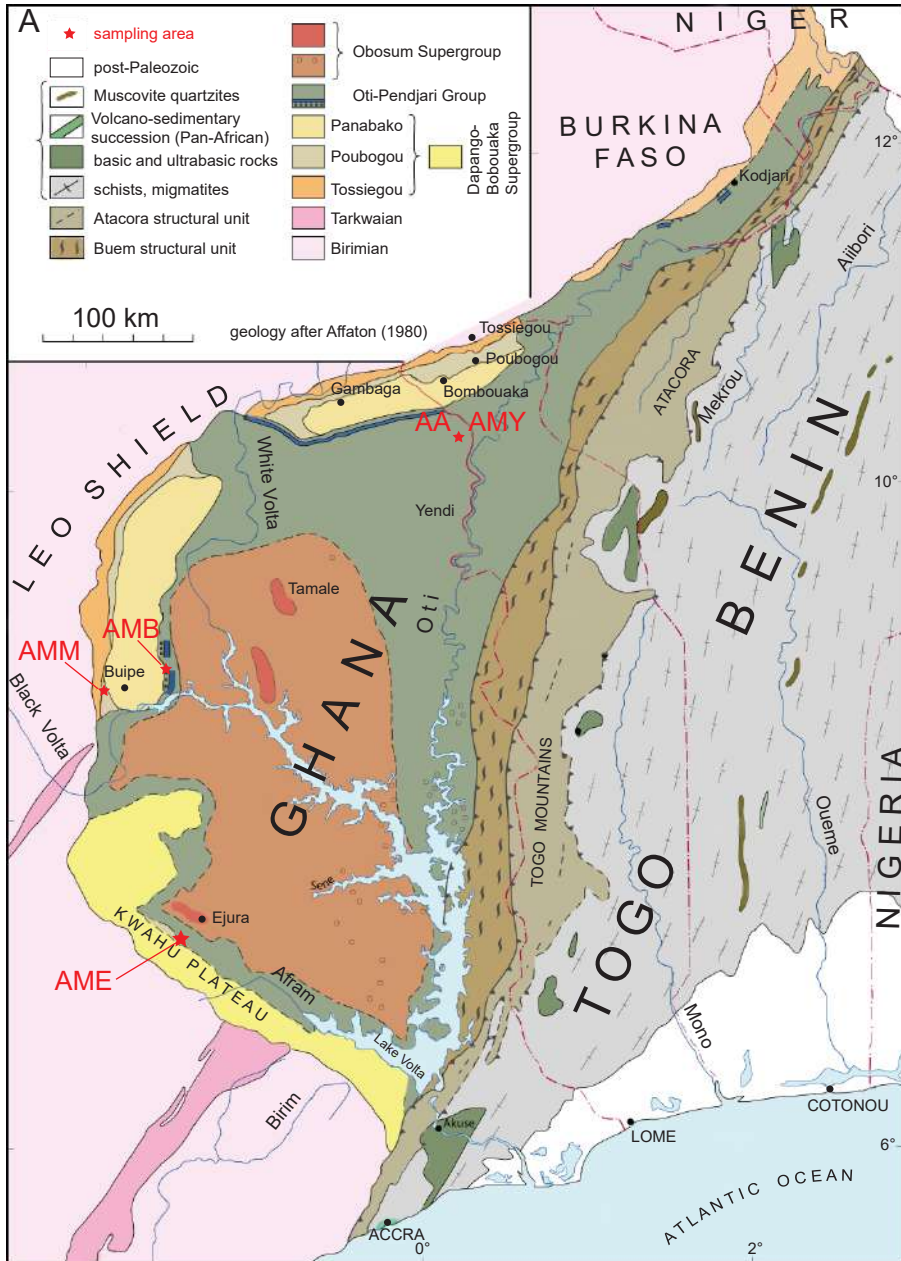
Fig. 10. Chemostratigraphic profile for the Kodjari Formation in Volta Basin, Ghana. Negative $\delta^{13}\text{C}_{\text{carb}}$ values are consistent with those of the Marinoan glaciation cap carbonate (cf. Halverson et al., 2005). **A.** AMB section from the limestone quarry near Buiepe. **B.** AA section in the northeast.

Fig. 11. Species richness and chemostratigraphic profile through the Pendjari Formation outcrop. Decline in OWM species richness and transition from the lower Ediacaran DPA taxa to LELP taxa characteristic of the late Ediacaran occurs independent of palaeoenvironmental conditions. $\delta^{13}\text{C}$, TOC, and $\delta^{15}\text{N}$ indicate deposition in an oxic environment with a large dissolved nitrate reservoir.

Fig. 12. Size comparison of *Multifronsphaeridium* and *Variomargosphaeridium* species size maxima and minima across different localities. With exceptions of the largest specimen of *M.*

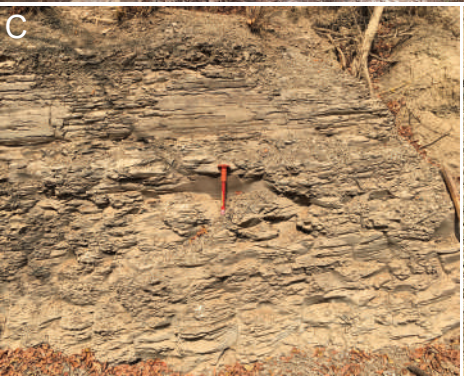
2113 *pelorium* from Australia ([Grey, 2005](#)), there is overlap between vesicle diameter and process
2114 lengths across most taxa within both genera.

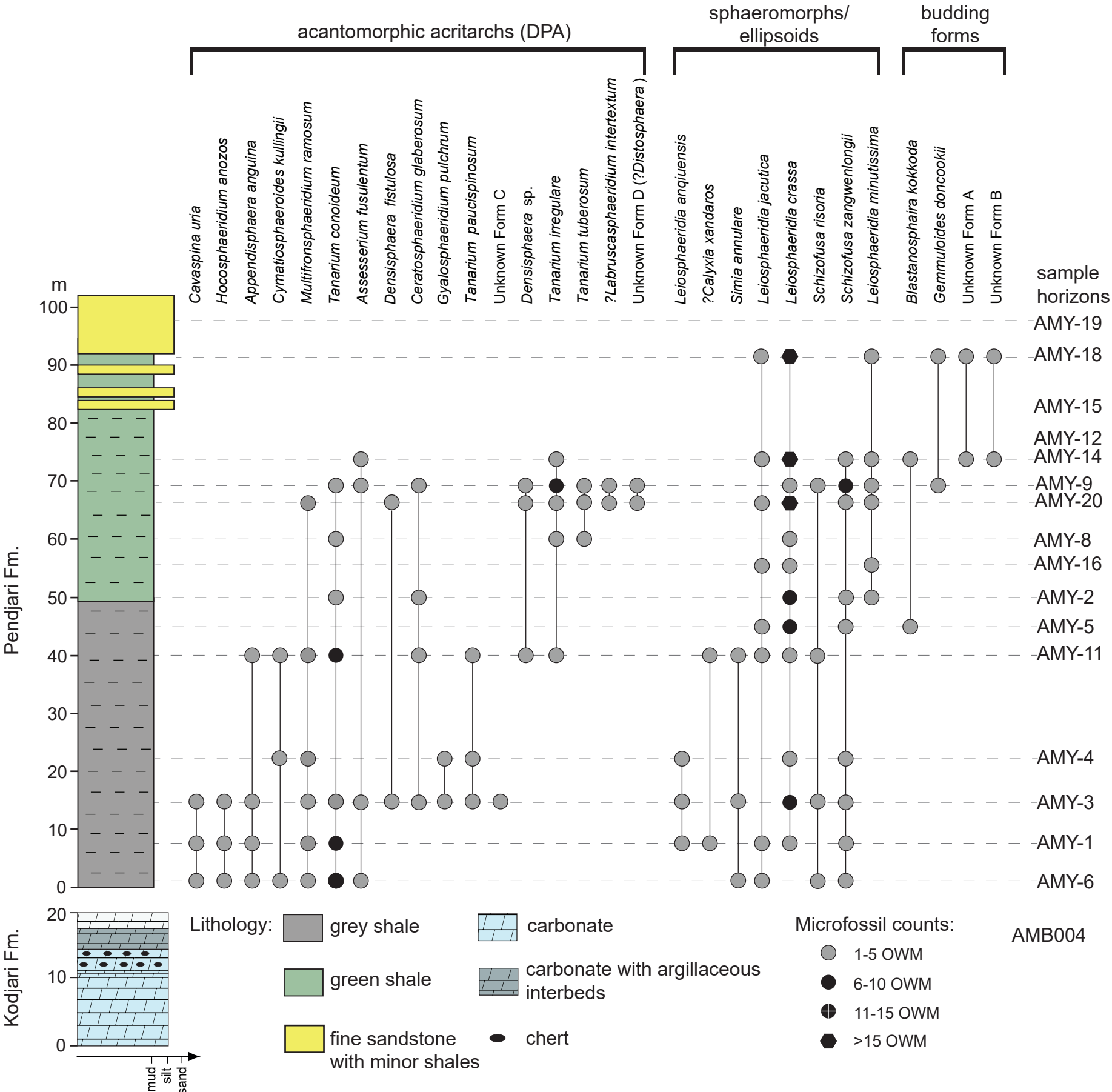
2115
2116 **Table 1.** Global distribution of OWM taxa found in the Pendjari Formation. Most taxa are shared
2117 with early Ediacaran assemblages in Australia and Siberia.



