

A unique record of prokaryote cell pyritization

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ABSTRACT

Prokaryotes, including bacteria, are a major component of both modern and ancient ecosystems. Although fossilized prokaryotes are commonly discovered in sedimentary rocks, it is rare to find them preserved *in situ* alongside macrofossils, particularly as pyritized cells in sites of exceptional fossil preservation. We examined prokaryotes preserved in the Lower Cretaceous Crato Formation of Brazil and demonstrate the widespread presence of spherical microorganisms preserved on the surface of Crato invertebrate fossils. These microorganisms were pyritized, covering decaying carcasses, $1.14 \pm 0.01 \mu\text{m}$ in size, hollow with smooth surfaces, and can be found as aggregates resembling modern prokaryotes, particularly, coccoid bacterial colonies. It is likely that the observed microorganisms covered the carcasses before permissive conditions were established for pyritization, which must have been so rapid as to inhibit the autolysis of their delicate membranes. This is a new record of prokaryote fossils preserved in pyrite in association with macrofossils, which highlights the unique diagenetic and paleoenvironmental conditions of the Crato Formation that facilitated this mode of fossilization.

INTRODUCTION

Prokaryotes, including bacteria, play a major role in ecosystems and provide some of the earliest evidence of life on Earth (e.g., Homann, 2019; Javaux 2019). Bacteria in the fossil record can be preserved in stromatolites, thrombolites, and simple microbial mats (e.g., Noffke et al., 2003; Peters et al., 2017; Gueriau et al., 2020). They can also be phosphatized (Cosmidis et al., 2013) in association with decaying macrofossils, replicating the anatomy of the degrading tissue (e.g., Wilby and Briggs, 1997). In some cases, bacteria can be preserved as carbonaceous material or in pyrite, but this type of preservation is biased toward cyanobacteria that have relatively resistant cell walls (Wilson and Taylor, 2017; Demoulin et al., 2019). Outside of these narrow windows of preservation (see also Toporski et al., 2002), bacterial occurrences in the fossil record become rarer and highly debated

(e.g., Nims et al., 2021). Numerous spherical and elongated microstructures associated with macrofossils have been reported globally and were interpreted as the remains of microorganisms that contribute to the decomposition of organic material (e.g., Lindgren et al., 2015; Schweitzer et al., 2015). However, these microstructures were interpreted as melanosomes by other researchers (e.g., Vinther, 2015, 2016, and references therein). Interestingly, although pyritization is a main pathway for macrofossil preservation in the fossil record and is mediated by sulfate-reducing bacteria, there is little evidence of prokaryote pyritization alongside macrofossils. This is because preservation by pyrite in Lagerstätten is commonly believed to be too coarse to preserve minute organisms such as prokaryotes. Our study aims to investigate microorganism preservation in the Lower Cretaceous Crato Formation of northeastern Brazil.

The Crato Formation was deposited in a stratified lacustrine environment (Martill et al., 2007; Osés et al., 2016; Varejão et al., 2019; Barling et al., 2020) or perhaps a semi-arid wetland (Ribeiro et al., 2021), and yielded a diverse fos-

sil assemblage (Martill et al., 2007). The preservation fidelity varies among different taxa but is extremely high for insects (Fig. 1A). Many structures are preserved in minute details down to the sub-micron scale (Figs. 1B–1E; Barling et al., 2015). This remarkable degree of preservation is ensured through early diagenetic conditions that permit the replication of labile structures by calcium phosphate and/or by framboidal and nanocrystalline pyrite (Osés et al., 2016; Barling et al., 2020; Dias and Carvalho, 2021). While some fossils in the Crato Formation might have been preserved as carbonaceous remains, as evidenced by an insect specimen (Bezerra et al., 2018), recent investigations on 138 fossil insects suggest that the vast majority of fossils were initially preserved in pyrite and subsequently oxidized into iron oxides/hydroxides (Figs. 1F and 1G; Bezerra et al., 2023). The high reactivity of the early diagenetic environment and the exquisite preservation of fossils make the Crato Formation a unique candidate for investigating potential prokaryote cell pyritization. Discovery of prokaryotic pyritization emphasizes the extraordinary early diagenetic conditions that contributed to the exquisite preservation of the Crato biota and constitutes a paradigm shift in our understanding of pyritization fidelity in Lagerstätten. It also establishes a benchmark for comprehending the pyritization in other exceptionally preserved biotas across different spatial and temporal contexts.

