LETTERS

Large colonial organisms with coordinated growth in oxygenated environments 2.1 Gyr ago

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The evidence for macroscopic life during the Palaeoproterozoic era (2.5–1.6 Gyr ago) is controversial^{1–5}. Except for the nearly 2-Gyr-old coil-shaped fossil Grypania spiralis^{6,7}, which may have been eukaryotic, evidence for morphological and taxonomic biodiversification of macroorganisms only occurs towards the beginning of the Mesoproterozoic era (1.6–1.0 Gyr)⁸. Here we report the discovery of centimetre-sized structures from the 2.1-Gyr-old black shales of the Palaeoproterozoic Francevillian B Formation in Gabon, which we interpret as highly organized and spatially discrete populations of colonial organisms. The structures are up to 12 cm in size and have characteristic shapes, with a simple but distinct ground pattern of flexible sheets and, usually, a permeating radial fabric. Geochemical analyses suggest that the sediments were deposited under an oxygenated water column. Carbon and sulphur isotopic data indicate that the structures were distinct biogenic objects, fossilized by pyritization early in the formation of the rock. The growth patterns deduced from the fossil morphologies suggest that the organisms showed cell-to-cell signalling and coordinated responses, as is commonly associated with multicellular organization⁹. The Gabon fossils, occurring after the 2.45-2.32-Gyr increase in atmospheric oxygen concentration¹⁰, may be seen as ancient representatives of multicellular life, which expanded so rapidly 1.5 Gyr later, in the Cambrian explosion.

Our samples come from the Francevillian Group, which belongs to a well-recognized lithostratigraphic succession, outcropping across $35,000 \text{ km}^2$ in southeastern Gabon^{11,12}. This group is exposed in the intracratonic basins of Plateau des Abeilles, Lastoursville and Franceville (Fig. 1), and reaches a maximum thickness of about 2,000 m.

The group consists of five unmetamorphosed and undeformed sedimentary formations, FA to FE, bounded by conformable surfaces^{11,12}. The lower part of the sequence (FA Formation) comprises fluvial deposits of a low-stand system tract dominated by onshore-to-coastal sandstones. In the FB Formation, marine deltaic deposition is indicated by facies development and sedimentary structures such as load casts, water escape structures, cross-stratification and hummocky cross-stratification. Shallower water conditions are observed in the FC Formation, whereas subsequent deposits (FD and FE) show

intercalated volcanic and continental sediments accumulated during the ultimate filling phase of the basin (Supplementary Fig. 1).



basin (inset) and the location of the fossiliferous site (star) near the town of Franceville.

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More than 250 pyritized specimens embedded within their sedimentary matrix were collected *in situ* from at least 18 thin horizons, identified within the FB2 black shale lithofacies (Supplementary Fig. 2). In some cases, the layers containing the specimens were locally coated with iron oxides, owing to oxidation of pyrite crystals. The specimens range in shape from elongated to nearly isodiametric forms, with occasional finger-like protrusions (Fig. 2, Supplementary Fig. 3). Their length and width range from 7 to 120 mm and from ~5 to 70 mm respectively, and their thickness varies from ~1 to 10 mm. We estimate a density of up to 40 specimens per m², with forms of different sizes and shapes and disparate orientations occurring together (Supplementary Figs 3, 4).

We used micro-computed tomography (micro-CT)-based threedimensional (3D) imaging to characterize the outer and inner morphologies of the structures (see Supplementary Information). Most specimens show a pattern of radial fabric at the outer edge of their undulate or lobate periphery (Figs 2, 3, 4a–c, Supplementary Figs 5–8); this is often curved, so as to meet the outer rim at a roughly perpendicular angle. In some cases, the radial fabric does not reach the outer rim (Fig. 4d), whereas in others it is simply lacking. The central parts of the larger forms are commonly thrown into smooth, transverse folds, which do not reach the outer edge and which are externally expressed as wrinkling of the structure (Figs 3, 4b–c,



Figure 2 | **Examples of black shale bedding surfaces. a**, **b**, Bearing macrofossils in colony form from the FB2 level. Scale bars, 1.0 cm.