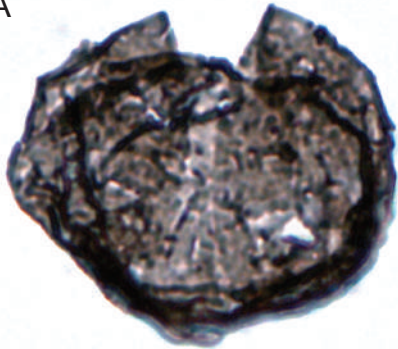
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TIME	GROUP	FORMATION	LITHOLOGY
Paleozoic	Tamale/ Obosum	Obosum	sandstones, conglomerates
		Tamale	
Unconformity			
Late Neoproterozoic	Oti-Pendajri	Pendjari	argillaceous shales, minor sandstones
		Kodjari	601.3 ± 2.0 Ma (1) carbonates, tillites
Unconformity			
Late Mesoproterozoic	Kwahu/ Bambouaka	Panabako	1100-1000 Ma (2) sandstones
		Poubogou	993 ± 65 Ma (3) shales, sandy shales
		Tossiegou	sandstones, minor shales
Unconformity			



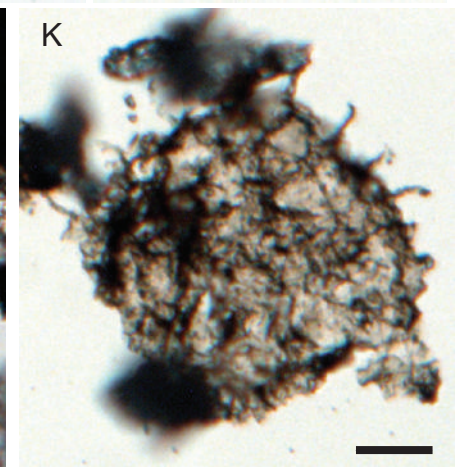
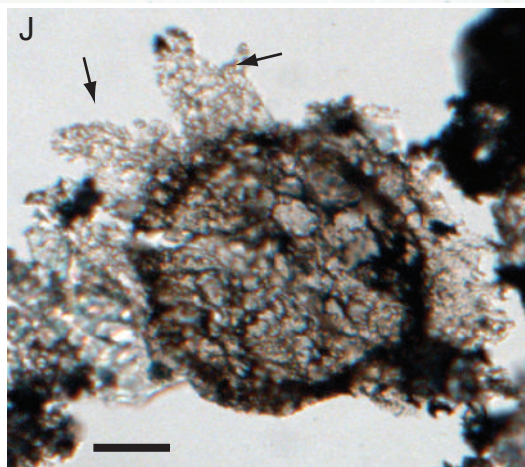
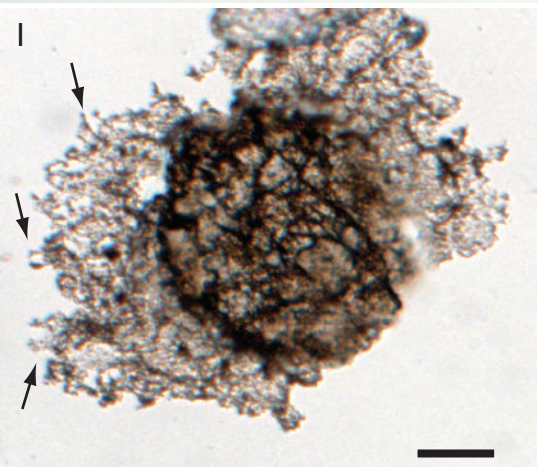
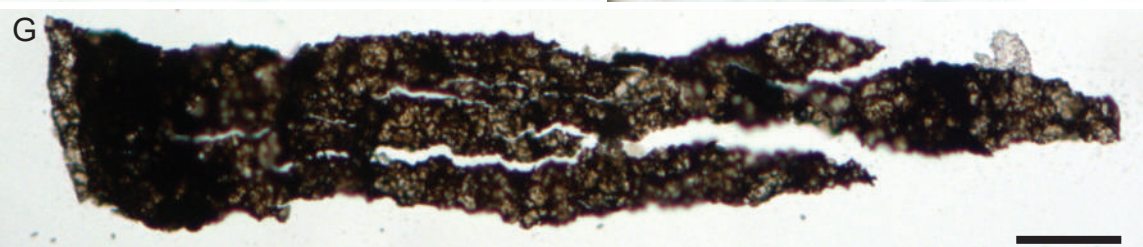
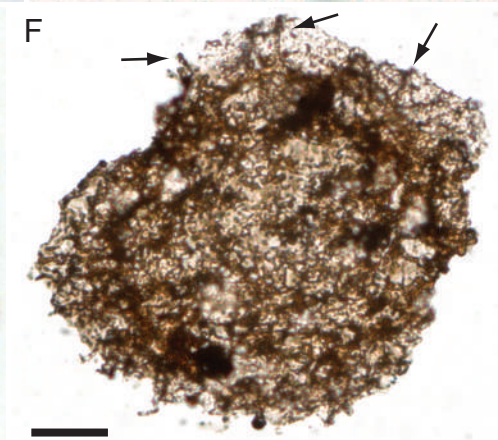
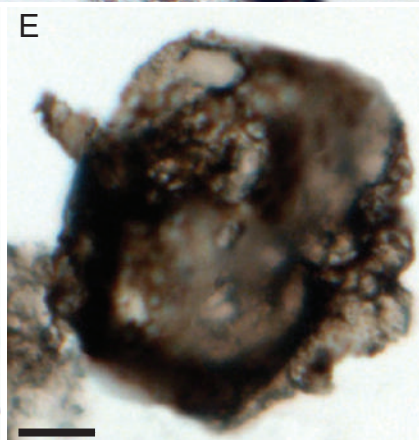
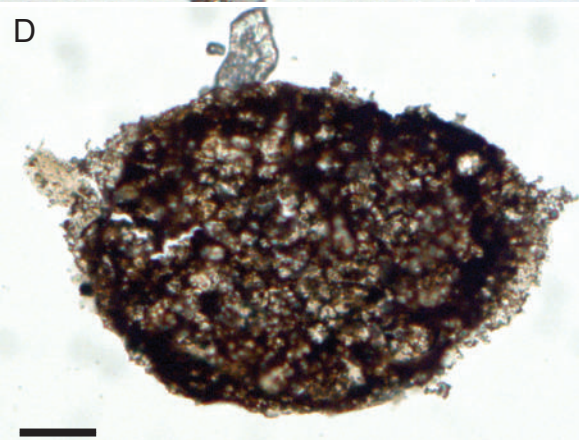
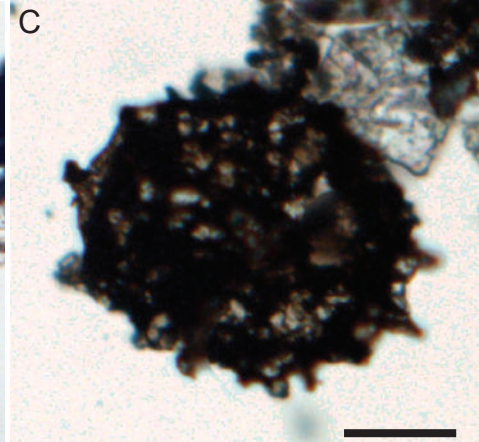
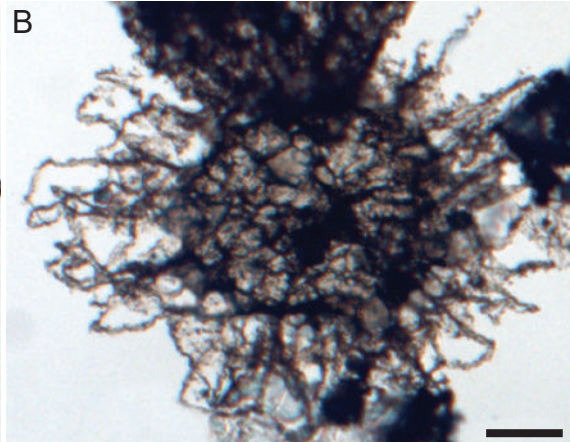
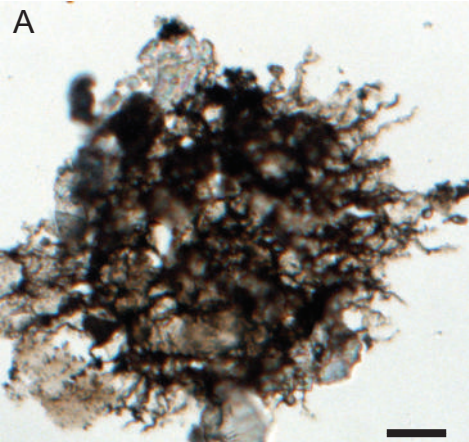