MATERIAL AND METHODS

We analyzed 119 fossil insect specimens. All specimens are registered at the Museu de Paleontologia Plácido Cidade Nuvens (MPPCD) at the Universidade Regional do Cariri in Crato, Brazil. More than 3500 scanning electron microscope (SEM) images were captured, depicting the micron-scale preservational fabrics, and

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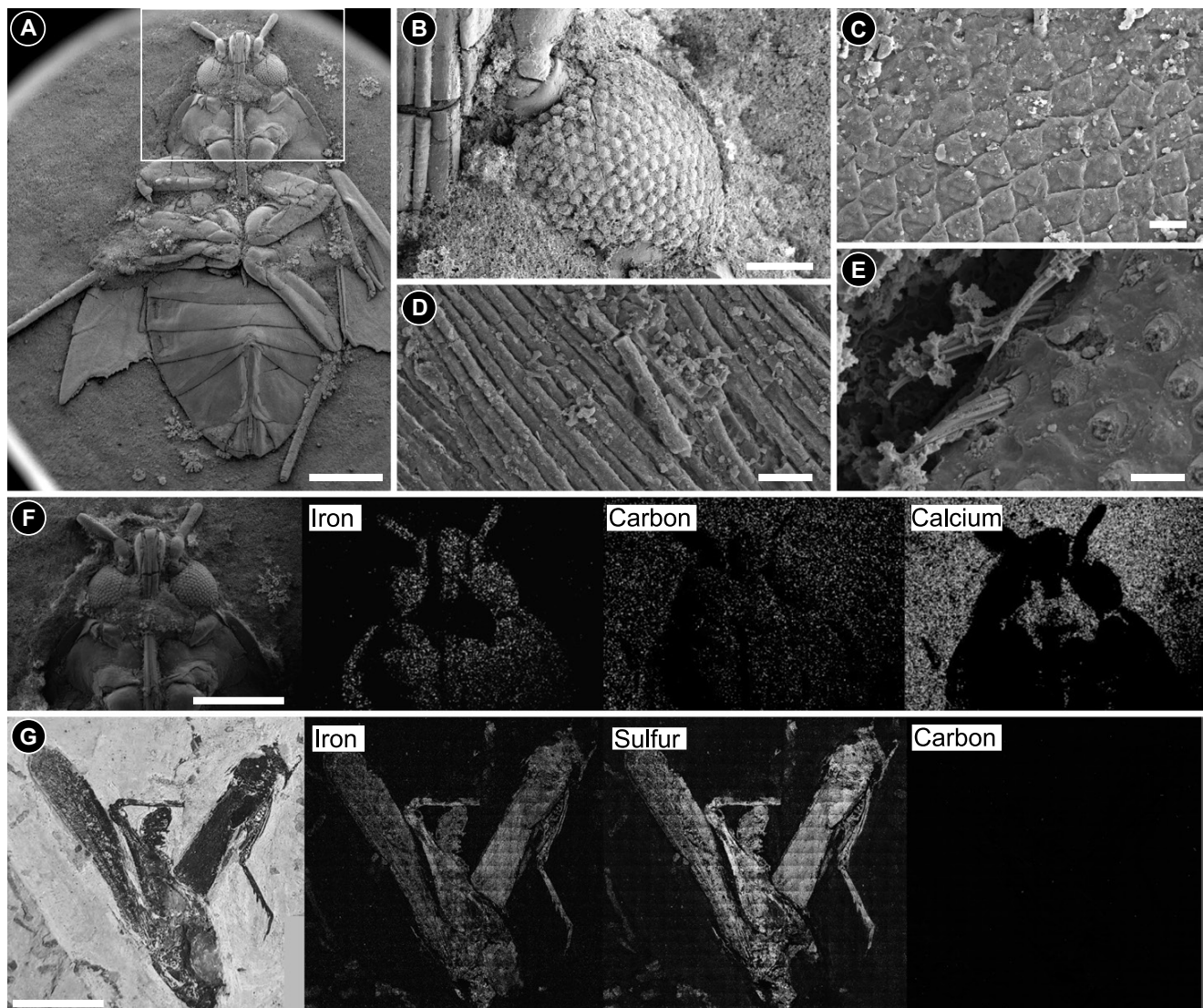