Figure 3 | *In situ* macrofossil specimen from the FB2 Formation. **a**, Lower side of the fossil (top) with its impression left in the black shales (bottom), showing peripheral radial fabric and wrinkled appearance. **b**, Micro-CT-based virtual reconstruction (volume rendered in semi-transparency), showing radial fabric and two inner pyrite concretions. **c**, Longitudinal virtual section running close to the estimated central part of the specimen, evidencing the fold pattern. Scale bars, 1.0 cm.

Supplementary Fig. 6–8, 11). Laminae of the host shale are draped around the folds (Supplementary Fig. 13), showing that the folding occurred before compaction. X-ray diffraction analyses show no mineralogical difference between the clay matrices in the specimens and the host shale (Supplementary Fig. 14, Supplementary Table 1).

The larger specimens often also contain a central pyrite body (Figs 3, 4c, d, Supplementary Figs 8, 11), which is developed differently. Sometimes it forms a median layer within the folded sheet (Supplementary Figs 6–8), but it is more often nodular (Figs 3b, 4c–d, Supplementary Figs 8, 11), sometimes deflecting the transverse folds (Fig. 4c, Supplementary Fig. 11). We measured topographic thickness along geometrically homologous virtual sections, which indicated progressive thinning towards the periphery (Supplementary Figs 9, 10).

Differences in X-ray attenuation within the specimens are largely due to the differential distribution of octahedral pyrite crystals. The peripheral radial fabric is characterized by pyrite-free regions expressed in the microfabric as canals or slits (Supplementary Figs 12, 15). Secondary-ionization mass-spectrometric analysis of the pyrite reveals very light δ^{34} S values of about -25% to -30% in the fossilized sheets, with the central pyrite nodule tending towards heavier values of 5% to 15‰, particularly in the outer margins (Fig. 5, Supplementary Table 2). The sheet, which represents the main body of the fossilized structure, was therefore pyritized during early diagenesis, when sulphate reducers were in direct contact with the effectively unlimited sulphate pool of the overlying water column. The high fractionations suggest sulphate concentrations in excess of 200 μ M (ref. 17) (Supplementary Fig. 17). The pyritized nodules apparently formed later, from pore fluids more depleted in sulphate, and the pattern of sulphur isotopes suggests that



Figure 4 | Micro-CT-based reconstructions and virtual sections of four specimens from the FB2 macrofossil record of Gabon. Samples show a disparity of forms based on: external size and shape characteristics; peripheral radial microfabric (missing in view d); patterns of topographic thickness distribution; general inner structural organization, including occurrence of folds (seen in views b and c) and of a nodular pyrite concretion in the central part of the fossil (absent in views a and b). a, Original specimen. b, Volume rendering in semi-transparency. c, Transverse (axial) two-dimensional section. d, Longitudinal section running close to the estimated central part of the specimen. Scale bars, 5 mm. Specimens from top to bottom: G-FB2-f-mst1.1, G-FB2-f-mst2.1, G-FB2-f-mst3.1, G-FB2-f-mst4.1.

pyritization began at the centre and continued towards the outer margins, during which process the remaining sulphate became progressively more depleted in light isotopes. The sulphur isotope patterns thus support the interpretation that the pyritized sheets represent early diagenesis of original biological fabric, whereas the occasional central lump of pyrite is a later, post-burial, diagenetic feature that is not likely to reflect original morphology.

The differences in the organic carbon δ^{13} C content recorded between five specimens and their associated host shale sediment also support the fossilized structures representing a distinct organic entity (Supplementary Table 3). Plants and biomineralized animal tissues of the Phanaerozoic eon are commonly pyritized; pyritization of soft tissues is rare but typically results in faithful replication. This preservation is thought to be favoured by a low content of organic molecules and high content of reactive iron in the pore-waters¹⁸.