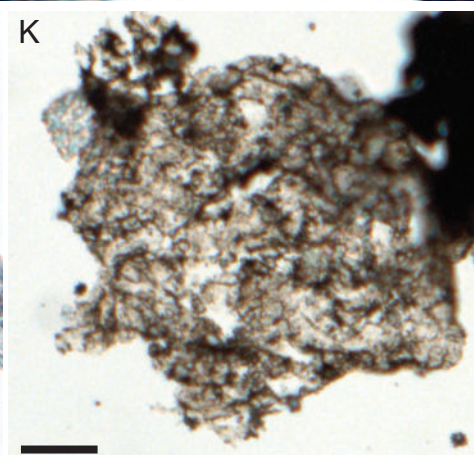
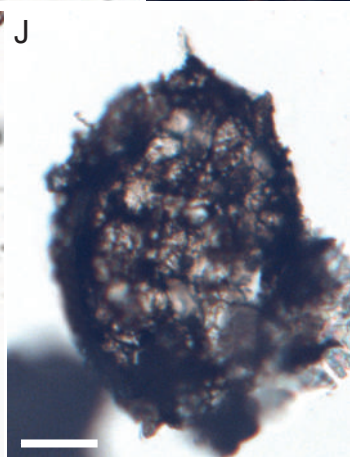
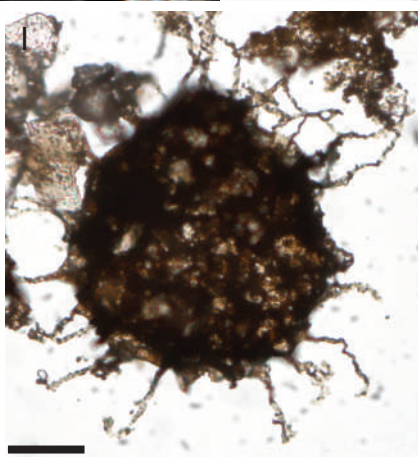
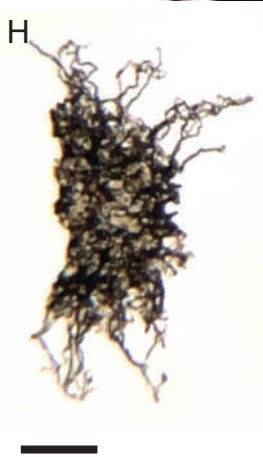
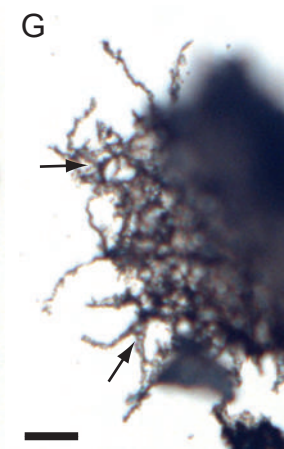
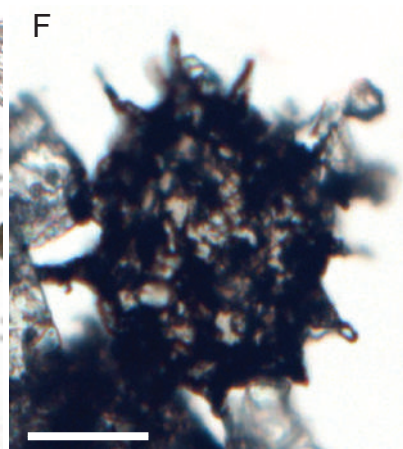
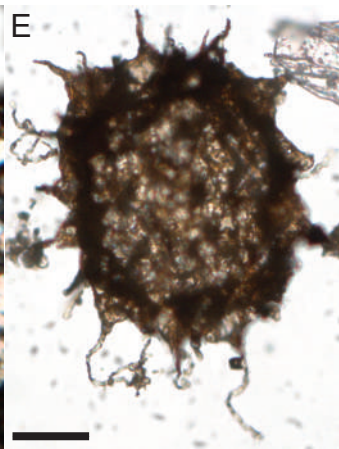
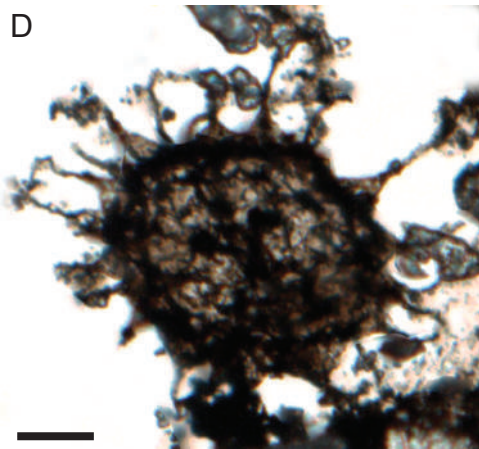
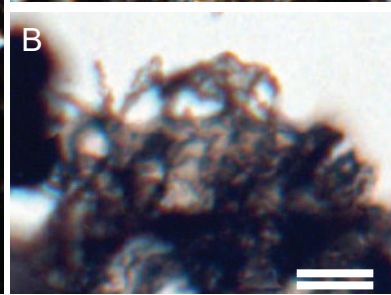
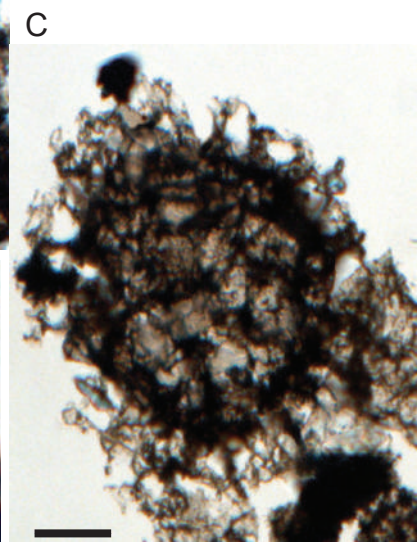
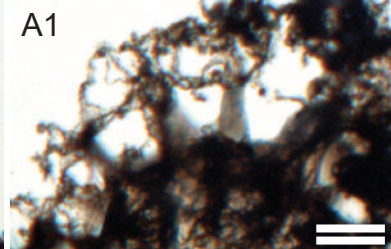