Figure 1. Scanning electron micrographs (SEM) of Crato Formation (northeastern Brazil) insect fossils, demonstrating their remarkable preservation. (A) Complete and articulated Hemiptera (true bugs) fossil (Museu de Paleontologia Plácido Cidade Nuvens specimen MPPCD I 4179). (B) Higher magnification image of Hemiptera fossil in A showing preservation of ommatidia (individual visual units of an arthropod compound eye). (C) Diamond-shaped cuticular scales from a possible Hemiptera (MPPCD I 4183). (D) Gill filaments preserved from Ephemeroptera (mayfly) nymph (MPPCD I 4184). (E) Diptera (true flies) setae (bristle-like sensory structures) preserved with ridges (MPPCD I 4185). (F) Elemental mapping on the head region of the weathered Hemiptera fossil (white box in A), showing the presence of iron in the fossil, calcium in the matrix, and the absence of organic remains such as carbon (or sulfur) from the fossil. (G) Non-weathered Orthoptera (grasshoppers, locusts, and crickets) (MPPCD I 4192), showing the presence of iron and sulfur in the fossil. Scale bars are 1 mm in A and F; 100 μ m in B; 10 μ m in C–E; and 1 cm in G.

~150 energy dispersive X-ray spectra (EDS) were also made of areas of interest to better visualize spatial elemental concentrations. The SEM and EDS equipment used were a JEOL JSM-6100 SEM, a JEOL JSM-6060LV SEM-EDS, an EVOMA10 Zeiss SEM-EDS, and a FEI Quanta FEG 650 SEM-EDS. Specimens were coated with gold, and most of them were examined at a working distance of 13 mm (this distance varied between 11 and 32 mm according to the topographic relief of the specimen). The voltage used for analyses ranged between 8 and 20 kV, with most specimens analyzed at 16 kV.

The spot size used in these analyses is 60 nm. Probe currents varied between 5 pA and 200 pA, allowing for images of uncoated specimens to be captured at magnifications up to 85,000 \times .

RESULTS AND DISCUSSION

Microscopic structures in the shape of spherules were found in association with Crato Formation insect fossils (Fig. 2). There are two distinct morphologies of these microscopic spherules. The first type is undoubtedly of mineralogical origin, consisting of hyperabundant sub-spherical globules of varying sizes that can

either form a distinct layer within the cuticle or replace it altogether (see Barling et al., 2015, their figs. 14A–14F). The second type of spheroids is much rarer and typically smaller than 2 μ m in size, appearing on the surface of fossil insect cuticle rather than within it, sometimes a bit flattened (Fig. 2). These spherules are not specific to a particular anatomy or taxon of Crato insect, because they are found on the abdomen, thorax, wings, limbs, and cerci (paired appendages on the rear-most segments of many arthropods) of different insect taxa (Fig. 2). Moreover, they can be isolated or preserved in aggregates