We find no evidence to support an inorganic origin of the structures from the FB2 black shale level, whether concretions resulting from epitaxic/crystal growth processes, or features of diagenetic, sedimentary, hydrothermal, or tectonic origin. There is a superficial resemblance between the Gabon structures and the Ediacaran dubiofossil *Mawsonites spriggi*, which has been interpreted as a sand volcano interacting with biomats¹⁹; however, this interpretation accounts for neither the fine internal radial fabric nor the inner fold



Figure 5 | Section through specimen G-FB2-f-mst4.3. δ^{34} S values (coloured spots, see scale) are measured in the central pyrite nodule (centre) and surrounding sheet material (top and bottom) by secondary-ionization mass spectrometry. See Supplementary Information.

pattern of the Gabon fossils, and there is no structural evidence of sediment injection in association with the fossils. The Gabon fossils also resemble radially growing pyrite or marcasite crystals, or 'pyrite suns', which are occasionally found in Phanaerozoic shales. However, a micro-CT-based comparison of the inner structures clearly shows that the 'pyrite suns' have a much more regular and linear radial fabric than the Gabon specimens, and that this fabric extends all the way to the centre of the structure, without any evidence of flexible folding (Supplementary Fig. 16). Indeed, we are unaware of any inorganic processes that can generate the style of flexible folding and irregular radial fabric that we observe in the Gabon fossils (Fig. 4).

The accumulated evidence suggests that the structures are biogenic. The fold pattern seen in the centre of most of the specimens indicates deformation of a flexible sheet, implying an originally cohesive structure of organic composition. The radial fabric is commonly deflected to meet the rim of the specimen, suggesting that the original material was growing by peripheral accretion of flexible organic matter. We conclude that the Gabon structures fulfil the general criteria of biogenicity applied to fossil-like forms in the early rock record²⁰ (Supplementary Table 4). The presence of abundant organic matter in the FB Formation^{21,22} (Supplementary Table 5), including steranes of eukaryotic origin²³, is consistent with this interpretation.

We consider it most likely that these structures represent fossilized colonial organisms. Bacterial colonies growing on surfaces are known to coordinate their behaviour, resulting in regular shapes and distinct fabrics⁹; radial fabrics are common, and are thought to be due to repulsive chemotaxis²⁴. Most studies of bacterial colony growth have been done on monocultures in Petri dishes, where colonies exceed centimetre size⁹. In nature, 'fairy-ring' colonies, formed by cyanobacteria and diatoms and reaching a diameter of 15 cm, have been

reported²⁵. Nonetheless, structures similar to those from Gabon are unknown in the available fossil record and, because of their complex inner structural morphology and the sterane signature in the FB rocks, it is also possible that they represent colonial eukaryotes.

Microbial mat-forming communities, including organisms whose phototactic behaviour modifies the mat shape, are inferred to have been prevalent in marine and lacustrine environments from the early Archaean eon²⁶. Because of their sediment-binding properties, such mats often leave characteristic structures in carbonates and siliciclastic rocks. Such structures, however, including those formed in shales and mudstones, do not resemble the Gabon fossils²⁷. Colonies with regular fabric resulting from coordinated-growth behaviour, as we infer for the Gabon fossils, represent a degree of organization different to that of such mat-forming communities. They require cell-tocell signalling and coordinated responses, akin to that required for multicellular organization⁹. The Gabon fossils represent the earliest evidence for such signalling and coordinated-growth behaviour on the scale of macroorganisms.

One fundamental selective advantage of multicellularity is large size²⁸, but ambient oxygen levels must be high enough to allow aerobic organisms to grow large. Our iron-speciation analyses reveal low ratios of highly reactive iron to total iron $(Fe_{HR}/Fe_T)^{29}$, consistent with sediment deposition under an oxygenated water column (Supplementary Fig. 18). This implies that these fossil organisms, living on the sediment surface, were likely to engage in aerobic respiration. This is consistent with the timing of deposition, some 200 to 250 Myr after the first accumulation of oxygen into the atmosphere^{10,30}.