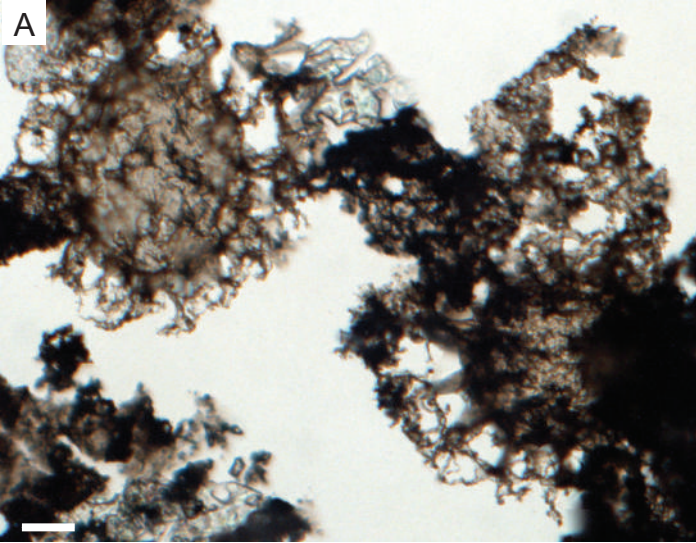
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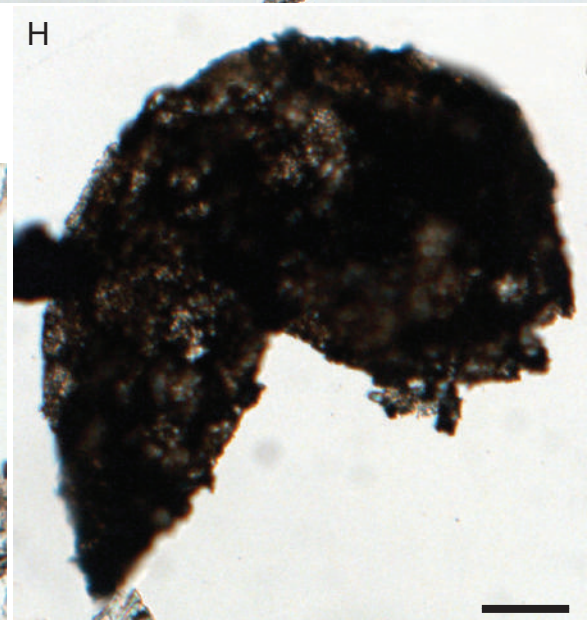
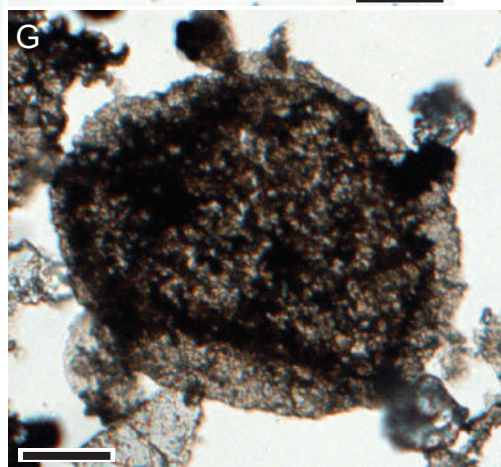
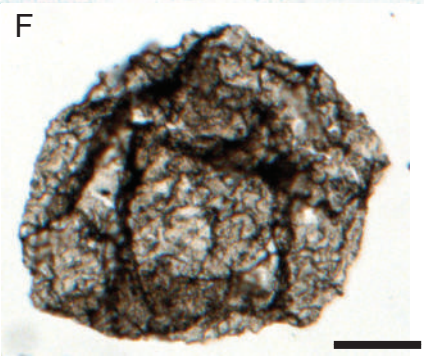
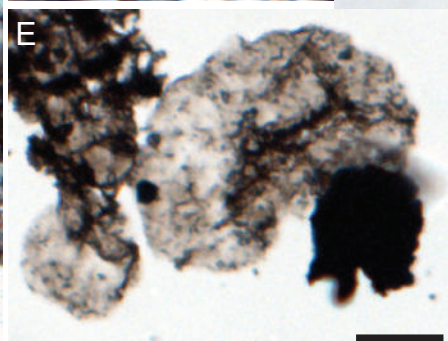
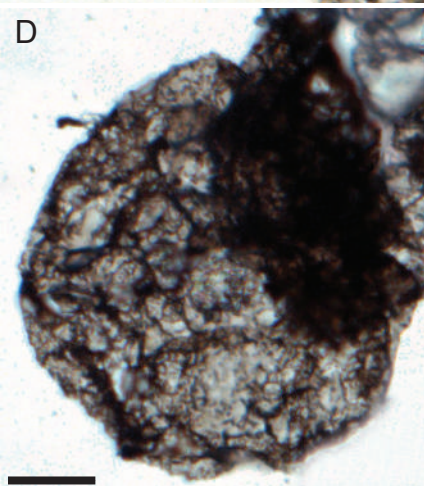
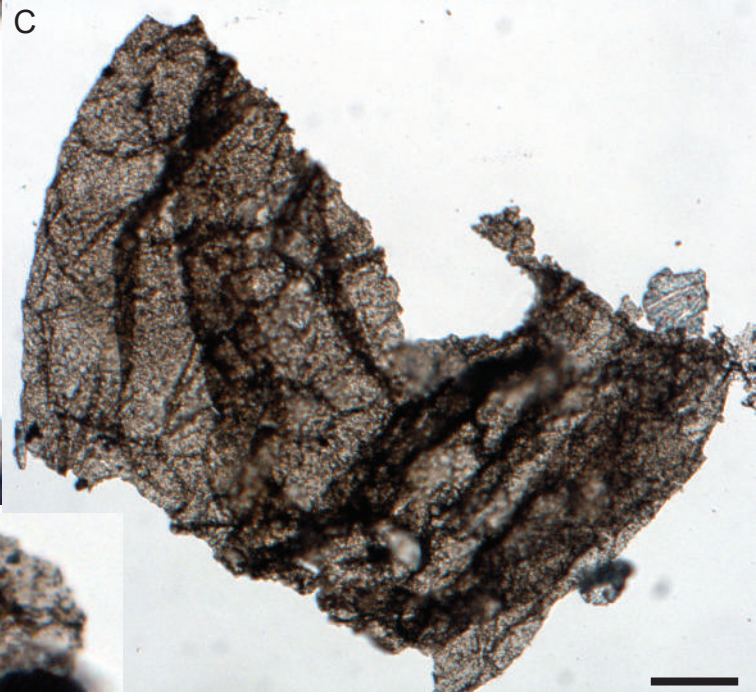
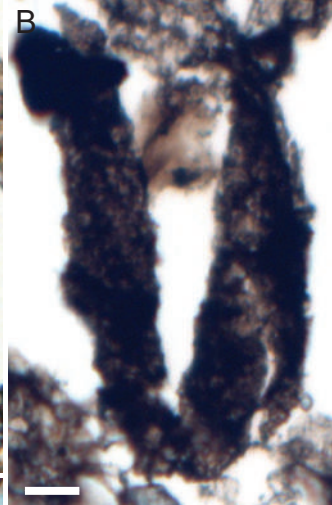
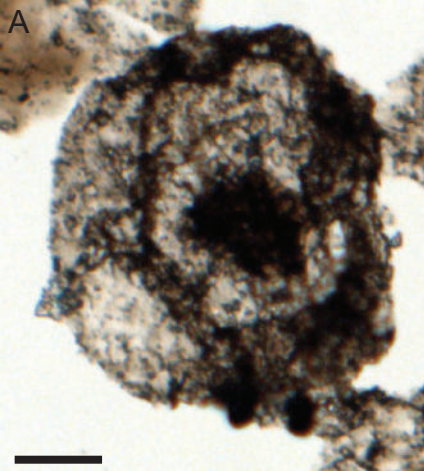