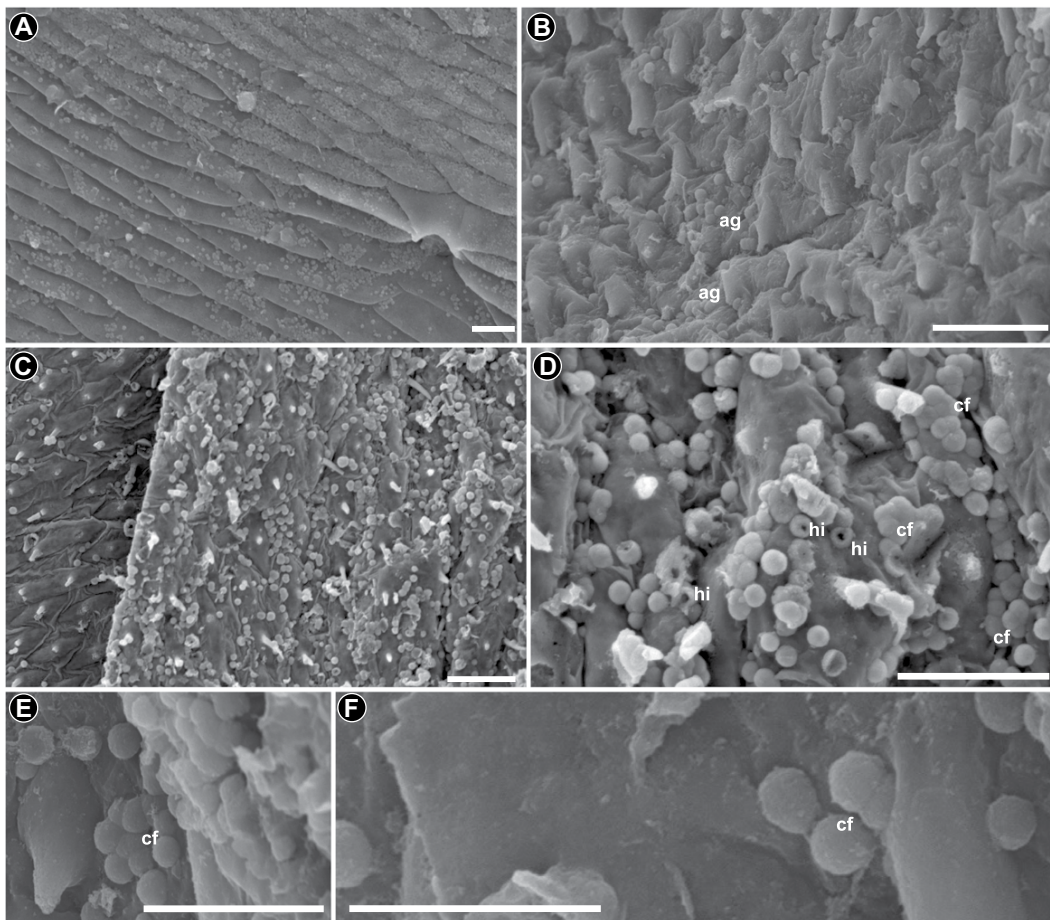


Figure 2. Scanning electron micrographs of microscopic spherules interpreted here as prokaryotes, likely bacterial fossils covering *Blattodea* (cockroaches and termites) (Museu de Paleontologia Plácido Cidade Nuvens specimen MPPCD I 4121) abdomen (A) and *Coleoptera* (beetles) (MPPCD I 4126) abdomen (B, E, F) and wing (C, D) specimens from the Crato Formation in northeastern Brazil. Fossilized prokaryotes are found isolated or in aggregates (A, B). Bacterial fossil cells show little size variability (C), smooth surfaces, and hollow interiors (D). Possible cell fission can be preserved (E, F), but this might also be an artifact resulting from flattened prokaryotes pressed against each other. ag—aggregates; hi—hollow interior, cf—cell fission. Scale bars = 10 μm .

(Figs. 2A and 2B). The random distribution of these spherules on the outer surface of specimens rules them out as melanosomes, as the latter structures should be part of the tissue itself and not simply laid on its outer surface.

Numerous geochemical processes can lead to the formation of pseudo-microfossils (Barge et al., 2016; McMahon and Cosmidis, 2021). Pseudo-microfossils are typically created by strong thermodynamic and/or chemical gradients while in liquid water, such as the redox boundary that preserved the Crato Formation insects (Barling et al., 2020; McMahon and Cosmidis, 2021). Pseudo-microfossils are rarely reported in the literature, but fluorapatite and carbon-sulfur biomorphs are known to produce similar morphologies to the microscopic structures observed by us (McMahon and Cosmidis, 2021). However, fluorapatite spherulites transform from dumbbell-shaped to spherical (transitional morphological stages should be observed) and occur in the size range of tens of microns (McMahon and Cosmidis, 2021). Additionally, carbon-sulfur biomorphs contain accompanying coarse (1 μm diameter, $\sim 15 \mu\text{m}$ length) filaments (McMahon and Cosmidis, 2021). Neither dumbbell nor filament structures have been observed accompanying the microscopic