Although we cannot determine the precise nature and affinities of the 2.1-Gyr macroorganisms from the Francevillian B Formation of Gabon, we interpret these fossils as ancient representatives of multicellular life, which expanded so rapidly 1.5 Gyr later.

METHODS SUMMARY

We assessed textural relations between the pyritized sheet and the shale matrix embedding the macrofossils on sections, using a Nikon Eclipse E600. We carried out scanning electron microscopy on a JEOL 5600 LV, equipped with an Oxford EDX for mineralogical analyses. We obtained X-ray diffraction patterns from randomly-oriented powders and oriented preparations using a PANalytical X'Pert diffractometer (Ni-filtered Cu-K α radiation), equipped with an accelerator detector (2° 2 θ analysis angle).

We ran high-resolution micro-CT on X8050-16 Viscom AG equipment. We made reconstructions using DigiCT v.2.3 (Digisens), 64-bit version, running on a 2.5 GHz Dell T7400 Precision Windows XP 64 workstation with 32 GB of DDR RAM and two NVIDIA graphic cards (Quadro FX 5600 and Telsa C870). We carried out virtual sections and 3D rendering on AVIZO v.5 (Mercury Computer Systems). We carried out SRXTM tomographic microscopy at the X02DA TOMCAT beamline of the Swiss Light Source at the Paul Scherrer Institute (http://www.psi.ch/).

We studied organic matter using Rock-Eval III pyrolysis ('Oil Show Analyzer'). We took isotopic measurements ($\delta^{13}C_{carb}$) on a VG Sira 10 triple collector mass spectrometer. We investigated iron speciation using the sequential extraction protocol, and determined sulphide concentrations by the chromium reduction method (CRM). We measured the concentration of iron in all iron fractions, except for pyrite, by atomic absorption spectrometry. We measured the δ^{34} S composition of bulk rock on Ag₂S precipitates from samples of the sulphide that was liberated by CRM. We added about 200 µg to a tin cup with V₂O₅ and combusted it using a Thermo elemental analyser coupled via a Conflow III interface to a Thermo Delta V Plus mass spectrometer. We analysed S isotopes (32 S, 33 S and 34 S) by secondary-ionization mass spectrometry using a Cameca IMS1270e7.

For further details of sample treatment and analytical procedures, see Supplementary Information.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions A.E.A. conceived and headed the project. A.E.A., S.B., D.E.C., E.H., A.B., R.M., J.-J.D., P.J. and A.Meunier designed research. A.E.A., A.Mazurier, E.H., F.O.O. and P.S. did field research. A.E.A. and F.O.O. analysed sedimentology. A.E.A., S.B., F.T.F., P.S. and D.V. analysed morphology. A.E.A., S.B., R.M. and A.Mazurier carried out microtomographic analyses. E.J. analysed palynology.

A.E.A., C.F., F.O.O. and A.Meunier analysed mineralogy. S.B., D.E.C., A.B., E.H., P.B., A.-C.P.-W., A.R. and M.W. carried out isotope and geochemical analyses. F.G.-L. provided geological samples. A.E.A., S.B., D.E.C., A.B., R.M., A.Mazurier, E.H., P.B., C.F., F.T.F., F.G.-L., P.J., E.J., F.O.O., A.-C.P.-W., A.R., D.V., M.W. and A.Meunier analysed data. A.E.A., S.B., D.E.C., R.M. and E.H. wrote the main part of the manuscript. A.B., A.Mazurier, P.B., J.-J.D., C.F., F.T.F., F.G.-L., P.J., E.J., A.-C.P.-W., A.R., D.V., M.W. and A.Meunier provided critical input to the manuscript.

Author Information The repository of the fossils is the Department of Geosciences, University of Poitiers, France. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to A.E.A. (abder.albani@univ-poitiers.fr).