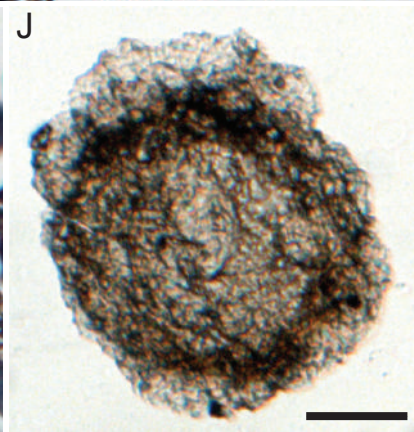
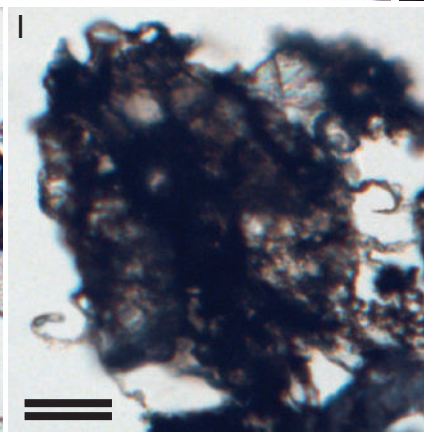
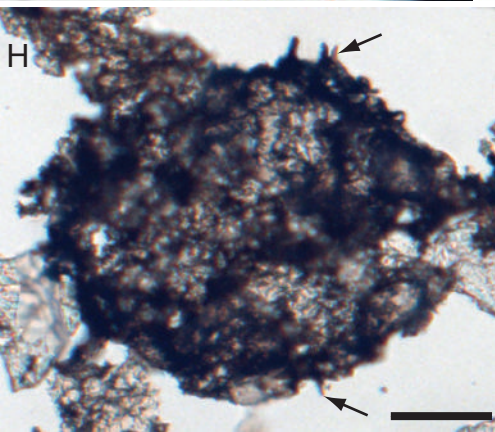
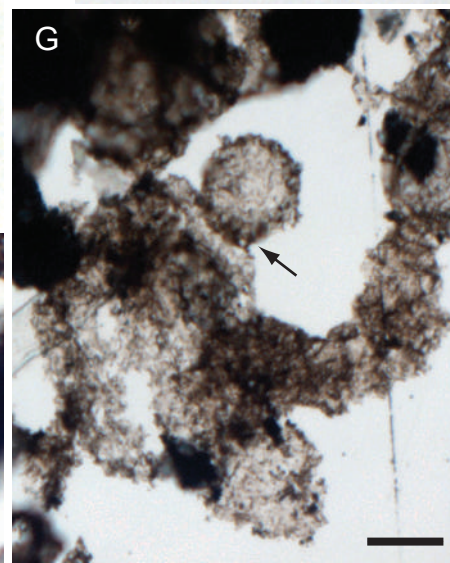
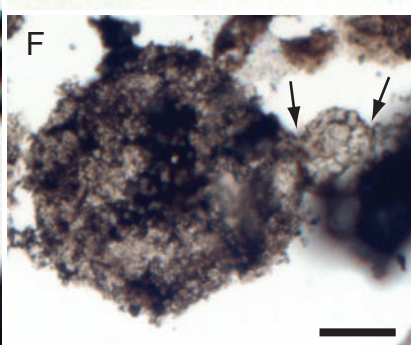
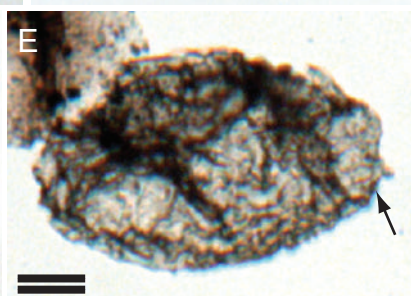
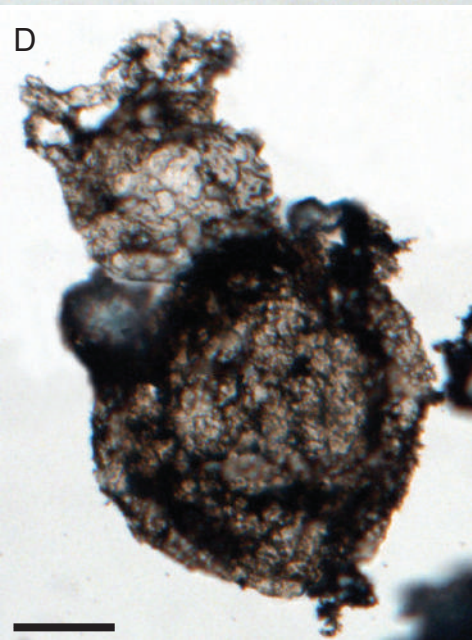
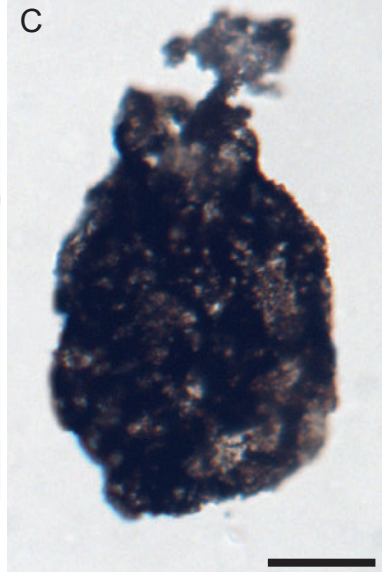
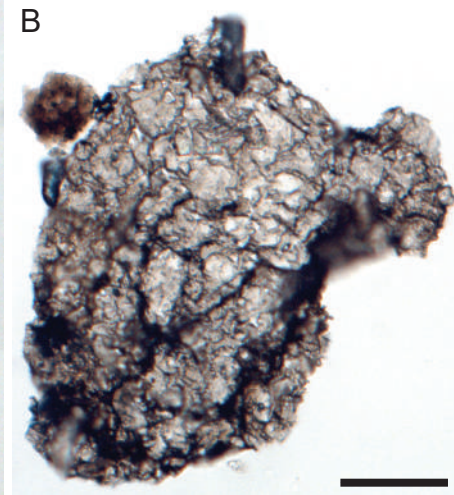
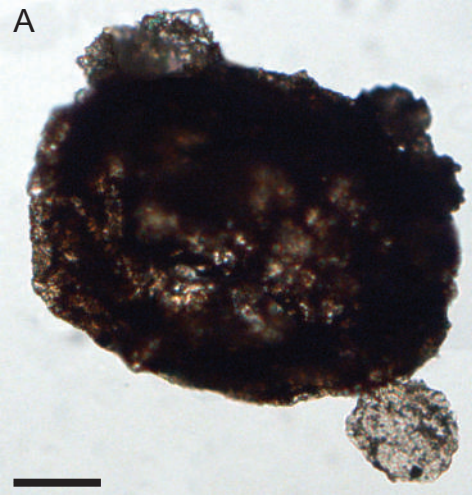
B