spherules here, thus eliminating fluorapatite and carbon-sulfur as an origin for these microscopic spherules. Abiotic structures formed of Fe-oxides have been reported from Rio Tinto (Spain) (Barge et al., 2016) and can be comparable in size to the ones observed herein. However, the Rio Tinto structures show a remarkable size variation and tend to be more elongated and have a less-regular surface than the Crato microstructures (Barge et al., 2016). The uniform size range (between 0.5 and 1.9 μm ; Figs. 2C and 3A), hollow interiors (Fig. 2D), and possible stages of cell division (Figs. 2D and 2E) observed in Crato fossils strongly suggest that these structures are not of biomorphic or mineralogical origin, as these are characteristics rarely observed in biomorph pseudo-microfossils (McMahon and Cosmidis, 2021). Instead, a particular resemblance is observed between these spherules and modern prokaryotes, particularly coccoid bacteria, both of which aggregate in the same manner and are comparable in size). Furthermore, these spherules were preserved in Fe-oxides (Fig. 3B), exhibiting the same chemical signature of the initially pyritized and subsequently oxidized insect fossils, both adjacent to the macrofossils and discreetly in the host matrix (Figs. 3C and 3D). Prokaryotes can be preserved in Fe-oxides

from the original environment rather than being replicated by pyrite first (Gueriau et al., 2020). However, considering that non-weathered macrofossils from the Crato Formation are largely preserved in Fe and S (see Barling et al., 2015, their fig. 5) and possess the same fidelity of preservation, we favor the hypothesis that these prokaryotes were originally preserved in pyrite and were later oxidized, in the same manner as the associated insect macrofossils.

The enrichment of iron and the lack of carbon in these microorganisms demonstrates that they are mineralized, rather than organic-walled, and are therefore not modern contamination (McMahon et al., 2018). This is because Fe ions are known to cause oxidative damage to prokaryotic membranes (McMahon et al., 2016), and there is no model to explain how elements such as iron could be incorporated into modern prokaryotes during specimen storage, nor would we expect modern prokaryotes to be present as hollow cell membranes with no remnants of their internal cytoplasm. Thus, it is most likely that iron enrichment occurred when early diagenetic conditions were suitable for their preservation in pyrite under sulfate reducing conditions. The mineralization front responsible for pyrite precipitation likely developed on or around the

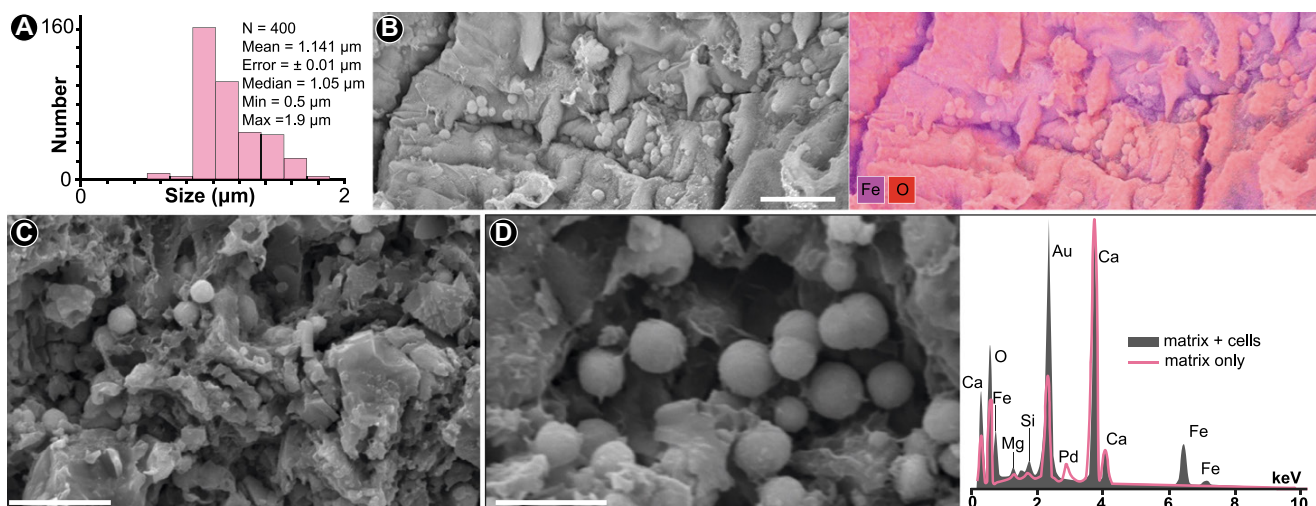


Figure 3. Histogram showing prokaryote size range in the Crato Formation (northeastern Brazil) (A) in addition to scanning electron microscopy with energy dispersive X-ray analysis data showing that the microfossils are preserved in iron oxide in a similar manner to the accompanying insect tissue with no differences between the cuticle and the microorganisms (B; Museu de Paleontologia Plácido Cidade Nuvens specimen MPPCD I 4126). These microorganisms are also observed in the carbonate matrix surrounding the fossil (C, D), yielding a spectrum characterized by Fe and Ca peaks when aggregates are present. Conversely, when prokaryotes are absent, the spectrum shows Ca peaks only. This essentially indicates that the prokaryotes are the structures rich in Fe within the matrix. Note the Au peak results from the gold plating of the sample. Scale bars are 10 µm in B and C, and 4 µm in D.

cell membrane, as iron originated from the surrounding sediment, and this phenomenon would account for the hollow interiors observed in the preserved cells. Furthermore, an additional argument against the possibility of modern contamination lies in the fact that contemporary cells typically undergo collapse, fracturing, and degradation when subjected to intense beam exposure (i.e., SEM). However, this scenario is not applicable herein, as the investigated microorganisms retained their original shapes, sizes, and distribution throughout the analyses, owing to their mineralized membranes.

These findings suggest that pyritization occurred during early diagenesis in the Crato Formation and must have initially transpired at the nanometer scale (Canfield and Raiswell, 1991; Barling et al., 2020). Once conditions for pyritization were established (i.e., availability of Fe and reduced sulfates), prokaryotes were pyritized. The establishment of sulfate-reducing conditions for pyritization must have been abrupt to inhibit the autolysis of cell membranes (Vinther, 2016). However, it remains unclear why other characteristics commonly associated with prokaryotes in general, and bacteria in particular, such as rods, filaments, and exopolymeric substances, are not preserved, even though these structures are reported elsewhere in the Crato Formation replicated in calcium carbonate (Catto et al., 2016). Conducting decay experiments on bacteria could provide valuable insight into this matter.

Although rare, pyritized prokaryotes can be found in the fossil record (e.g., Love and Murray, 1963; Love, 1964; Folk, 2005; Wilson and

Taylor, 2017; Yalikun et al., 2018). Of these, only Wilson and Taylor (2017) reported microfossils in association with macrofossils. Furthermore, those microfossils were cyanobacteria, which are larger in size and have thicker (cellulose-rich) membranes than the microorganisms reported herein. They therefore had more resistant carcasses that could persist for longer periods before disintegrating (Vinther, 2015), thereby expanding their preservation potential and increasing the likelihood of persisting until conditions became conducive for pyritization (Wilson and Taylor, 2017). With this in mind, the microorganisms observed herein represent the first example of labile non-cyanobacterial microorganisms preserved pyritized in Lagerstätten. Even the most famous sites with soft-tissue pyritization fail to provide evidence of similar microorganism preservation (Briggs, 2003). This raises many new questions and opens new avenues for future research: Why are pyritized prokaryotes largely absent from other Lagerstätten, and what precise mechanism allows for this type of pyritization in the Crato Formation? However, at this stage, it is evident that pyritization should not be considered as too coarse to preserve microorganisms. Under favorable conditions, pyritization can indeed preserve structures with high fidelity at the micron- and even sub-micron scale.

CONCLUSIONS

We propose that spheroidal structures scattered across the surface of Crato Formation insect fossils are fossilized prokaryotes, likely coccoid bacterial body fossils, based on their

morphology, mineralogy, size, and aggregation pattern. This is a new record of three-dimensional bacterial prokaryotic body fossils preserved in pyrite in association with macrofossils in Lagerstätten. These remarkable fossils highlight the unique diagenetic and paleoenvironmental conditions of the Crato Formation that facilitated pyritization at the micron and even sub-micron scale.

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