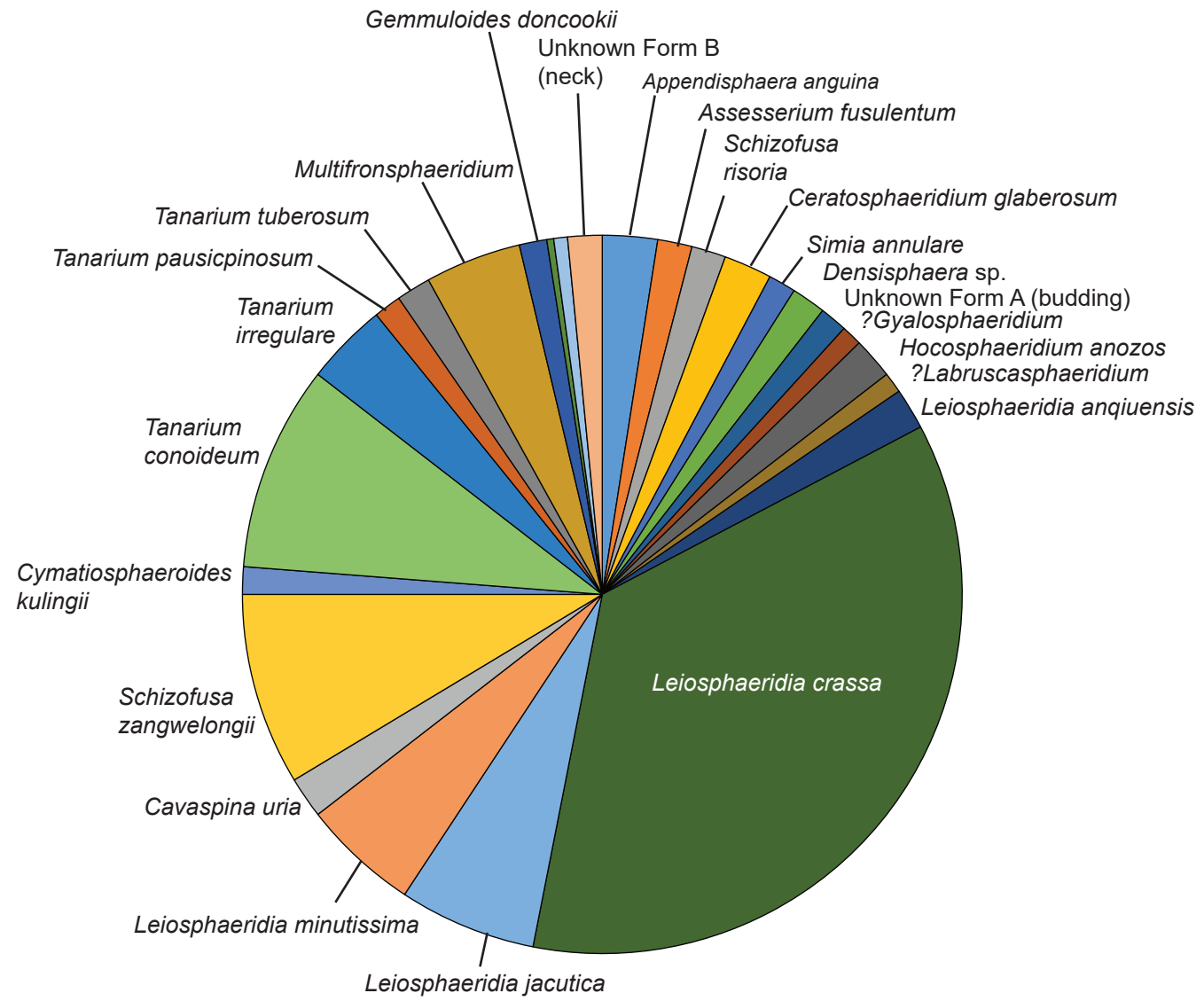




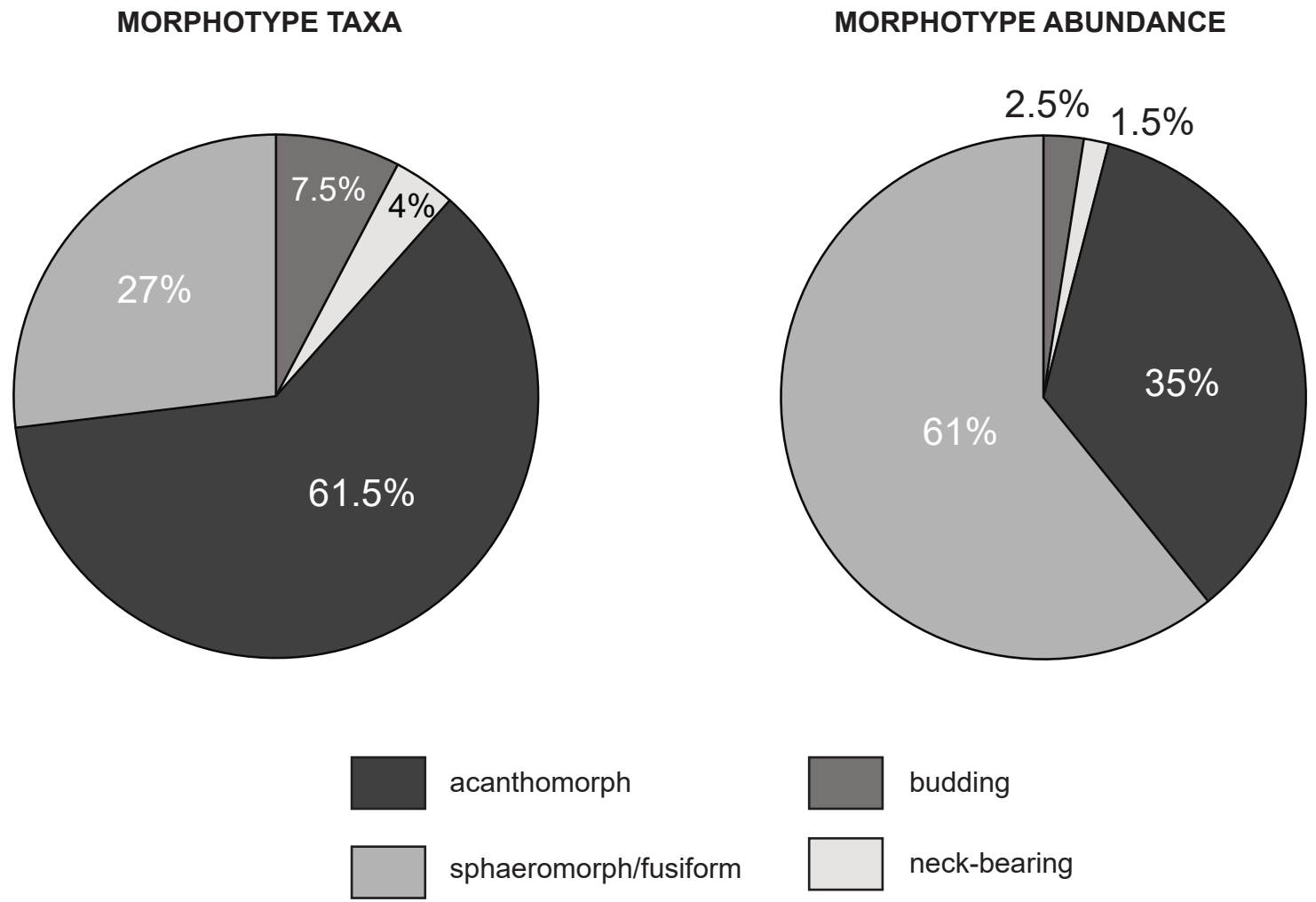




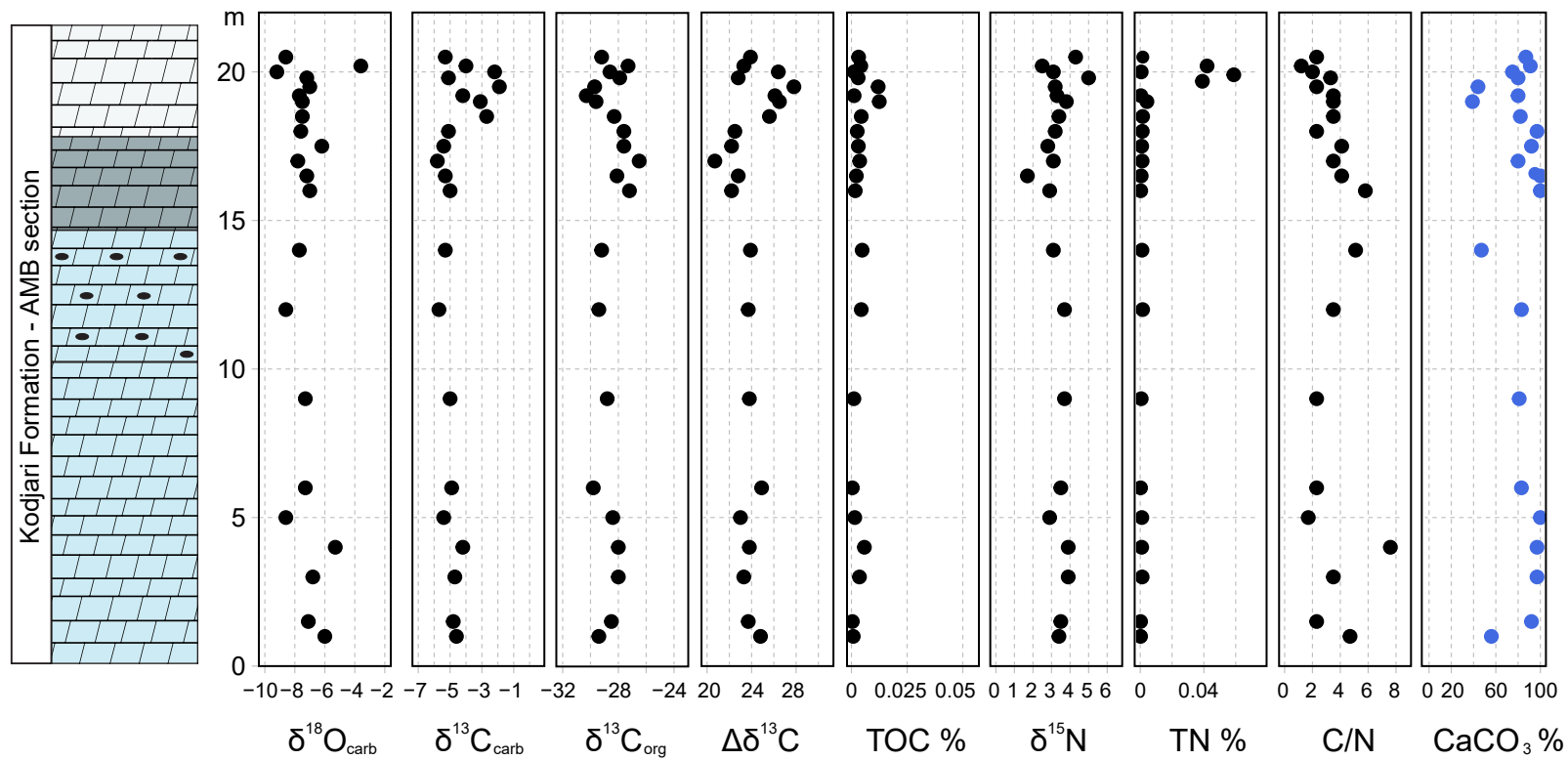
A



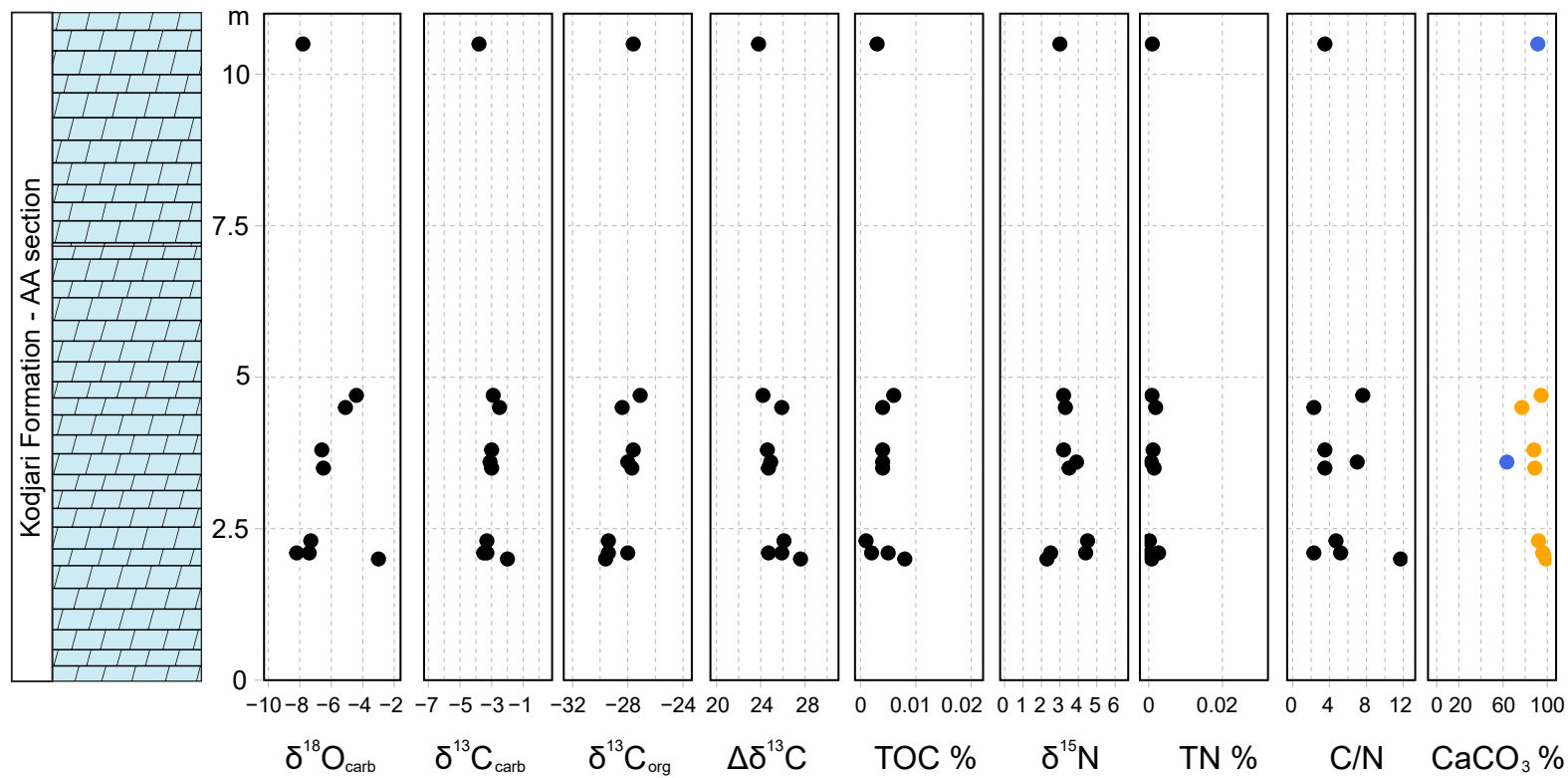
B



A



B



carbonate

carbonate with argillaceous
interbeds

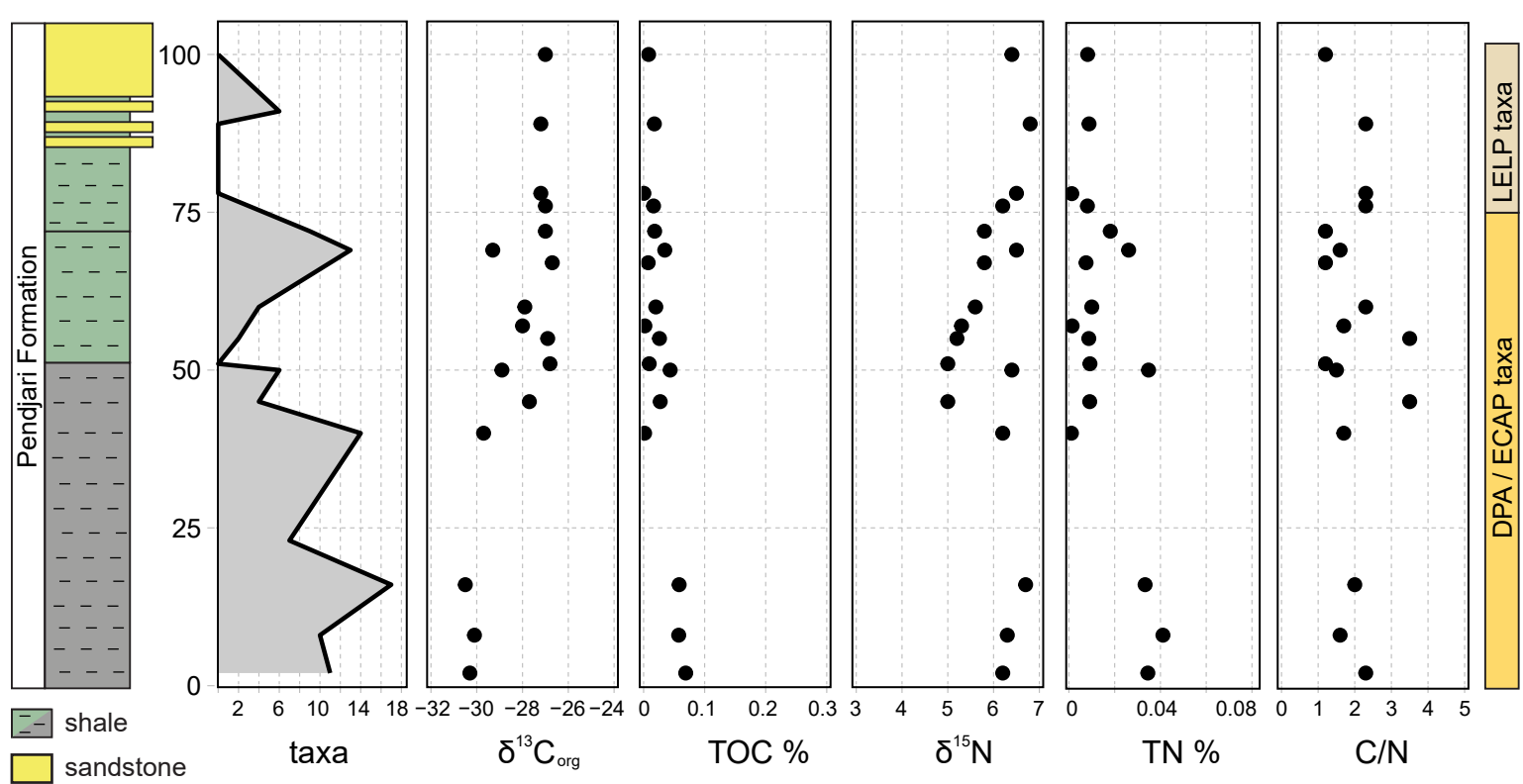
chert



calcite



dolomite



Taxon	Ghana (this study)	Australia	Baltica	Brazil	China	India	Norway	Siberia
<i>Appendisphaera anguina</i>	●	●			●?			
<i>Assesserium fusulentum</i>	●			●			●	●
<i>Blastanosphaera kokkoda</i>	●	●?		●				
<i>Cavaspina uria</i>	●	●	●		●			●
? <i>Calyxia xandaros</i>	●	●						
<i>Ceratosphaeridium glaberosum</i>	●	●	●	●	●		●	●
<i>Cymatiosphaeroides kullingii</i>	●	●			●			
<i>Densisphaera fistulosa</i>	●					●		●
<i>Densisphaera</i> sp.	●							●
<i>Gemmuloides doncookii</i>	●							
? <i>Gyalosphaeridium pulchrum</i>	●	●			●	●		●
<i>Hocosphaeridium anozos</i>	●	●			●			
? <i>Labruscasphaeridium intertextum</i>	●	●						●
<i>Leiosphaeridia anquiensis</i>	●				●			
<i>Leiosphaeridia crassa</i>	●	●	●	●		●	●	●
<i>Leiosphaeridia jacutica</i>	●	●				●	●	
<i>Leiosphaeridia minutissima</i>	●						●	
<i>Multifronsphaeridium ramosum</i>	●		●		●		●	●
<i>Schizofusa risoria</i>	●	●			●			
<i>Schizofusa zangwenlongii</i>	●	●		●	●	●	●	●
<i>Simia annulare</i>	●			●				
<i>Tanarium conoideum</i>	●	●			●	●		●
<i>Tanarium irregulare</i>	●	●					●	●
<i>Tanarium paucispinosum</i>	●	●			●			●
<i>Tanarium tuberosum</i>	●	●		●	●			●
Unknown Form A (budding)	●	●						●
Unknown Form B (neck-like)	●		●?				●?	
Unknown Form C	●							
Unknown Form D	●	●?						